

**COMPARING DENSITY ANALYSES AND CARNIVORE ECOLOGY IN  
MADAGASCAR'S SOUTHEASTERN RAINFOREST**

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# COMPARING DENSITY ANALYSES AND CARNIVORE ECOLOGY IN MADAGASCAR'S SOUTHEASTERN RAINFOREST

Brian Daniel Gerber

## Abstract

Madagascar is renowned for its biodiversity, but also for forest loss, fragmentation, and degradation, making it a global conservation priority. With few studies dedicated to Madagascar's carnivores, little is known about their ecology. My objectives were to 1) compare density estimation techniques applicable to enumerating rare and/or elusive carnivores, 2) investigate Malagasy carnivore distributions, abundance and density, and occupancy/use across four sites that vary in forest disturbance, and 3) explore temporal activity patterns of rainforest carnivores. I found the spatially-explicit-capture-recapture models were empirically superior, as they are flexible and account for spatial variation in detection probability and area estimation. I found both endemic and exotic carnivore composition varied among four rainforest sites: Primary, Selectively-logged, Fragments <2.5 km and Fragments >15 km from contiguous-primary rainforest. All endemic carnivores were present in the Primary and Selectively-logged rainforest, while endemic carnivore species richness decreased and exotic carnivore species richness increased in the fragmented forests. Malagasy civet (*Fossa fossana*) density  $\pm$  SE was significantly less in the Selectively-logged compared to the Primary rainforest ( $1.38 \pm 0.22$ ,  $3.19 \pm 0.55$  civets/km<sup>2</sup>, respectively); they were absent from both fragmented forests. Fossa (*Cryptoprocta ferox*) density  $\pm$  SE was not different between the Primary and Selectively-logged rainforests ( $0.12 \pm 0.05$ ,  $0.09 \pm 0.04$  adults/km<sup>2</sup>, respectively); a single animal was detected in the Fragments <2.5 km, while none were detected in the Fragments >15 km. Malagasy carnivores had varied temporal activity overlap (5.8-88.8%). *C. ferox* preferred crepuscular activity, but overall exhibited a cathemeral activity pattern.

**Intended authorship and target journals for manuscripts included in this thesis:**

**Chapter Two:**

Empirical evaluation of closure violations, effects of lure, and abundance and density estimation for mesocarnivores using photographic-sampling data of the Malagasy civet

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\*In review: Submitted on September 29<sup>th</sup>, 2010 to *Population Ecology*

**Chapter Three:**

The impact of forest logging and fragmentation on carnivore species composition, density, and occupancy in Madagascar's southeastern rainforests

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## **Chapter Four:**

Temporal activity patterns of Malagasy rainforest carnivores

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## Chapter 1 – Madagascar Conservation and Carnivore Ecology

### Introduction:

The island of Madagascar is one of the most biologically rich areas on the planet and one of the world's leading conservation priorities because of the serious threats to its unique biodiversity (Myers et al. 2000). It is home to 771 endemic vertebrates (2.8% of global total; Myers et al. 2000), including 99 species of lemur and nine species of carnivore (Goodman and Helgen 2010; Irwin et al 2010). While Madagascar is renowned for its wealth of endemic flora and fauna (Vences et al. 2009), it is also well known for its forest loss, fragmentation, and degradation.

The main challenge to biodiversity conservation in Madagascar is forest conversion to a human dominated landscape through slash and burn agriculture, mining, and logging (Mittermeier et al. 2005). Humbert and Cours Darnes (1965) estimated that in 1953 forest covered 107,430 km<sup>2</sup>, while the Joint Research Centre Project estimated that only 55,328 km<sup>2</sup> were still remaining by 1999. These analyses showed a mean rate of 9.5% forest loss per year between 1950 and 1993 and a 1.6% mean rate of forest loss per year between 1993 and 1999 (Dufils 2003; Humbert and Cours Darne 1965). Most recently, Madagascar is estimated to have only 16% primary forest cover remaining (Harper et al. 2007). The remaining eastern rainforest, which in 2000 was estimated at 41,668 km<sup>2</sup>, is confined to a slim band running longitudinally along the eastern escarpment of the island and is highly fragmented (Harper et al. 2007). Among all forest types, greater than 80% of forests is within 1 km of a non-forest edge (Harper et al. 2007), such that edge effects (Laurance et al. 2002) have likely altered forest structure and function significantly across much of Madagascar.



Based on these estimates of deforestation from 1950 to 2000, it has been predicted that 9.1% of Madagascar's species have become extinct or are assured for extinction within this time period. In addition to the 32.9% of species predicted to have gone extinct prior to 1950, Madagascar may have lost 42% of its biodiversity since human colonization (Allnutt et al. 2008). The extinction potential may be even worse considering that most climate predictions suggest almost all Madagascar vegetation types will shrink by 2080 (Hannah et al. 2008).

One taxonomic group of special concern in conservation planning activities due to its uniqueness and potential importance in ecosystem structure and function is the Malagasy Carnivora clade, which includes nine extant species and seven genera belonging to the endemic Family Eupleridae (Gaubert et al. 2005; Yoder et al. 2003; Goodman and Helgen 2010). Eupleridae species previously belonged to a monophyletic Viverridae clade based on comparative morphometric analyses, but were relatively recently reorganized within the Feliformia sub-order (Fig. 1; Species accounts provided in Appendix A). Genetic evidence suggests that the Malagasy carnivores are most closely related to the dominantly African Family Herpestidae. Roughly 19 to 26 million years ago, an over-water dispersal event brought carnivores to Madagascar (Krause 2010). The lack of Carnivora competition allowed the original colonizers to radiate into a broad range of niches. Only a single carnivore species, *Cryptoprocta spelea*, is known to have gone extinct. While considerable study of many Malagasy taxa has directly benefited conservation planning, the dearth of studies on Madagascar's threatened carnivore species (IUCN 2010) has excluded them from consideration (Kremen et al. 2008). All nine species of extant Malagasy carnivores are categorized on the IUCN Red List (IUCN, 2010; Endangered: giant-striped mongoose *Galidictis grandidieri*; Vulnerable: fossa *Cryptoprocta ferox*, narrow-striped mongoose *Mungotictis decemlineata*,

brown-tailed mongoose *Salanoia concolor*; Near Threatened: Malagasy small-toothed civet *Eupleres goudotii* and *Eupleres major*, Malagasy civet *Fossa fossana*, broad-striped mongoose *Galidictis fasciata*; Least Concern: ring-trailed mongoose *Galidia elegans*). Knowledge is lacking on the basic ecology and anthropogenic impacts on the populations and habitat use of all Malagasy carnivores (Irwin et al. 2010). Further, given the known impact of carnivores on lemur prey in fragmented forests (Irwin et al. 2009), there is concern for lemur persistence as Madagascar's forests shrink, fragment, and degrade due to increasing demands from a growing human population (Achard et al. 2002; Green and Sussman 1990).

The potential influence of carnivores on ecosystem structure and function also make them a crucial component of any conservation plan (Noss et al. 1996). Not only do carnivores often have the largest area requirements (Miquelle et al. 2005; Sergio et al. 2008), they can also exert regulatory effects on threatened and endangered prey, potentially causing extirpation in fragmented habitats (Buskirk 1999, 2003; Crooks and Soule 1999; Terborgh et al. 2001). Carnivores may impact prey species through direct mortality (Paine 1969) and indirect behavioral effects, such as altering prey distribution and habitat selection. To best plan landscape conservation strategies within the context of Madagascar's Durban vision, which aims to triple the total protected area in Madagascar and create corridors between new and existing protected areas (Norris 2006), it is critical to understand the population ecology of the IUCN-listed Malagasy carnivores (IUCN 2010).

To meet this overarching need for information on carnivore population ecology in Madagascar, my study had three main objectives:

- 1) **Evaluate density estimation techniques useful in enumerating rare and/or elusive carnivore populations (Chapter 2).**
- 2) **Examine population state variables of endemic and exotic rainforest carnivores to gain insight into Malagasy carnivore ecology and the impact of forest logging and fragmentation (Chapter 3).**
- 3) **Provide a quantitative evaluation of the temporal activity patterns of Madagascar's carnivores in the eastern rainforests (Chapter 4).**

In the sections that follow, I provide background information and justification for each of these objectives in greater depth than I am able to do so in each individual chapter which are formatted as publications.

**Objective 1:**

**Evaluate density estimation techniques useful in enumerating rare and/or elusive carnivore populations.**

*Background:*

Estimating population abundance and density is fundamental to the study of ecology as well as critical for appropriate conservation action. A now common approach to estimating the abundance and density of rare and/or elusive species is the photographic-capture of individuals and the use of the mark-recapture analytical framework (Karanth et al. 2004; Kays and Slauson 2008). Identifying uniquely marked individuals over two or more sampling occasions (usually days or weeks) provides the necessary closed capture-recapture data to estimate the probability

of detection,  $\hat{p}$ , and thus abundance,  $\hat{N}$ . The technique for correcting simple animal counts ( $M_{t+1}$ ) or minimum number known alive (MKNA) by incorporating the sampling detection process has long been recognized as the underpinning to accurately estimating abundance (McKelvey and Pearson 2001; Nichols 1992; Williams et al. 2001). However, to compare populations across areas, it necessary to estimate animal density ( $\hat{D} = \hat{N}/\hat{A}$ ), which requires an accurate estimate of the sampling area ( $\hat{A}$ ) and is fraught with many challenges (Parmenter et al. 2003).

Since the initial use of the photographic-capture methodology (Karanth 1995; Karanth and Nichols 1998; Karanth and Nichols 2002), termed camera-trapping, it has been quickly adopted as a tool for estimating abundance/density of a diverse array of species, with particular utility for studies of large and medium terrestrial carnivores (Dillon and Kelly 2007; Gerber et al. 2010; Heilbrun et al. 2006; Jackson et al. 2006; Kelly et al. 2008; O'Brien et al. 2003; Silveira et al. 2009; Silver et al. 2004). Over the years, substantial effort has been put towards the refinement and standardization of using camera-traps to provide better data for comparisons across studies (Balme et al. 2009; Dillon and Kelly 2007; Dillon and Kelly 2008; Kelly 2008; Maffei and Noss 2007; Silveira et al. 2003; Soisalo and Cavalcanti 2006; Wegge et al. 2004). Concurrently, there have been significant developments in the analyses of closed capture-recapture data (Borchers and Efford 2008; Royle et al. 2009; White 2005; White 2008) for the purposes of estimating abundance or density. Despite the availability of newer, flexible analyses implemented in the software programs MARK (White and Burnham 1999), DENSITY (Efford et al. 2009), and SPACECAP (Singh et al. 2010), carnivore photographic-capture studies often still rely on a very limited set of analytical tools, namely program CAPTURE (Rexstad and Burnham 1991), coupled with ad hoc boundary-strip methods to convert abundance to density (Table 1).

### *Chapter 2 Objectives:*

In my comparative examination of the strengths and weaknesses of mark-recapture analytical techniques for enumerating carnivore abundance/density using photographic-capture data, I identified two major challenges: the potential biases of edge effects while grid sampling and/or the use of attractants during sampling. In Chapter 2, I use data collected on the Malagasy civet, *F. fossana* to 1) compare and make recommendations regarding methods to account for geographic closure violation in estimating density, 2) evaluate the effect of lure on closure, abundance/density estimation, maximum movement distances, and temporal activity patterns while photographic-sampling, as well as make recommendations for use of lure/bait in future mesocarnivore studies, and 3) empirically compare the performance of four density estimators when it is necessary to use closed capture-recapture models with a geographically open and ill-defined study area and make recommendations for future studies.

### **Objectives 2 and 3:**

- **Examine population state variables of endemic and exotic rainforest carnivores to gain insight into Malagasy carnivore ecology and the impact of forest logging and fragmentation.**
- **Provide a quantitative evaluation of the temporal activity patterns of Madagascar's carnivores in the eastern rainforests.**

### *Background:*

Carnivores are generally sensitive to habitat loss, fragmentation, and degradation (Crooks 2002; Sergio et al. 2008; Weaver et al. 1996) due to their low densities, high area and energy

requirements, and persecution by humans (Cardillo et al. 2004; Noss et al. 1996). The decline or extirpation of a large- or meso-carnivore can dramatically alter ecosystem dynamics and result in trophic cascades, which could lead to species extirpations (Berger et al. 2001; Hebblewhite et al. 2005; Ripple and Beschta 2006; Roemer et al. 2009; Terborgh et al. 2001). Many carnivore species can be useful indicators of habitat disturbance (Soulé and Terborgh 1999) and/or biodiversity (Sergio et al. 2005; Sergio et al. 2006), making them effective focal species for conservation planning (Carroll et al. 2001; Paul et al. 2008; Thorne et al. 2006). As such, carnivores can be critical for biodiversity conservation and ecosystem integrity (Noss et al. 1996; Sergio et al. 2008; Terborgh et al. 1999).

Understanding the ecology of top and mesocarnivores in Madagascar is especially important, as 1) most Malagasy carnivores and many of their lemur prey are listed as threatened or endangered, 2) little is known about the predator-prey dynamics linking the two groups, 3) threats to Malagasy carnivore and lemur populations continue to be exacerbated by ongoing habitat loss and fragmentation, and 4) as land is protected and corridors restored as part of the Durban Vision, a lack of knowledge inhibits the inclusion of habitat requirements and movement dynamics of the top predators in the planning process (IUCN 2010; WorldBank 2005). The Durban Vision aims to identify new protected areas to protect Madagascar's rich biodiversity and establish corridors linking protected areas (Norris 2006).

While there have been decades of intensive research on Madagascar's lemurs, very little is understood regarding carnivore predation pressure and impacts on lemurs across habitats or seasons. As primates represent the largest mammalian prey biomass of the forests of Madagascar, carnivore predation is likely to be a significant factor in lemur social structure, behavior, ecology and evolution. Carnivores can affect prey through direct mortality of prey

(Paine 1969), as well as indirectly through behavioral effects such as altering prey distribution and habitat selection (Lima and Dill 1990; Schmitz et al. 1997). To accomplish the conservation goals of the Durban Vision, it is essential to understand variations in carnivore demographic parameters, habitat use, and lemur predation across Madagascar's diverse biomes from undisturbed to highly disturbed systems.

The 2010 IUCN Red List of Threatened Species identifies all Malagasy carnivore's populations as declining or currently unknown (IUCN 2010). Major threats to carnivores include habitat loss and fragmentation, and harvesting by local people (Golden 2009; IUCN 2010; Kerridge et al. 2003). Of the lemur species in the southeastern rainforests of Madagascar that are endangered, IUCN lists two as critically endangered (*Prolemur simus*, *Varecia variegata*) and three as endangered (*Haplemur aureus*, *Propithecus edwardsi* *Propithecus diadema*; IUCN, 2010).

To date, only short-term or rapid-assessment studies of Malagasy carnivores have been conducted in the eastern rainforests (Dollar 1999a; Dollar 1999b; Dollar et al. 1997; Dunham 1998; Gerber et al. 2010; Goodman 1996; Goodman et al. 2003; Goodman and Pidgeon 1999; Rasolonandrasana 1994). Long-term research studies have thus far centered in the western dry-deciduous forests and have only focused on *C. ferox* (Dollar 2006; Hawkins 1998). There are limited peer-reviewed research articles available that address Malagasy carnivore ecology (Britt et al. 2004; Goodman 1996; Goodman et al. 2003; Goodman et al. 1997; Goodman and Pidgeon 1999; Hawkins and Racey 2005, 2008, 2009; Rand 1935; Rasoloarison et al. 1995; Woolaver et al. 2006; Wright et al. 1997). Natural history accounts, book chapters and non-peer reviewed publications are also available, but are still relatively few (Albignac 1975; Albignac 1969; Albignac 1971, 1973; Britt et al. 2001; Dollar 1999a; Dollar 1999b, 2000; Dollar et al. 2007;

Dunham 1998; Goodman and Benstead 2003; Karpanty and Wright 2007; Rasolonandrasana 1994). Only a single study has addressed population parameters of Malagasy carnivores in the eastern rainforests, which was a pilot study leading to this thesis work (Gerber et al. 2010). Besides this pilot study, Dollar (1999b), Dunham (1998), and Kerridge et al. (2003) have conducted limited carnivore trapping efforts and subsequent radiotelemetry studies (*C. ferrox*: 1-yr, 2 adults tracked; *G. elegans*: 11 trapped, 7 tracked; *F. fossana*: 22 trapped, 4 tracked) in the eastern rainforests. The overall paucity of published information on Malagasy carnivores is an accurate representation of the state of knowledge of these species.

#### *Madagascar Conservation:*

Using available GIS information (Kremen et al. 2008), we know that current protected areas across Madagascar total 40,733 km<sup>2</sup> (Fig. 2) When classified by forest type, there is a total protection of 23,021 km<sup>2</sup> of rainforest, 10,440 km<sup>2</sup> dry forest, and 1,439 km<sup>2</sup> spiny forest. However, taking into account the dispersion and isolation of most protected areas, there are only five rainforests, four dry forests, and no spiny forests with greater than 1,000 km<sup>2</sup> protected. Similar to other developing countries, Madagascar has been successful in restraining deforestation within their protected areas, but forest loss surrounding protected areas has been considerable (DeFries et al. 2005). At Ranomafana National Park, one of Madagascar's most-prized protected areas, endemic flora diversity is higher and exotics lower within the park than compared to adjacent unprotected forest (Brown et al. 2009). While park boundaries may afford some species adequate protection, human disturbance within the Ranomafana National Park can have a significant effect on lemurs (DeFries et al. 2009) and could be a potentially important



factor determining whether carnivores can persist in isolated protected areas (Woodroffe and Ginsberg, 1998).

Conservation activities in Madagascar are currently moving very slowly and/or on hold due to ongoing political turmoil which derailed active nationwide conservation progress since March, 2009. Prior to the conflict, now former President Marc Ravalomanana outlined an ambitious conservation goal in the Durban Vision, which planned to protect a total of 60,000 km<sup>2</sup> of new protected areas and establish corridors linking the new and existing protected areas. The Durban vision specifically targeted wildlife corridors connecting existing parks in order to protect rare habitats, watersheds, and the continuity of species' ranges (Norris 2006; WorldBank 2005). The application of spatial data and knowledge of a diverse set of endemic taxa has helped to prioritize conservation by identifying optimal expansions of Madagascar's protected areas (Kremen et al. 2008). The proposed areas would potentially add 2,522 km<sup>2</sup> of dry forest and 11,009 km<sup>2</sup> rainforest to the current protected areas, albeit, some of which has suffered from fragmentation and degradation. Two shortcomings of the proposed conservation plan are the lack of consideration of vegetation zones shifting due to climate change and the exclusion of the Malagasy carnivores, likely due to the paucity of information on their population ecology and sensitivity to anthropogenic disturbances (Gerber et al. 2010; Irwin et al. 2010). Given the isolation and generally limited size of Madagascar's protected areas, there may not be a single protected area that can maintain a viable population of the largest extant carnivore, the fossa (*Cryptoprocta ferox*; Hawkins and Racey 2005) over a long period. Since many of the proposed new conservation areas do not significantly add to already established protected areas, these proposed areas may still not ensure any one area is large enough for a viable population of *C. ferox*. Conservation activities that identify forest corridors to maximize connectivity for both

carnivores and other species movements in the face of climate change induced vegetation shifts would be of great value.

*Chapter's 3 and 4 Objectives:*

My study seeks to provide much needed data on the population and behavioral ecology of carnivores in the rainforests of Madagascar to help address the substantial need for such information in conservation planning efforts. In Chapter 3, I use non-invasive photographic-sampling to 1) quantify carnivore species composition, density, and occupancy across a continuum of disturbed rainforest habitats to begin to understand the impacts of forest logging and fragmentation on Malagasy carnivores, and 2) investigate the influence of exotic carnivore species, human activity, landscape characteristics, and micro-habitat on the occupancy of Malagasy rainforest carnivores. In Chapter 4, I use the temporal activity information derived from photographic captures to 1) evaluate the temporal activity patterns of Madagascar's native and exotic rainforest carnivores across a continuum of disturbed rainforest, and 2) compare activity pattern overlap among carnivores to examine temporal niche partitioning and potential conflict between native and exotic species.

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Table 1. Photographic-capture studies designed to estimate abundance or density and their use of mark-recapture software programs, statistical models used in program CAPTURE, closure evaluation tests, and effective sampling area estimation method. Summary statistics from relevant literature found using the Institute for Scientific Information Web of Science. Search date 1/16/10, using “camera” and “trap”.

Criterion	Number of Studies		
	Applicable to Criterion <sup>a</sup>	Total <sup>b</sup>	%
Study Objective			
Density	29	30	97
Abundance	1	30	3
Closure Evaluation Test			
Otis 1978	21	30	70
Not Mentioned	7	30	23
Stanley Test	2	30	7
Pradel	2	30	7
Mark-Recapture Software Program			
CAPTURE	28	30	93
MARK	2	30	7
Neither	1	30	3
CAPTURE Model Use			
M <sub>h</sub> Jackknife Only	23	28	82



M <sub>h</sub> Jackknife and Other Models	2	28	7
Not M <sub>h</sub> Jackknife Model	3	28	11
CAPTURE's Model Selection selected M <sub>0</sub> , but researcher used M <sub>h</sub> Jackknife	16	23	70
Area Estimation Method <sup>c</sup>			
HMMDM Only	15	28	54
Multiple Methods (HMMDM+MMDM)	9	28	32
No Buffer	2	28	7
Home Range Radius	2	28	7
MMDM Only	0	28	0

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<sup>a</sup>Total number of studies may not sum to total, as some studies uses multiple methods or models.

<sup>b</sup>See Appendix B for complete literature citations

<sup>c</sup>HMMDM and MMDM are the half and complete mean maximum distance moved of animals detected, respectively

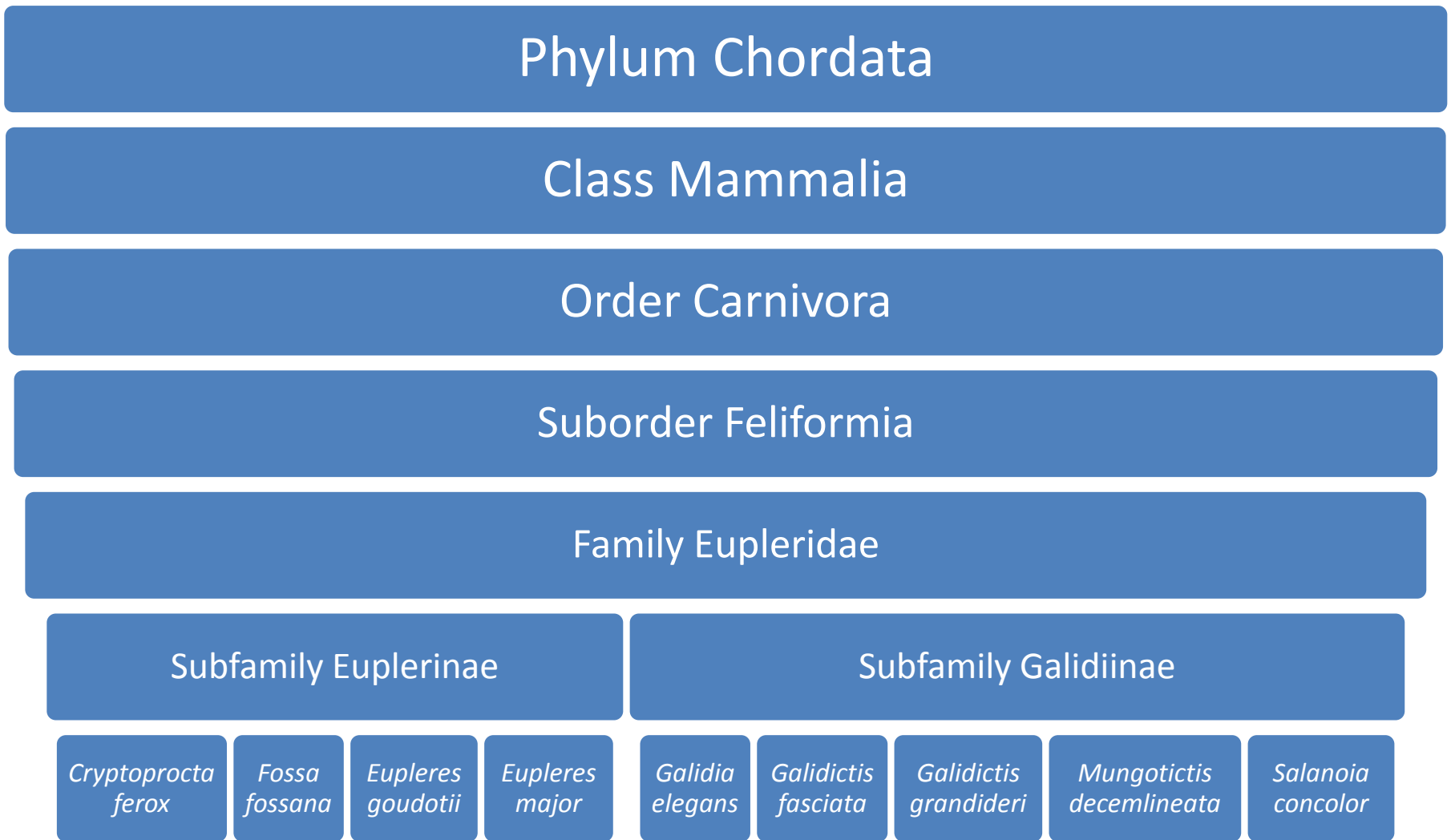


Figure 1. Madagascar's extant carnivore phylogeny.

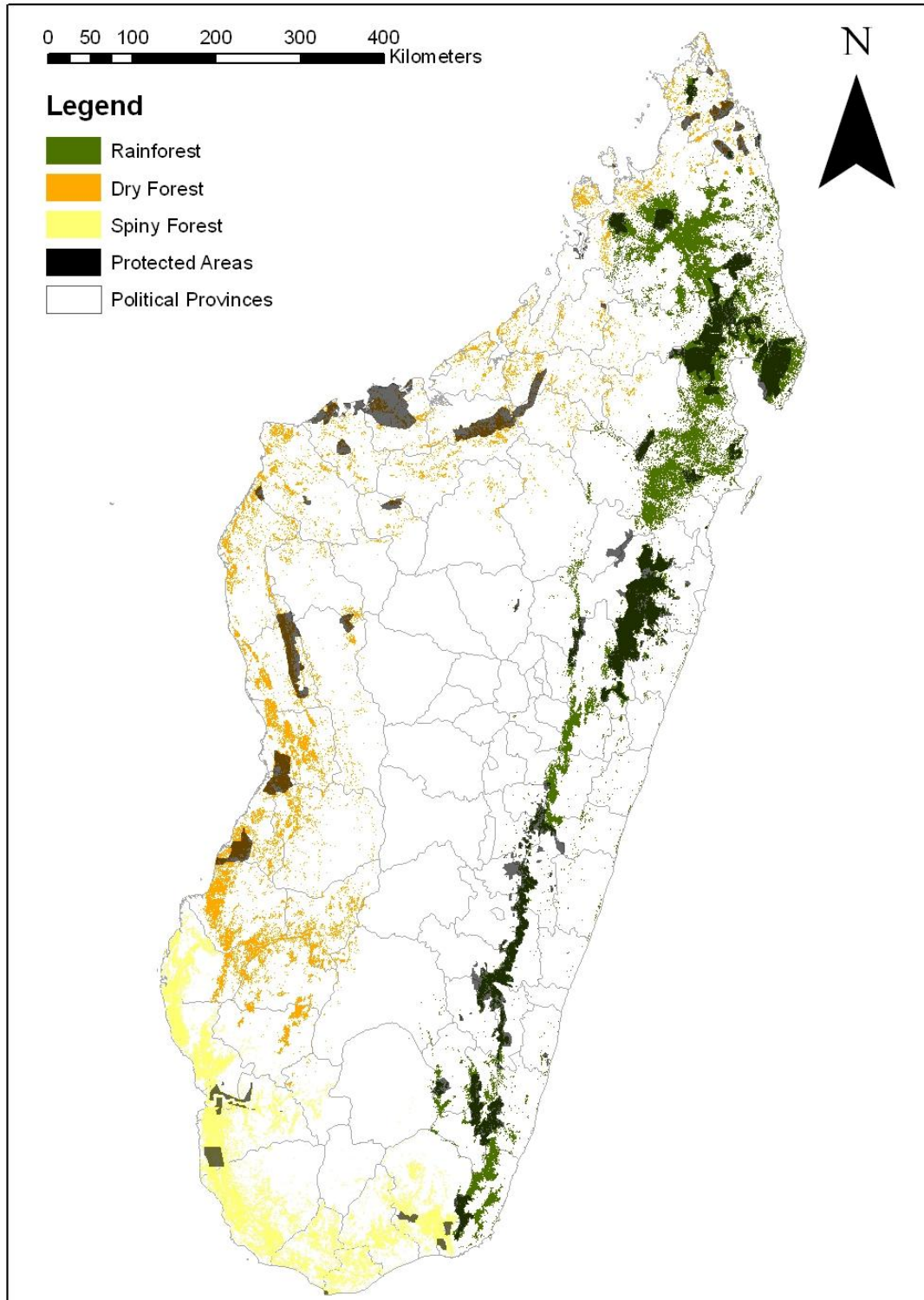


Figure 2. Madagascar primary forest cover (2005) and protected areas. Forest cover was provided by Conservation International (2010).

## Chapter 2 - Empirical evaluation of closure violations, effects of lure, and abundance and density estimation for mesocarnivores using photographic-sampling data of the Malagasy Civet

### Abstract:

1. Estimating abundance and density of rare and/or elusive carnivores with capture-recapture analyses is increasingly common. However, providing unbiased and precise estimates is still a challenge due to 1) strict assumptions of geographic closure, which large-ranging carnivores often violate, 2) uncertainties in area estimation when using ad hoc boundary-strip methods to compensate for edge effects, and 3) the use of bait or lure to attract animals to the detection device, which is rarely tested for potential biases.
2. We use photographic-sampling data of the Malagasy civet *Fossa fossana* collected with and without lure to evaluate tests of geographic closure and to determine effects of lure on geographic closure, abundance and density estimation, maximum movement distances, and temporal activity patterns. In addition, we compare the performance of four density estimators: 1) dividing the superpopulation ( $\hat{N}_s$ ) by the effective sampling area ( $ESA$ ), calculated with different ad hoc boundary-strip methods ( $\hat{D} = \hat{N}_s/ESA$ ), 2) dividing Core-only abundance ( $\hat{N}$ ) by the sampling area ( $\hat{D} = \hat{N}/A$ ), 3) estimating density directly with a maximum-likelihood (ML-SECR) and 4) Bayesian spatially-explicit capture-recapture model (B-SECR).
3. SECR model density estimates  $\pm$  SE were the least precise as they incorporate spatial variation (CV = 0.11-0.13), but consistent with each other (ML-SECR =  $1.38 \pm 0.18$ , B-

SECR =  $1.24 \pm 0.17$  civets/km<sup>2</sup>), while estimates relying on boundary-strip methods do not incorporate spatial variation, varied greatly and were generally larger than SECR model estimates (1.26 - 2.85 civets/km<sup>2</sup>). The use of lure did not influence geographic closure, abundance and density estimation, maximum movement distances, or temporal activity patterns, but did provide more precise population estimates than when not using lure.

4. ***Synthesis and Applications.*** Utilizing lure to sample carnivores can provide significant benefits, including improved precision with less effort, which can permit either greater sampling coverage or reduced project costs. Estimating carnivore density with ad hoc boundary-strip methods often leads to overestimation and/or increased uncertainty in density estimates as they do not incorporate spatial variation. This may lead to inaction or poor decisions by management agencies that can jeopardize populations, especially those already at risk. In contrast, SECR models free researchers from making subjective decisions with boundary-strip methods and estimate density directly, providing more comparable and valuable population estimates.

### **Introduction:**

Unbiased and precise estimates of abundance and density are fundamental to the study of population ecology and essential for effective conservation and management decisions. A common approach to estimating the abundance and density of a species is to capture, mark, and recapture animals to apply capture-recapture (hereafter 'C-R') analyses (White et al. 1982). While previously less common, utilizing C-R to quantify the populations of carnivores is increasingly widespread. This is due to the successful implementation of remote sampling techniques, such as hair snares or scat collection which allow the isolation of individually-

identifiable DNA markers and photographic-sampling of species with uniquely identifying physical marks (Long et al. 2008).

Given the small sample sizes encountered in most carnivore studies and the nearly universal finding that detection probability is affected by heterogeneity among animals and occasional trap responses (Noyce et al. 2001; Boulanger et al. 2004a; Boulanger et al. 2004b), carnivore biologists primarily implement closed, versus open, C-R models to estimate abundance ( $\hat{N}$ ), but see Karanth et al. (2006). To compare populations across areas it is necessary to convert abundance to density ( $\hat{D}$ ), yet traditional C-R analyses provide no direct estimate of  $\hat{D}$ .  $\hat{N}$  must be divided by the sampling area ( $A$ ) to estimate density ( $\hat{D} = \hat{N}/A$ ). However, unless the sampling area is confined by natural barriers (Mace et al. 1994), at least some sampled individuals will have home ranges that extend beyond the edges of the sampling area, thus violating the basic assumption of geographic closure and positively biasing  $\hat{D}$  due to this “edge effect” (White et al. 1982; Boulanger and McLellan, 2001). Given that 1) many carnivores have large home ranges and 2) financial and logistical constraints generally prohibit sampling areas of necessary size (Bondrup-Nielsen, 1983) or simultaneously tracking animals across these edges (White and Shenk, 2001), the edge effect is likely to be substantial when sampling carnivores using grids (Greenwood et al. 1985; Mowat and Strobeck, 2000; Boulanger and McLellan, 2001).

If we assume movements across the sampling area edge are random,  $\hat{N}$  will likely not be biased, but will correspond to the superpopulation ( $\hat{N}_s$ ), or those animals that occupy the sampling area and an unknown amount of the surrounding area (Kendall, 1999). To accurately estimate density of what is actually a geographically open population using closed C-R models, it is necessary to estimate the effective sampling area (*ESA*; Wilson and Anderson, 1985), or the

area that pertains to the  $\hat{N}_s$  estimate ( $\hat{D} = \hat{N}_s/ESA$ ). Despite this frequent need to estimate the *ESA*, there is still much debate on a robust solution; most recommendations suggest variations on ad hoc boundary-strip methods (Soisalo and Cavalcanti, 2006; Maffei and Noss, 2007; Dillon and Kelly, 2008; Balme et al. 2009).

Spatially-explicit C-R models (Efford et al. 2009b; Royle et al. 2009) incorporate the spatial component of the sampling array in the C-R framework, thereby estimating density directly without the need of an ad hoc *ESA* estimate. Field studies have recently provided empirical support for the use of a maximum likelihood spatially-explicit C-R model (ML-SECR; Obbard et al. 2010) and a Bayesian spatially-explicit C-R model (B-SECR; Gardner et al. 2010) to estimate density of geographically open populations of a large ranging carnivore, *Ursus americanus*.

In addition to the challenge of dealing with geographically open populations, carnivores often have low detection rates, even with intense sampling efforts, which inhibit the application of even closed C-R analyses (White et al. 1982; McCarthy et al. 2009). Thus, carnivore C-R studies, especially those using hair snares, often utilize bait (food reward) or lure (non-food reward) to attract animals to the detection device to more effectively (re)capture individuals (Obbard et al. 2010; Gardner et al. 2010). In contrast, photographic-sampling studies less frequently use bait or lure (Trolle et al. 2007; Gerber et al. 2010), but rather often place cameras on trails to increase detection (Dillon & Kelly 2007). Few studies have examined the influence that these attractants may have on C-R population estimation. Using attractants can potentially increase the sample size of detected and/or repeated detections of individuals, and thereby increase detection probability for closed C-R analyses. The advantages include more efficient model selection, increased estimate precision, and the need for less sampling length/effort, thus

reducing project costs (White et al. 1982). However, attractants may also introduce bias to the density estimate, irrespective of, or in combination with, the edge effect (Mowat and Strobeck, 2000; Gardner et al. 2010), by disrupting natural spatial and temporal movement patterns within the sampling area, “pulling” animals onto the sampling area, and/or deterring a proportion of the population (e.g. by sex or age) from being detected (Noyce et al. 2001).

To appropriately estimate carnivore density given the potential biases of edge effects and/or attractants, it is necessary to assess and account for violations of the closure assumption in C-R abundance and density estimation. In this paper, we 1) compare and make recommendations regarding methods to account for geographic closure violation in estimating density of the Malagasy civet *Fossa fossana*, Müller 1776, 2) evaluate the effect of lure on closure, abundance and density estimation, maximum movement distances, and temporal activity patterns while photographic-sampling, as well as make recommendations for use of attractants in future mesocarnivore studies, and 3) empirically compare the performance of four density estimators when it is necessary to use closed C-R models with a geographically open and ill-defined study area and make recommendations for future studies.

## **Materials and Methods:**

### *Study Area and Species*

We studied Madagascar’s third largest endemic carnivore, the near-threatened *F. fossana*, at the Sahamalaotra trail-system within Ranomafana National Park from 9 June-8 August, 2008 (Fig. 1; IUCN, 2010). Sahamalaotra is montane rainforest, characterized by a 20-25 m tree canopy dominated by *Tambourissa* and *Weinmannia* (Turk, 1997). *F. fossana* is a



mesocarnivore averaging 1.6 kg and 0.91 m in length; populations are declining due to habitat loss and local hunting (Kerridge et al. 2003; IUCN, 2010).

### *Field Methodology*

We deployed 26 passive-infrared camera sampling stations on trails in a systematic grid with a random starting point using Deercam DC300's (DeerCam, Park Falls, USA) and Reconyx PC85's (Reconyx, Inc., Holmen, Wisconsin). The photographic-sampling grid was designed based on a preliminary study (Gerber et al. 2010) and had 3.98 stations km<sup>-2</sup> with an average distance and standard deviation of  $566 \pm 93$  m between adjacent stations. Sampling stations consisted of two independently-operating camera-traps mounted on opposite sides of a trail to provide a photographic-capture of both flanks of each animal, thus improving individual identification in recaptures. Cameras were approximately 20 cm above the ground and set to be active for 24 hours/day.

We sampled for 61 nights; during the first 36 nights we did not deploy attractants. Starting on the 37<sup>th</sup> night, 1-2 kg of chicken meat was secured within three layers of metal-wire-mesh at all sampling stations for an additional 25 nights of sampling. Chicken was inaccessible for consumption and acted as a scent-lure. We hung most of the chicken lure 2 m directly above the sampling station on a line tied between two trees. We also staked a small piece of chicken wrapped tightly in three layers of metal-wire-mesh on the ground. We checked sampling stations every five days to ensure continued operation, replacing batteries, film, and memory cards when necessary. We replaced chicken at least every other visit to ensure a maximum-volatile olfactory signal. By maintaining a strict schedule, we ensured that there was no time

when lure was absent from any sampling station, thus reducing among-station heterogeneity (Zielinski and Kucera, 1995).

### *Animal Identification and Capture Histories*

Using *F. fossana*'s individually-identifiable spot pattern (Gerber et al. 2010), two researchers independently agreed on the individual-identity of 96% of all capture events ( $N = 469$ ) used to construct the capture histories necessary for closed C-R analyses. A capture event was all photographs of an individual within a 0.5 hour period (O'Brien et al. 2003). We created three datasets for comparison, 1) capture/recaptures from the complete sampling period (61 nights), 2) capture/recaptures from only the non-lure period (36 nights), and 3) capture/recaptures from only the lure period (25 nights). A sampling occasion was a 24-hour period from 12:00 PM to 11:59 AM.

### *Assessing Closure Violation*

We assumed demographic closure and used three methods to evaluate geographic closure. First, we used the closure hypothesis test of Otis et al. (1978), which assumes only heterogeneity in the recapture probability. Second, we emulated the Stanley and Burnham (1999a) closure test that assumes only time variation in recapture probability using the Pradel model (Pradel, 1996) in Program MARK (v 5.1; White, 2008). Third, we used the full capabilities of the Pradel model to evaluate geographic closure by estimating site fidelity ( $\phi$ ), recruitment ( $f$ ), recapture probability ( $p$ ), and the composite variable of sampling area population growth rate ( $\lambda$ ; Boulanger and McLellan, 2001). We included a priori biologically plausible models in this full Pradel analysis. Models included the effect of lure (*lure*) as a simple time

effect between the non-lure and lure periods, males versus females (*sex*), and general location of animals on the camera grid (*location*). We classified *location* for each individual as either “Core”, individuals that were on-average detected within the interior of the sampling area, or “Edge”, animals that were only detected at camera stations on the edge of the sampling area.

We evaluated models using Akaike’s Information Criterion with a small sample size bias correction ( $AIC_c$ ) and considered all models with  $\Delta AIC_c < 2$  equally parsimonious; we model-averaged estimates to incorporate uncertainty (Burnham and Anderson, 2002). We calculated the relative importance of a parameter ( $R_i$ ) as the sum of  $AIC_c$  weights of all models containing the variable. We estimated overdispersion ( $\hat{c}$ ) with a bootstrap goodness-of-fit test using the Cormack-Jolly-Seber model (Boulanger and McLellan, 2001). Interactive models were prohibitive, thus using our global model  $\phi(location + lure + sex) p(location + lure + sex)$ , we estimated  $\hat{c}$  equal to 1.17. A  $\hat{c}$  correction was incorporated into model selection, so we present  $QAIC_c$  values. If geographic closure is met using the Pradel analysis, we expect site fidelity ( $\phi$ ) to be one, immigration ( $f$ ) to be zero, and thus the study area population growth rate ( $\lambda$ ) to be one.

#### *Abundance and Density Estimation*

We used four methods to estimate density using the complete, non-lure, and lure datasets for *F. fossana*. We defined a significant difference between methods when the 95% confidence intervals of two means overlap no more than half the average margin of error; this is equivalent to a conservative hypothesis test at  $\alpha = 0.05$  (Cumming and Finch, 2005).

First, we assumed random movement across the sampling edge (Kendall, 1999) and estimated  $\hat{N}_s$  for all three datasets using the Huggins closed C-R model (Huggins, 1991) in

Program MARK. We constructed models using heterogeneity ( $h$ , 2-point mixture model), time ( $time$ ), behavior ( $b$ ),  $sex$ , mean-capture distance to the sampling area edge ( $distedge$ ), and mixed combinations. A  $lure$  effect was included in the complete dataset. We evaluated model fit using  $AIC_c$ . We calculated density by dividing the model-averaged  $\hat{N}_s$  by the  $ESA$  and calculated variance using the delta method (Karanth and Nichols, 2002).

We derived four variations of the  $ESA$  by calculating the expected half ( $1/2MMDM^*$ ) and expected full ( $MMDM^*$ ) mean maximum distance moved as the  $MMDM$  is known to increase with increasing recaptures (Tanaka, 1972). We calculated  $MMDM^*$  for observed animals as,

$$E(\bar{W}_i) = W^*(1-e^{-(i-1)b}) \quad (\text{eqn 1})$$

where  $\bar{W}_i$  is the  $MMDM$  for animals captured ( $i$ ) times,  $W^*$  is the expected maximum distance moved for the given population, and  $b$  represents a model parameter (Jett and Nichols, 1987).

We evaluated  $W^*$  using a likelihood function, hereafter referred to as  $MMDM^*$ , in two ways, 1) using all animals detected at least twice ( $MMDM^*$ ) and 2) using the *Core* subset of animals ( $MMDM-Core^*$ ). We assumed *Core* animals are less likely to have truncated maximum movement distances. In contrast, *Edge* animals are very likely to have a maximum distance moved of zero (having not been detected at multiple stations) or a truncated distance as their home range is mostly outside the sampling area.  $MMDM^*$ ,  $1/2MMDM^*$ ,  $MMDM-Core^*$ , and  $1/2MMDM-Core^*$  values were applied as circular buffers to each sampling station, dissolving overlapping areas to calculate the  $ESA$ . We removed villages, roads, and agricultural land (non-habitat) from these buffered areas and restricted area estimation north of the Namorana river (Fig. 1) as it likely restricts regular movement (Gerber et al. 2010).

Second, we used the Huggins model to estimate  $\hat{N}$  of only the *Core* animals. We assume *Core* animals' home ranges are contained in the study area, thus  $\hat{N}$  pertains directly to the

sampling area ( $A$ ) and no ad hoc buffer value was needed. We used the same candidate models from the  $\hat{N}_s$  analysis to evaluate capture histories. We model-averaged to obtain Core-only  $\hat{N}$  and divided by  $A$  to calculate density; the variance was derived by dividing  $\hat{N}$  variance by the square of  $A$  (Weinberg and Abramowitz, 2008).

Third, we use Program DENSITY's *ML-SECR* model (v. 4.4; Efford, 2009a) to directly estimate density. The likelihood function was evaluated with a 2-dimensional numerical integration using 4096 evenly distributed points within a rectangular area extending 1 km beyond the sampling area edge. We assumed home range centers were Poisson distributed, removed non-habitat, and again restricted area estimation north of the Namorana river. We compared the fit of three detection functions (half-normal, hazard-rate, and negative-exponential) to model detection probability variation away from an animal's home range center. We used a conditional-likelihood function to model both  $g_0$  (detection process when a single detector is located at the center of an animal's home range) and  $\sigma$  (spatial scale detection process away from the center of the home range) using a priori biologically plausible models. The same variables modeling detection probability in the  $\hat{N}_s$  were used, except we excluded the *distedge* covariate. Model fit was evaluated using  $AIC_c$  and we model-averaged results to derive  $\hat{D}$  and associated variance.

Fourth, we used the R package SPACECAP (v. 1.0) to apply the *B-SECR* model to estimate density. To compare with the *ML-SECR* estimates, we used the same 2-dimensional numerical integration, removed non-habitat and restricted area estimation north of the Namorana river. We allowed incorporation of a trap response in the model for all three datasets and ran 60000 Markov chain Monte Carlo iterations. SPACECAP is limited to the half-normal detection function.

### *Effect of Lure on Movement and Temporal Activity Patterns*

To test the effect of lure on individual's movements, we calculated the maximum distance moved (*MaxDM*) for all individuals and *Core* animals only, before and after lure was applied. We tested whether individuals detected during both sampling periods change their *MaxDM* using the Wilcoxon Signed Rank test (Zar, 1998). We also tested whether *MMDM* of individuals captured  $\geq$  two times in each the non-lure and lure sampling periods is different using all individuals (*MMDM*) and *Core* animals only (*MMDM-Core*) using the Wilcoxon Ranked Sum test (Zar, 1998). Lastly, we contrast the *MMDM\** and *MMDM-Core\** for the non-lure and lure sampling periods.

We evaluated the effect of lure on the temporal activity of *F. fossana* by testing if activity distributions from data collected with and without lure were different using the non-parametric circular Mardia-Watson-Wheeler statistical test (MWW; Batschelet 1981). In addition, we estimated the mean temporal overlap between activity distributions using a kernel density analysis (Ridout and Linkie, 2009). We defined a sample as the median time of all photographs of the same individual within a 0.5 hour period, thus avoiding the issues of non-independence of consecutive photographs (O'Brien et al. 2003). We applied a kernel estimator from Ridout and Linkie (2009; see eqn 3.3, smoothing parameter of 1.00). We tested for a shift in the proportion of activity in four temporal classes based on sunrise/sunset times during this study: dawn (5:25-7:24), day (7:25-16:27), dusk (16:28-18:27), and night (18:28-5:24). We derived the proportion of activity for each temporal class from the kernel probability distribution and used a contingency table analysis with a likelihood ratio test to examine if animals spent a different amount of time in any temporal class after lure was applied at the sampling stations. We

considered a difference ( $\alpha = 0.05$ ) in the activity distributions between the non-lure and lure datasets and/or a shift of activity among the four temporal classes to indicate a change in activity pattern due to lure.

## **Results:**

### *Animal Identification and Capture Histories*

We photographically captured 22 individual *F. fossana* from 61 sampling nights (Table 1). Eighteen of 22 individuals were detected in both the non-lure and lure periods; two unique individuals were detected only in the non-lure period and two unique individuals only in the lure period. We observed *F. fossana* attempt to remove the staked-ground lure in only 6% of digital-camera capture events and did not observe any chicken being removed in 915 film images or 2296 digital images.

### *Assessing Closure Violation*

We found the *F. fossana* population to be geographically closed or open depending on the method employed. The Otis et al. (1978) test did not reject the closure assumption during the non-lure period ( $Z = -1.153$ ,  $P = 0.12$ ), but did for both the lure period ( $Z = -2.771$ ,  $P = 0.002$ ) and the complete dataset ( $Z = -2.982$ ,  $P = 0.001$ ). The Stanley and Burnham (1999a) test similarly rejected the closure assumption, as the model constraining site fidelity ( $\phi$ ) to one and immigration ( $f$ ) to zero was given no support using only the Stanley and Burnham models (QAIC<sub>c</sub> Weight = 0.00; Table 2).

We found no evidence of permanent closure violation using the full Pradel analysis as the top model included site fidelity ( $\phi$ ) and immigration ( $f$ ) as constant, and recapture probability

( $p$ ) varying by *location* and the use of *lure* (Table 2). Model-averaged  $\lambda \pm \text{SE}$  for the complete, non-lure, and lure datasets were estimated at  $1.00 \pm 0.004$ ,  $1.00 \pm 0.006$ , and  $0.995 \pm 0.008$ , respectively. While there was no evidence of permanent closure violation, recapture probability  $\pm \text{SE}$  was significantly higher for *Core* animals (Non-lure =  $0.35 \pm 0.04$ , Lure =  $0.48 \pm 0.04$ ) than *Edge* animals (Non-lure =  $0.13 \pm 0.02$ , Lure =  $0.21 \pm 0.03$ ), indicating potential closure violation by *Edge* animals temporarily emigrating from the sampling area, thus producing an edge effect.

#### *Effect of Lure on Abundance, Density, Movements, and Activity*

Detection probability was affected by heterogeneity, behavior, sex, and lure in most of our selected models for  $\hat{N}_s$ , Core-only  $\hat{N}$ , and  $\hat{D}$  of *F. fossana* (Table 3). We found that complete-dataset models estimating  $\hat{N}_s$  for *F. fossana* included effects of  $h$  ( $R_i = 100\%$ ), *distedge* ( $R_i = 100\%$ ),  $b$  (trap-happy;  $R_i = 100\%$ ), *sex* ( $R_i = 100\%$ ), and *lure* ( $R_i = 93\%$ ) on the probability of detection. All models included  $h$  ( $R_i = 100\%$ ) in detection probabilities to estimate Core-only  $\hat{N}$ . Additionally, a trap-happy  $b$  effect on the detection probability was clear in the Core-only  $\hat{N}$  complete dataset ( $R_i = 100\%$ ) and the non-lure ( $R_i = 97\%$ ), but not in the lure dataset ( $R_i = 49\%$ ). Males were detected more often than females when using the complete dataset for Core-only  $\hat{N}$  ( $R_i = 98\%$ ), but an effect of *sex* was less evident for the non-lure ( $R_i = 68\%$ ), and lure ( $R_i = 15\%$ ) datasets. In the *ML-SECR* model, we found the negative-exponential function fit all three datasets best and variation in  $g_0$  and  $\sigma$  was best explained by  $h$  and/or *sex* (Table 3). Model selection for the *B-SECR* analysis is unavailable in SPACECAP (v. 1.0), thus estimates are a priori “best” models.

We found no effect of lure on estimates of  $\hat{N}_s$ ,  $\hat{N}$  (Table 4), and  $\hat{D}$  for each density estimation technique (Table 5). We found higher average detection probabilities  $\pm \text{SE}$  in our



analyses of  $\hat{N}_s$ , when using lure (capture probability =  $0.33 \pm 0.08$ , recapture probability =  $0.45 \pm 0.05$ ) than while not using lure (capture probability =  $0.07 \pm 0.03$ , recapture probability =  $0.31 \pm 0.09$ ). This increase in (re)capture probability increased the population estimate precision, as the coefficients of variation decreased when using lure, except for the SECR model estimates.

We found no effect of lure on the *MaxDM* of all individuals ( $W = 9.0, P = 0.156$ ), nor *Core* individuals only ( $W = 0.00, P = 1.0$ ). Similarly, we found no effect of lure on the *MMDM* of all individuals ( $Z = 1.125, P = 0.260$ ), nor *Core* individuals only ( $Z = -0.317, P = 0.752$ ). The use of lure only changed *MMDM\** by 18 m and *MMDM-Core\** by 6 m (Table 5); this later increase translates into a negligible increase of 0.2% in the *ESA*. The large difference between *MMDM\** and *MMDM-Core\** reflects the exclusion of animals with poorly sampled *MaxDM*.

We did not observe any shift in temporal activity pattern after lure was applied ( $W = 0.38, P = 0.83$ ). The mean overlap of activity  $\pm$  SE between the non-lure and lure datasets was  $95.51 \pm 0.02\%$ . We found no significant difference in the proportion of activity during the dawn, day, dusk, and night periods for the non-lure and lure sampling periods ( $X^2 = 0.78, P = 0.68$ ). *F. fossana* were predominantly active at night (85%) as compared to dusk (9%), dawn (6%), and day (<1%).

### *Comparison of Density Estimation Analyses*

Given that we found no effect of lure on  $\hat{D}$  (Table 5), we used the complete dataset to compare density estimation methodologies. We found  $\hat{D}$  derived as  $\hat{N}_s/ESA$  varied considerably depending on the buffer value used to calculate the *ESA*; the  $1/2MMDM^*$  buffer produced the smallest *ESA* ( $7.99 \text{ km}^2$ ) and thus the highest density estimate (Fig. 2). We found no differences in  $\hat{D}$  as estimated using 1)  $\hat{N}_s/MMDM-Core^*$ , 2) Core-only  $\hat{N}/A$ , 3) *ML-SECR*, and 4) *B-SECR*

( $\alpha = 0.05$ , Fig. 2). Our estimate precision was lowest with both *SECR* methods as these analyses include uncertainty and process variation in abundance and area estimation that is often underestimated with other density estimators.

### **Discussion:**

It is critical to test the assumption of geographic closure when using closed C-R models to estimate abundance and density, and to fully understand if the use of attractants biases these estimates. We recommend the Pradel model to test geographic closure in carnivore studies, because it 1) is flexible in modeling recapture variation, especially to account for the common occurrence of heterogeneity, 2) uses model selection procedures to estimate the components of geographic closure, and 3) is not affected by high Type 1 errors, as are the other tests when there is a behavioral effect (White et al. 1982; Stanley and Burnham, 1999b), or heterogeneity (Stanley and Burnham, 1999b). However, when sample sizes are inadequate to use the Pradel model, as with many large carnivore studies, Otis et al. (1978) and Stanley and Burnham (1999a) can be useful when model assumptions are met (which were not in this study); otherwise, no test of closure is appropriate.

Despite concern that attractants might compromise geographic closure, we found no indication that *F. fossana* were permanently immigrating to or emigrating from our study area. This is likely a combination of the distance the lure could be detected and the territorial behavior of *F. fossana*. If the maximum distance *F. fossana* could detect the lure was small compared to its home range, only animals already overlapping sampling stations would be affected. Thus, lure could increase the detection of an animal within a small area around the sampling station. Alternatively, if the detection distance of the lure was large, animals would not be “pulled” onto

the sampling area because of territoriality. Like many terrestrial carnivores, *F. fossana* likely defends a territory, thus preventing individuals from moving into an area they do not normally occur. For example, the Malay Civet (*Viverra zibellina*, Gray 1832), which similarly occupies secondary rainforest, is territorial (Jennings et al. 2006). Further evidence that *F. fossana* may be territorial was that the negative-exponential function best fit our data in the *ML-SECR* analyses, describing a sharp decline in movement away from the home range center. Given that habitat extended well beyond the majority of our sampling area, we would expect that weak territorial behavior would have resulted in the selection of a more gradual distance function (e.g. half-normal) for these data (Obbard et al. 2010).

We found the use of lure did not alter abundance or density estimates of *F. fossana*, regardless of estimation method. Similarly, we found no effect of lure on maximum movement distances or temporal activity pattern of *F. fossana*. The latter is an important finding for photographic-sampling studies, which often evaluate temporal activity.

Given the challenges of detecting carnivores frequently enough to effectively apply closed C-R analyses, we suggest lure can be used while remotely sampling territorial animals without risking closure violations, alterations of abundance, density, or temporal activity pattern. Our findings are particularly relevant to methodologies such as hair snares that often employ attractants to detect carnivores. Higher detection rates from using lure can increase estimate precision and reduce needed sampling effort and costs. Although not employed in this study, post-hoc collapsing of sampling occasions can also increase detection probabilities and thus increase precision (Dillon and Kelly, 2007); however, sampling efforts may still need to be quite large. We do suggest that if lure is used, a rigid schedule be maintained for reapplying the lure, as to reduce sampling heterogeneity.

Carnivore C-R studies using a grid design also face the dual challenges of the effects of sampling layout on (re)capture probabilities and the determination of the appropriate area for density analyses. We found the *ML-SECR* and *B-SECR* models estimated density significantly lower than all but one of our estimates using an ad hoc buffer value to determine the effective sampling area. In agreement with Obbard et al. (2010), we found that using a buffer of  $\frac{1}{2}MMDM^*$  on  $\hat{N}_s$  overestimated density compared to *SECR* model estimates, while our *MMDM-Core\** density estimate was similar and not statistically different than either *SECR* density estimate. The *MMDM* buffer has been supported by several studies (Parmenter et al. 2003; Soisalo and Cavalcanti, 2006; Trolle et al. 2007; Dillon and Kelly, 2008); however, there is no theoretical framework for why this value should provide consistent and reliable density estimates. Obbard et al. (2010) argued that empirical support for  $\hat{N}_s/MMDM$  may reflect the underestimation of  $\frac{1}{2}MMDM$  due to few recaptures per individual (Tanaka, 1972), the truncation of movement distances due to the sampling area edge (Soisalo and Cavalcanti, 2006), and the inclusion of zero distances moved (Dillon and Kelly, 2007). In our study, we still found that the  $\hat{N}_s/\frac{1}{2}MMDM-Core^*$  density estimate was significantly higher than *SECR* model estimates even though 73% of our *F. fossana* individuals were recaptured  $\geq 5$  times, we modeled recapture rate, and we strategically ameliorated the issues of the sampling area edge by using *Core* animals, which had no zero distances moved. Further, in contrast to Obbard et al. (2010), we use a distance to sampling area edge covariate (*distedge*) to incorporate closure violation bias on variation in detection probability to more robustly estimate  $\hat{N}_s$  (Boulanger et al. 2004a). While our corrected  $\hat{N}_s$  and  $\frac{1}{2}MMDM-Core^*$  buffer still produced a higher density than either *SECR* model, our estimate was less dramatically different (71-76%) than Obbard et al. (2010) found in some cases using the  $\frac{1}{2}MMDM$  buffer (20-200%). Ultimately, the appropriate buffer value will

depend on the characteristics of the sampling array layout (size, shape, and trap spacing) and the unknown home ranges of the sampled animals that may differ in size, shape, overlap, and proportion contained within the sampling area (Parmenter et al. 2003).

Given the uncertainties of using  $1/2MMDM$  and  $MMDM$  to buffer  $\hat{N}_s$  in density estimation, carnivore studies often use both values, reporting two density estimates (Trolle et al. 2007). This is unsatisfying for conservation organizations attempting to identify populations and species at risk, as  $1/2MMDM$  densities are almost twice that of using  $MMDM$ . Given the known constraints on measuring  $MMDM$  and the uncertainties in the appropriateness of any buffer value to calculate the  $ESA$ , it is best to abdicate ad hoc boundary-strip methods given the availability of newer statistical methods that ameliorate these issues (Efford et al. 2009b; Royle et al. 2009).

Of all four density estimators considered, the Core-only analysis ( $\hat{D} = \hat{N}/A$ ) produced the most precise density estimate and was congruent with both  $SECR$  model estimates. We assume animals with a mean capture distance  $>$  zero from the sampling area edge, which on average were captured 86% of the time at sampling stations away from the edge, were completely contained within the sampling area. Without tracking *Core* animals to account for the true proportion of time *Core* animals spend on and off the sampling area (White and Shenk, 2001), we cannot validate this assumption. Also, by assuming area is known exactly, we deflate the density variance by neglecting to account for uncertainty, leading to potentially erroneous confidence in our estimate.

Determining the correct area of a sampled population to ameliorate the edge effect is the limiting factor in producing robust estimates of density in the C-R framework. We agree with Obbard et al. (2010) and Gardner et al. (2010) that  $SECR$  models are preferable to either traditional ad hoc boundary strip methods or Core-only analyses to estimate density. The  $SECR$

models incorporate the very real likelihood that the sampling layout has an effect on the detection process and area estimation (Boulanger et al. 2004b; Dillon and Kelly, 2007). We encourage other carnivore C-R studies to employ SECR models, as they 1) have a sound theoretical and statistical framework, 2) free researchers from making subjective decisions on how to calculate the *ESA*, thus making density estimates across studies more comparable, 3) relax the geographic closure assumption and account for the edge effect, and 4) provide conservation agencies with important population information in a single answer from one underlying methodology, rather than a range of answers from multiple methodologies.

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Table 1. Photographic-sampling summary of the Malagasy civet (*Fossa fossana*), sampled with and without lure from 26 camera stations at the Sahamalaotra trail system within the rainforests of Ranomafana National Park, Madagascar from 9 June-8 August, 2008.

Sampling Period	Sampling Occasions (Nights)	Individuals Detected	Recaptures <sup>a</sup> (C-R, SECR)	Male	Female
Complete	61	22	264, 428	11	11
Non-Lure	36	20	128, 185	11	9
Lure	25	20	136, 243	11	9

<sup>a</sup>Recaptures for closed capture-recapture (C-R) analyses and for spatially-explicit C-R analyses which allows animals to be caught at multiple stations on the same occasion

Table 2. Model selection results evaluating the effects of lure on geographic closure for the Malagasy civet (*Fossa fossana*), sampled with and without lure from 26 camera stations at the Sahamalaotra trail system within the rainforests of Ranomafana National Park, Madagascar from 9 June-8 August, 2008.

Models <sup>a</sup>	QAICc	$\Delta$ QAICc	$w_i$	Model Likelihood	No. Parameters	QDeviance
Full Pradel Analysis <sup>b</sup>						
$\phi(\cdot) p(\text{location} + \text{lure}) f(\cdot)$	1030.45	0.00	0.68	1.00	5	929.24
$\phi(\text{location}) p(\text{location} + \text{lure}) f(\text{location})$	1033.32	2.87	0.16	0.24	7	927.92
Stanley and Burnham Models <sup>c</sup>						
$\phi(\cdot) p(\text{time}) f(\cdot)$	1177.34	148.08	0.00	0.00	62	933.22
$\phi(1) p(\text{time}) f(\cdot)$	1199.88	170.62	0.00	0.00	61	958.99
$\phi(\cdot) p(\text{time}) f(0)$	1206.45	177.21	0.00	0.00	61	965.57
$\phi(1) p(\text{time}) f(0)$	1224.20	194.95	0.00	0.00	60	986.52

<sup>a</sup> $\phi$ , site fidelity;  $p$ , recapture probability;  $f$ , immigration onto the study area. Parameters with “(1)” and “(0)” indicate the parameter is fixed. “.” indicates a constant value.

<sup>b</sup>*Location* is a group, where animals have either a mean-capture distance greater than zero or zero from the grid edge. *Lure* is a time effect between the non-lure and lure sampling periods

<sup>c</sup>*Time* as recapture probability variation by each sampling night (24-hour period from 12:00 PM to 11:59 AM)

Table 3. Top abundance and density estimation models (model likelihood >0.125) incorporating detection probability variation of the Malagasy civet (*Fossa fossana*), sampled with and without lure from 26 camera stations at the Sahamalaotra trail system within the rainforests of Ranomafana National Park, Madagascar from 9 June-8 August, 2008.

Analysis	Dataset	Model Selection <sup>a</sup>	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>	Model Likelihood	No. Parameters	Deviance
Superpopulation ( $\hat{N}_s$ )	Complete	<i>b+h+sex+distedge+lure</i>	2855.40	0.00	0.93	1.00	11	2831.30
	Non-Lure	<i>b+h+distedge</i>	619.76	0.00	0.67	1.00	5	609.68
	Non-Lure	<i>b+h+distedge+sex</i>	621.39	1.62	0.30	0.44	6	609.26
	Lure	<i>b+h+distedge+sex</i>	528.84	0.00	0.59	1.00	6	516.67
	Lure	<i>h+distedge+sex</i>	530.02	1.18	0.33	0.55	5	519.90
Core-only	Complete	<i>b+h+sex+Lure</i>	1197.54	0.00	0.98	1.00	8	1183.40
Abundance ( $\hat{N}$ )	Non-Lure	<i>b+h+sex</i>	325.70	0.00	0.64	1.00	5	315.48



	Non-Lure	$b+h$	327.26	1.56	0.29	0.46	6	317.04
	Lure	$b+h$	274.32	0.00	0.47	1.00	4	266.11
	Lure	$h$	274.49	0.17	0.43	0.98	3	268.37
Maximum-Likelihood Spatially-Explicit Capture-Recapture Density( $\hat{D}$ )	Complete	Negexp $g_0(sex+lure) \sigma(h)$	2479.68	0.00	0.99	1.00	6	2426.87
	Non Lure	Negexp $g_0(h) \sigma(h)$	1165.86	0.00	0.64	1.00	5	1116.42
	Non Lure	Negexp $g_0(.) \sigma(h)$	1166.98	1.12	0.36	0.571	4	1121.16
	Lure	Negexp $g_0(sex) \sigma(sex)$	1668.47	0.00	0.68	1.00	4	1622.65
	Lure	Negexp $g_0(h) \sigma(h)$	1669.93	1.46	0.33	0.48	5	1620.49

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<sup>a</sup> $b$ , behavior effect;  $h$ , heterogeneity;  $sex$ , males vs. females;  $distedge$ , mean capture distance from grid edge;  $lure$ , a time effect between the non-lure and lure sampling period; ‘.’, fixed parameter;  $Negexp$ , negative-exponential distance function;  $g_0$ , detection probability at a home range center;  $\sigma$ , spatial scalar detection probability away from a home range center

Table 4. Population estimates, the coefficient of variation (CV), and trap success of the Malagasy civet (*Fossa fossana*), sampled with and without lure from 26 camera stations at the Sahamalaotra trail system within the rainforests of Ranomafana National Park, Madagascar from 9 June-8 August, 2008.

Population Analysis <sup>a</sup>	Sampling Period	Abundance $\pm$ SE	CV	Trap success (Capture Events / 100 Trap Nights) <sup>b</sup>
Superpopulation ( $\hat{N}_s$ )	Complete	22.74 $\pm$ 1.02	0.04	32.53
	No Lure	25.08 $\pm$ 3.79	0.15	23.89
	Lure	21.51 $\pm$ 2.21	0.10	45.86
Core-only ( $\hat{N}$ )	Complete	8.07 $\pm$ 0.28	0.04	22.37
	No Lure	8.12 $\pm$ 0.41	0.05	14.85
	Lure	8.00 $\pm$ 0.02	0.002	33.99

<sup>a</sup>Superpopulation is the population attributed to the sampling area plus an unknown amount of the surrounding area; Core-only is the population of the individuals that were on-average detected within the interior of the sampling area and assumed to be attributed to only the grid

<sup>b</sup>Capture events are all photographs within a 0.5 hour period; trap nights are the number of complete 24-hour periods during which at least one camera was functioning at a sampling station.

Table 5. Four density estimates and associated coefficient of variation (CV) of the Malagasy civet (*Fossa fossana*), sampled with and without lure from 26 camera stations at the Sahamalaotra trail system within the rainforests of Ranomafana National Park, Madagascar from 9 June-8 August, 2008.

Density Estimator <sup>a</sup>	Buffer Type <sup>b</sup>	Sampling Period <sup>c</sup>	Buffer Value (m)	ESA (km <sup>2</sup> ) <sup>a</sup>	Density (Individuals km <sup>-2</sup> ± SE)	CV	Significance ( $\alpha = 0.05$ ) <sup>d</sup>
$\hat{N}_s / \text{ESA}$	½MMDM*	No Lure	356	8.09	3.10 ± 0.47	0.15	A
		Lure	347	7.91	2.72 ± 0.28	0.10	A
	½MMDM-Core*	No Lure	588	11.05	2.27 ± 0.33	0.14	B
		Lure	591	11.47	1.88 ± 0.19	0.10	B
	MMDM*	No Lure	712	13.07	1.92 ± 0.29	0.15	C
		Lure	694	12.94	1.66 ± 0.17	0.10	C
	MMDM-Core*	No Lure	1175	17.73	1.41 ± 0.21	0.15	D
		Lure	1181	17.77	1.21 ± 0.12	0.01	D
$\hat{N} / A$	-	No Lure	-	6.53	1.24 ± 0.06	0.05	E
		Lure	-	6.53	1.23 ± 0.003	0.002	E
ML-SECR	-	No Lure	-	-	1.57 ± 0.35	0.22	F

		Lure	-	-	1.27 ± 0.29	0.23	F
B-SECR	-	No Lure	-	-	1.22 ± 0.17	0.14	G
		Lure	-	-	1.22 ± 0.19	0.15	G

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<sup>a</sup> $\widehat{N}_s$ , superpopulation;  $\widehat{N}$ , Core-only abundance; *ESA*, effective sampling area; *A*, sampling area; ML-SECR, maximum-likelihood spatially-explicit capture-recapture (SECR) model; B-SECR, Bayesian SECR model

<sup>b</sup> $\frac{1}{2}MMDM^*$  and  $MMDM^*$  are the expected half and full mean maximum distance moved.  $MMDM-Core^*$  values are based on a subset of *Core* animals

<sup>c</sup>Sampling nights: 36 non-lure, 25 lure

<sup>d</sup>Significance between the non-lure and lure datasets within each method, where different capital letters are significant, as determined when 95% confidence intervals of two means overlap no more than half the average margin of error (Cumming and Finch, 2005)

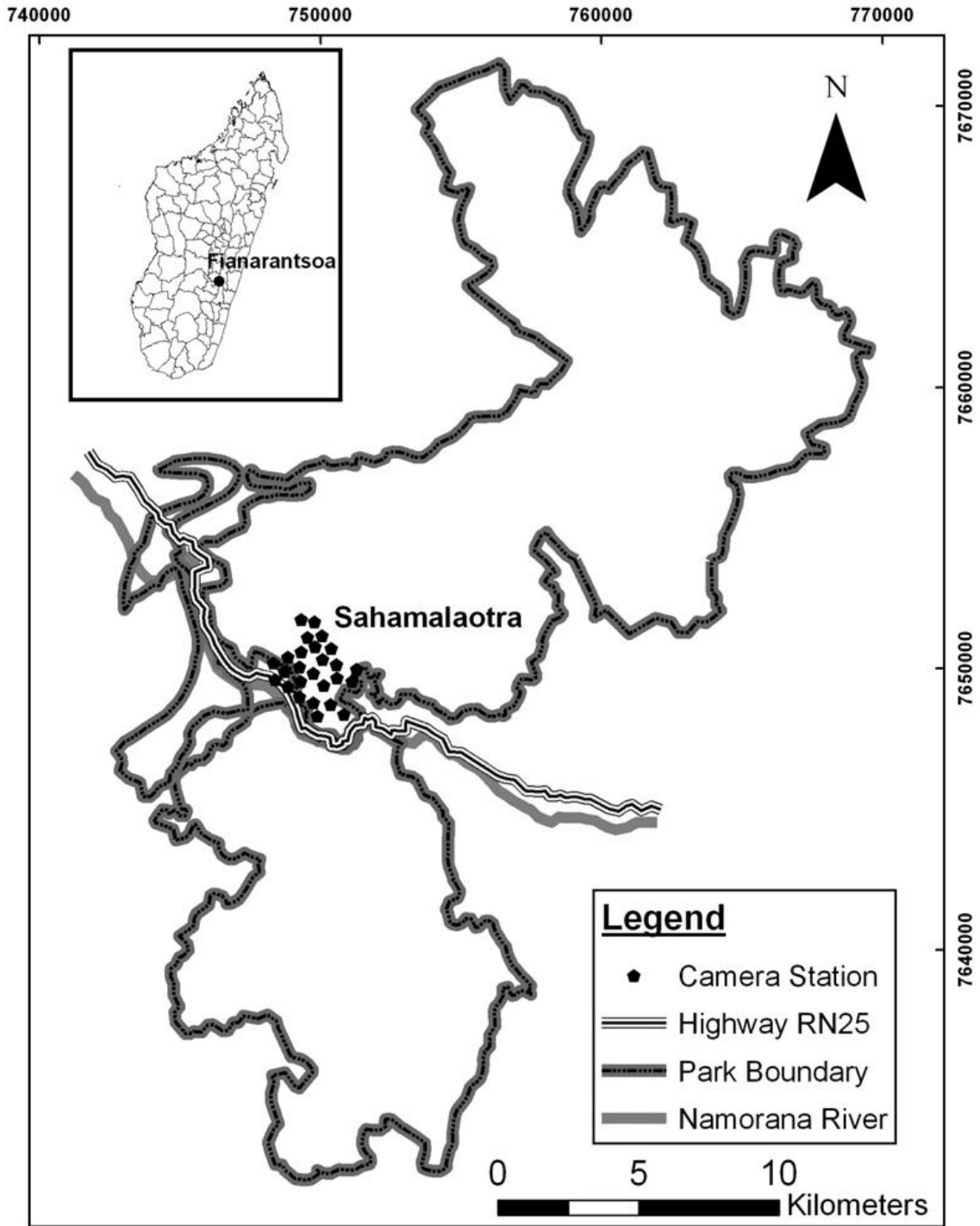


Figure 1. We placed 26 camera stations over a 6.53 km<sup>2</sup> area along the Sahamalaotra trail system within the rainforests of Ranomafana National Park, Fianarantsoa province in southeastern Madagascar from 9 June–8 August, 2008.

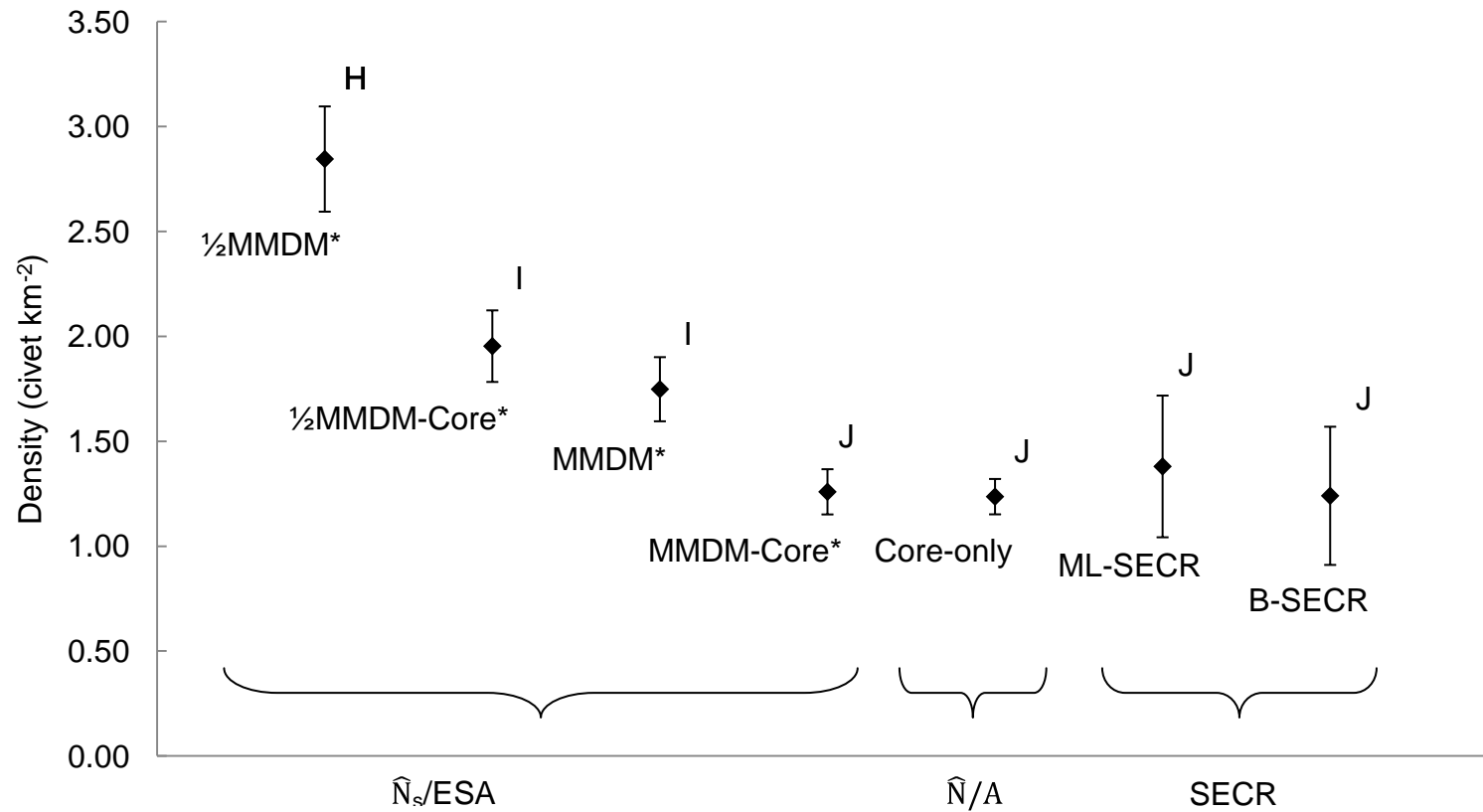


Figure 2. Density and 95% confidence limits using four methods of estimation on the complete dataset for the Malagasy civet (*Fossa fossana*) with statistical significance (95% confidence interval of two means overlap less than half the average margin of error) indicated with different capital letters ( $\alpha = 0.05$ ). Sampling was carried out using 26 camera stations at the Sahamalaotra trail system within the rainforests of Ranomafana National Park, Madagascar from 9 June-8 August, 2008.

### **Chapter 3 - The impact of forest logging and fragmentation on carnivore species composition, density, and occupancy in Madagascar's southeastern rainforests**

#### **Abstract:**

The endemic carnivores of Madagascar's southeastern rainforest face ongoing threats of forest loss and fragmentation, yet we know little about their ecology or how they respond to such disturbances. We evaluated carnivore species composition, density of two endemic carnivores (*Fossa Cryptoprocta ferox* and Malagasy civet *Fossa fossana*), and carnivore occupancy in continuous and fragmented rainforests in southeastern Madagascar to gain insight into the responses of these carnivores to forest loss, fragmentation, and degradation. We used photographic-sampling to survey carnivores at two contiguous (Primary and Selectively-logged) and two fragmented rainforests (Fragments <2.5 km and >15 km from intact primary forest). Carnivore composition varied among rainforests, with a higher number of native and lower number of exotic carnivores at the contiguous than fragmented rainforests. We found *F. fossana* absent from both fragmented rainforests and at a lower density  $\pm$  SE in the Selectively-logged ( $1.38 \pm 0.22$  individual/km<sup>2</sup>) than at the Primary rainforest ( $3.19 \pm 0.55$  individual/km<sup>2</sup>). *C. ferox* was detected briefly in the Fragments <2.5 km from intact rainforest and had similar densities between the Primary and Selectively-logged forests ( $0.12 \pm 0.05$  and  $0.09 \pm 0.04$  adults/km<sup>2</sup>, respectively), but was absent at the Fragments >15 km rainforest. We identified only two protected areas that could maintain >300 adult *C. ferox* in all of Madagascar. Broad-striped mongoose (*Galidictis fasciata*) occupancy in the fragmented rainforests was positively related to fragment size, while the ring-tailed mongoose (*Galidia elegans elegans*) was negatively associated with increasing exotic-wild cat (*Felis catus* and *Felis silvestris*, grouped) trap success

within and outside rainforest fragments. Our findings indicate that degraded rainforest fragments are of limited conservation value in supporting an intact endemic Malagasy carnivore community compared to primary and selectively-logged contiguous rainforest. However, degraded fragments may be of significant value in maintaining connectedness of carnivore populations across the landscape.

## **1. Introduction:**

Mammalian carnivores are generally sensitive to habitat loss, fragmentation, and degradation (Crooks 2002; Sergio et al. 2008) due to their low densities, high area and energy requirements, and persecution by humans (Cardillo et al. 2004; Noss et al. 1996). The decline or extirpation of a large- or meso-carnivore can alter ecosystem dynamics and result in trophic cascades, which could lead to further species extirpations (Berger et al. 2001; Ripple and Beschta 2006; Roemer et al. 2009). Carnivores can also be useful indicators of habitat disturbance (Soulé and Terborgh 1999) and biodiversity (Sergio et al. 2006), making them effective focal species for conservation planning (Carroll et al. 2001; Thorne et al. 2006). As such, understanding carnivore population ecology in a region can be critical in planning for the best actions to protect biodiversity and ecosystem integrity (Noss et al. 1996; Sergio et al. 2008; Terborgh et al. 1999).

The island of Madagascar is renowned for its wealth of endemic flora and fauna (Vences et al. 2009), but also for its forest loss, fragmentation, and degradation, making it a global biodiversity conservation priority. Only an estimated 16% of primary forest cover remains in Madagascar, with much of the remaining forest isolated in fragments with little area > 1 km from a forest edge (Harper et al. 2007). While studies of numerous Malagasy taxa have directly benefited conservation planning, the dearth of studies on Madagascar's carnivore species has



excluded them from consideration (Kremen et al. 2008). Knowledge is lacking on basic ecology and human impacts on the population ecology and habitat use of all Malagasy carnivores (Irwin et al. 2010), especially in the eastern rainforests where only short-term or rapid assessment studies have been conducted (Dollar 1999; Gerber et al. 2010; Goodman and Pidgeon 1999). Some insight can be gained from longer studies of conspecifics in the western dry forests (Dollar et al. 2007; Hawkins and Racey 2005), but due to increased primary production and variability of resources in rainforest, there is likely to be significant variation between forest types. Given the importance of carnivores to ecosystem dynamics and as focal species for conservation, it is critical to better understand Malagasy carnivore ecology.

Of the nine extant endemic carnivore species within the endemic family *Eupleridae* (Goodman and Helgen 2010; Yoder et al. 2003), five are known to occupy the southeastern rainforests (broad striped mongoose *Galidictis fasciata*, fossa *Cryptoprocta ferox*, Malagasy civet *Fossa fossana*, ring-tailed mongoose *Galidia elegans elegans*, small-toothed civet *Eupleres goudotii*; Gerber et al. 2010). All species are thought to be declining, except *G. e. elegans* which has an unknown population trend (IUCN 2010). Of particular concern is the population ecology of *C. ferox* and *G. e. elegans* as both are known to prey on lemurs (Goodman 2003c), many of which are also threatened (IUCN 2010). In the dry forests, lemurs can comprise greater than 50% of *C. ferox*'s diet. While there is likely significant geographic variation in *C. ferox*'s diet (Hawkins and Racey 2008), their impact can be considerable with extirpations of lemurs by *C. ferox* reported from contiguous and fragmented rainforests (Irwin et al. 2009).

Our objectives were to 1) use non-invasive photographic-sampling to quantify carnivore species composition, density, and occupancy across a continuum of disturbed rainforests to gain insight of the impacts of forest logging and fragmentation on Malagasy carnivores, 2) investigate

the influence of exotic carnivore species, human activity, landscape characteristics, and micro-habitat on the occupancy of Malagasy rainforest carnivores, and 3) estimate population sizes of *C. ferox* and *F. fossana* in Ranomafana National Park (RNP), and of *C. ferox* island-wide. These data will allow the incorporation of carnivore abundance, distribution, and habitat use into conservation planning in the rainforests of Madagascar, which is focused on the creation and restoration of forest corridors linking fragmented and continuous and protected and un-protected forest areas (Kremen et al. 2008; Norris 2006).

## **2. Materials and Methods:**

### **2.1. Study Area**

We carried out this research in four survey grids placed along Madagascar's eastern rainforest escarpment (Fig.1). We sampled the contiguous rainforests at the Valohoaka-Vatoranana (Primary) and Sahamalaotra (Selectively-logged) trail-systems located in the boundaries of RNP. We also sampled two fragmented rainforests at Mahatsinjo, Tsinjoarivo (Fragments <2.5 km) and Ialatsara Forest Station (Fragments >15 km). In this paper, we consider forest fragmentation to include the cumulative or synergistic effects of forest loss, fragmentation, and degradation as such disturbances are often concurrent (Laurance and Cochrane 2001).

RNP is recognized for its exceptional floristic and faunal diversity within Madagascar and among rainforests worldwide (Wright and Andriamihaja 2003). RNP encompasses 399 km<sup>2</sup> which experienced spatially-patchy logging prior to its establishment in 1991; it currently protects 329 km<sup>2</sup> of mid-altitude rainforest (Conservation International 2010). Our Primary rainforest grid was located within RNP and consisted of a mixture of unlogged forest with little

anthropogenic disturbance and an area of forest with minimal selective-logging (Wright 1997). Our Selectively-logged rainforest grid located within RNP experienced pre-1991 moderate logging pressure (JC. Razafimahaimodison, Pers. Comm.). Northwest of RNP, we sampled a protected fragmented rainforest separated by >15 km from the main tract of contiguous primary rainforest by a human-dominated landscape (Fig. 1). The Fragments >15 km grid encompassed four fragments ranging in size from 2-5 ha, five fragments 10-64 ha, and one fragment which was 240 ha, as determined by GPS-based mapping in November, 2008. These rainforest fragments were surrounded by a matrix of shrub, open-burned, exotic pine and eucalyptus, and minimal agriculture. Local people did not live within or between the fragments, but actively burned the matrix and used the area for travel and forest products. Lastly, we sampled a fourth grid 150 km north of RNP, located within a network of unprotected hilltop rainforest fragments that from its closest edge was <2.5 km from the large tract of contiguous primary rainforest (Fig.1). The Fragments <2.5 km grid was comprised of 19 fragments less than 7 ha, eight fragments of 10-40 ha and one fragment of 192 ha, as determined by combining GPS mapping in December, 2009 with IKONOS 2001 satellite imagery. Fifty-three household units with 1-6 houses per unit occupied the matrix surrounding the fragments, such that the matrix was dominated by agriculture and naturally regenerating shrub. Local people from these households used the fragments readily for a diversity of forest products (Irwin 2006). At both fragmented grids, forest edges were hard transitions to open habitat, caused by human activities, such as burning, grazing, and farming.

Surveys were conducted over a period of two years from May-December, 2008 (Primary, Selectively-logged, and Fragments >15 km grids) and October-December, 2009 (Fragments <2.5 km grid). The two contiguous grids within RNP were sampled in the cold-dry season (April-

October) and the two fragmented grids in the warm-dry season (November-February, Tecot 2008). A five year average (2005-2009) min-max daily temperature was 13-20 °C at RNP during the cold-dry season. The temperature during the warm-dry season sampling at the Fragments >15 km and Fragments <2.5 km grids were 15-24°C and 12-26°C, respectively. The five year average (2005-2009) daily rainfall  $\pm$  SD was  $6.2 \pm 11.4$  mm at RNP during the cold-dry season. The average rainfall  $\pm$  SD during the warm-dry season sampling at the Fragments >15 km and Fragments <2.5 km grids were  $5.1 \pm 8.4$  mm and  $7.4 \pm 14.0$  mm, respectively.

## 2.2. Rainforest Habitat Sampling

To evaluate impacts of habitat on carnivore species composition and population ecology, we measured landscape-, grid-, and camera-level (see sec 2.3) habitat features. Camera-level vegetation was sampled along four transects radiating in each cardinal direction from camera sampling stations. Along each transect, we established sampling points at 25, 50, and 75 m from the camera station. These transect points along with a point at the camera station made a total of 13 vegetation sampling points per camera station. At each of the 13 points, we recorded the diameter at breast height ( $D_{130}$ ) and the distance of the nearest tree ( $D_{130} \geq 10$  cm) in each quarter surrounding the center point. Also, at each point we recorded presence or absence of vegetation cover every 2 m for a total of 10 m in each cardinal direction for twenty point-intercepts, thus a total of 260 point-intercepts per camera station, following Davis et al. (In Press) methodology. Point intercept vegetation cover measurements included percent cover for down and dead trees ( $\geq 15$ cm  $D_{130}$ ), herbaceous ground plants (0-0.5 m), woody-shrubs (0.5-5 m,  $\leq 10$  cm  $D_{130}$ ), low canopy trees (0-5 m,  $\geq 10$  cm  $D_{130}$ ), medium canopy trees (5-15 m,  $\geq 10$  cm  $D_{130}$ ), and high canopy trees ( $\geq 15$  m,  $\geq 10$  cm  $D_{130}$ ). We used the nearest tree distances and  $D_{130}$  to estimate tree

density and basal area using an unbiased point-centered-quarter estimator (Pollard 1971). To test for grid-level differences in vegetation characteristics, we calculated the mean and standard error for each variable and used Welch's unequal variance ANOVA to test for differences among rainforest sites (Zar, 1998). We normalized data using either a log or square-root transformation. When the global test indicated a difference among grids, we used the Dunnett-Tukey-Kramer pairwise multiple comparison test adjusting for unequal variances and sample size (Dunnett, 1980).

We used ArcGIS 9.2 (ESRI, Redlands, CA) to measure landscape- and camera-level variables for each rainforest grid. We obtained data layers from available resources (Conservation International 2010; Kremen et al. 2008) and through collaborations with Madagascar National Parks, The Institute for the Conservation of Tropical Environments, Sadabe, and on the ground GPS mapping. We quantified fragment area, shape, and nearest neighbor metrics using FragStats (McGarigal et al. 2002). Additionally, we calculated nearest distances from camera stations to the matrix and villages.

### 2.3. Photographic-Sampling

We used a random starting point to establish a systematic grid of passive infrared camera stations along established trail-systems to photographically sample carnivores. Following recommendations for survey design (Karanth and Nichols 2002; White et al. 1982) and using the results from a preliminary study (Gerber et al. 2010), we deployed a minimum of 26 camera stations for at least 52 days at each rainforest grid (Table 1). Among all grids, the camera station density  $\pm$  SD was  $4.43 \pm 0.54$  stations  $\text{km}^{-2}$  with an average spacing  $\pm$  SD among adjacent stations of  $555 \pm 100$  m. Camera stations consisted of two independently-operating passive

infrared cameras, mounted on opposite sides of a trail. This allowed a photographic-capture of both flanks of every animal, thus improving individual identification in recaptures. We attached cameras 20 cm above the ground and set them to be active for 24 hours/day. Camera types included Deercam DC300 (DeerCam, Park Falls, USA) and Reconyx PC85 (Reconyx, Inc. Holmen, Wisconsin). We often used chicken meat as a scent lure to effectively sample these rare/elusive species and modeled effects on detection probability in occupancy and density analyses. Lure was deployed for the entire sampling period at the Primary and Fragments >15 km grids, but was only deployed for the second half of sampling at the Selectively-logged and Fragments <2.5 km grids. Previous work has found no effect of lure on the activity patterns of native and exotic carnivores at contiguous and fragmented rainforests (Gerber et al., in prep, Chapter 4), as well as no effect on *F. fossana* geographic closure, abundance and density estimation, or maximum movement distances (Gerber et al., in review). We checked camera stations every three to five days to ensure continued operation, replacing lure, batteries, film, and memory cards when necessary.

### 2.3.1. Carnivore Species Composition

Among the four rainforest grids, we compared both native and exotic carnivore species composition. While a positive detection leaves no doubt a species occurs within the study area, non-detection does not ensure a true absence. We used a binomial model using capture frequency and sampling effort to evaluate the number of trap nights needed to obtain a 95% probability of a single detection of native and exotic carnivores at each rainforest grid (Tobler et al. 2008). A trap night is defined as a 24-hour period during which at least one of the two cameras at a station was functioning.

### 2.3.2. Carnivore Density

We estimated carnivore density for *C. ferox* and *F. fossana* using capture-recapture analyses, as these species are individually-identifiable (Gerber et al. 2010). To minimize bias, two researchers independently agreed on the individual-identity of capture events to construct the necessary capture-histories for analyses. A capture event was defined as all photographs of the same individual within a 0.5 hour period. To evaluate the geographic closure assumption for *F. fossana*, we estimated the study grid population growth rate ( $\lambda$ ; Gerber et al., in review) using the Pradel model (Pradel 1996) implemented in program MARK (V. 5.1; White 2008). If closure is not violated,  $\lambda$  will equal one. Closure was evaluated for *C. ferox* using a hypothesis test that assumes only detection probability heterogeneity (Otis et al. 1978), as this dataset was too small for the Pradel model. To estimate density, we employed a maximum-likelihood spatially-explicit capture-recapture model (*ML-SECR*), implemented in program DENSITY (V. 4.4; Efford et al. 2009). We used the *ML-SECR* model rather than traditional ad hoc density estimators as it is better designed to estimate density and its variance when the sampling area is ill-defined due to geographic closure violations by temporary emigration from the study grid (Obbard et al. 2010; Gerber et al., in review). We applied a habitat-mask to remove villages, roads, and agricultural land (non-habitat) from the area estimation. We compared the fit of three detection functions (half-normal, hazard-rate, and negative-exponential) to model detection probability variation away from an animal's home range center. We used a conditional-likelihood function to model both  $g_0$  (detection process when a single trap is located at the center of an animal's home range) and  $\sigma$  (spatial scale detection process away from the center of the home range) using a priori biologically plausible models: including time variation (*time*), the effect of lure (*lure*) as a

difference between the non-lure and lure sampling periods, behavior effect (*b*), individual heterogeneity (*h*; Pledger's 2-point mixture), and males versus females (*sex*). Model fit was evaluated using Akaike's Information Criterion with a small sample size bias correction ( $AIC_c$ ). We model-averaged parameter estimates to incorporate model selection uncertainty (Burnham and Anderson 2002). We defined a significant statistical difference between estimates when the 95% confidence intervals of two means overlap no more than half the average margin of error. This is the equivalent to a conservative hypothesis test at  $\alpha = 0.05$  (Cumming and Finch 2005).

### 2.3.3. Carnivore Occupancy

We estimated the 1) average occupancy of our study grids for native and exotic carnivores, and 2) probability of occupancy, which we interpret as "use" of a 75 m radius surrounding the camera stations. We assumed closure while sampling and applied a single-season occupancy model, available in program PRESENCE (MacKenzie et al. 2005). We analyzed each species by grouping data from the two contiguous rainforest grids (Primary and Selectively-logged) and grouping separately the two fragmented rainforest grids (Fragments <2.5 km and >15 km), as each group was sampled within the same season and vegetation structure was more similar within a group. This allowed us to test differences between similar forests, include variables appropriate for both grouped forest types, and potentially share information across grids to more robustly estimate parameters.

We included covariates for both the probability of occupancy and detection to evaluate biologically-driven hypotheses. Covariates included camera-level vegetation and canopy cover variables (see sec 2.2), as well as the effect of lure as a survey covariate (*lure*). Landscape variables included rainforest fragment size (*Area*), nearest distance from camera stations to the



matrix (*Distmatrix*), camera station distance to the nearest village (*DistVillage*), Euclidian distance from each fragment to nearest neighboring fragment (*ENN*), camera station forest cover type as either rainforest or matrix (*ForestType*), a difference between grouped rainforest grids (*Grid*), the fragment shape as a shape index (*Shape*), and trail type as either maintained or secondary trail (*Trail*). Additionally, we evaluated the trap success of exotic carnivores and local people at camera stations as a measure of disturbance that may influence both native and exotic carnivore species. Trap success was calculated as the frequency of capture events by species at a station per 100 trap nights. Covariates were standardized (subtracting the mean and dividing by the standard deviation) to prevent numerical constraints with parameter estimation. To avoid multicollinearity, we examined correlations among variables and did not include variables with  $r > 0.6$  in the same model (Graham 2003). We used a two-step iterative modeling process by first including covariates that influence detection probability and secondly those covariates influencing occupancy using the best model for detection probability (Bailey et al. 2004). Our most parameterized (global) models were constrained to six parameters per response variable, based on sample size (Burnham and Anderson 2002). We evaluated global model fit by assessing the degree of overdispersion ( $\hat{c}$ ) using a goodness-of-fit test with 10,000 bootstraps and adjusted  $\hat{c}$  if chi-square tests indicate lack of fit ( $P < 0.05$ ; MacKenzie and Bailey 2004). We evaluated competing models using  $AIC_c$  as described in sec 2.3.2.

#### 2.3.4. RNP and Madagascar Carnivore Population Estimates

We extrapolated *C. ferrox* and *F. fossana* densities to estimate potential carnivore populations. We used ArcGIS to quantify available habitat from the most recent primary forest cover data (2005; Conservation International 2010) and to quantify the extent of current

protected areas (Kremen et al. 2008). Protected areas used here include a mixture of national parks, special reserves, and other designations with varying levels of protection status, as defined by Kremen et al. (2008). To investigate *F. fossana* and *C. ferox* abundance at RNP, we extrapolated this study's density estimates to available habitat defined as RNP primary forest coverage.

In addition, we estimated the potential island-wide population size of *C. ferox*, the number of distinct populations, and the connectedness of those populations by extrapolating this study's rainforest, adult-only, density estimates and an adult-only, dry forest estimate ( $0.18 \text{ km}^{-2}$ ; Hawkins and Racey, 2005). We assumed *C. ferox* were forest dependent (Hawkins and Racey 2005) and classified Madagascar's forests into zones of eastern rainforest, western dry forest, and southern spiny forest (Harper et al. 2007). We excluded the spiny forests from population estimates as there are no *C. ferox* density estimates from that region. In the rainforest and dry forest, we first identified forest fragments that could contain a single adult *C. ferox* (based on density estimates) and estimated population size of each fragment. Second, we removed fragments <25 ha to eliminate highly fragmented areas. Finally, we spatially joined all remaining fragments  $\leq 4.9$  km from each other as a single population of a forest complex, as movements of *C. ferox* in the human-dominated landscape are likely constrained to this distance (this study; Kotschwar 2010).

### **3. Results:**

#### 3.1. Vegetation Structure of Rainforest Grids

Grid-level vegetation structure differed greatly among all forests, but was most similar between fragmented forests (Table 2). We found the highest tree density and basal area in the Primary forest, followed by the Selectively-logged, and then the fragmented forests. There was

no difference in tree density and basal area between the two fragmented forests. High canopy cover was greatest at the Primary forest, while the Selectively-logged forest had the highest mid-canopy cover. Low canopy cover was generally low at all forests, except for the Fragments <2.5 km, which had ten times the low coverage compared to the Primary forest. We observed >78% shrub canopy cover in all forests, while dead and down cover was found to be highest at the Primary and Selectively-logged forests, which is consistent with our observations of ongoing dead wood extraction at the fragmented forests.

### 3.2. Carnivore Species Composition

We detected all known endemic southeastern rainforest carnivores in the Primary and Selectively-logged contiguous rainforests. We found reduced numbers of endemic carnivore species in the fragmented rainforests, with *G. fasciata* and *G. e. elegans* detected at both fragmented forests, *F. fossana* and *E. goudotii* absent from both fragmented forests, and *C. ferox* only detected at the Fragments <2.5 km. We observed exotic carnivores in all four rainforests. Only the domestic dog (*Canis familiaris*) was detected in the Primary and Selectively-logged forests, while three exotic species (*C. familiaris*, exotic-wild cat *Felis catus* and *Felis silvestris*, grouping the domestic and introduced African wildcat, *F. catus/silvestris*, as they are difficult to distinguish from each other), and the exotic small Indian Civet *Viverricula indica*) were found in both fragmented forests.

Among all rainforests, 423 trap nights or less were needed to achieve a 95% probability of a single detection of most carnivores. The two exceptions were *E. goudotii* at the Primary forest (1081 trap nights needed) and *C. ferox* at the Fragments <2.5 km (1375 trap nights needed). Assuming capture frequencies were similar among forests where species were detected

and not detected, our sampling effort at each forest was above the necessary trap nights to achieve a 95% probability of detecting all carnivores in each forest, except for *C. ferox* at the Fragments >15 km (Table 1). However, even at that site we had very close to the needed number of trap nights to detect *C. ferox*.

### 3.3. Carnivore Density

Two researchers independently agreed on the individual-identity of >96% of *F. fossana* and 88% of *C. ferox* capture events. We excluded two juvenile *C. ferox* each from the Primary and Selectively-logged forests due to lack of adequate recaptures; density estimates are thus for adults only. We detected a single *C. ferox* at the Fragmented <2.5 km grid, but could not conduct a density analysis with a single individual. The sex ratios of detected *C. ferox* and *F. fossana* were equal, except at the Primary forest where one more female *F. fossana* was detected (Table 1).

Closure was not rejected for *F. fossana* as  $\lambda$  was not different than 1.0 at the Primary ( $1.00 \pm 0.004$ ) or Selectively-logged contiguous rainforests ( $1.00 \pm 0.008$ ). Similarly, closure was not rejected for *C. ferox* at the Primary ( $Z = 1.281$ ,  $P = 0.899$ ) or Selectively-logged forests ( $Z = 1.362$ ,  $P = 0.913$ ).

We found the detection probabilities of *F. fossana* and *C. ferox* were affected by both *sex* and *h* (Table 3). We identified a single top model for *F. fossana* density estimation at both the Primary and Selectively-logged forests which included *sex* affecting detection at the home range center ( $g_o$ ; males higher than females) and *h* among individuals in the spatial scalar over which detection declines away from the home range center ( $\sigma$ ). Our use of *lure* at the Selectively-logged forest increased the detection probability of *F. fossana* at the home range center ( $g_o$ ), but

not the spatial scalar ( $\sigma$ ). We found less definitive evidence of effects on  $g_o$  and  $\sigma$  for *C. ferox*, but the inclusion of *sex* and *h* did improve fit over the null model.

*F. fossana* density was highest in the Primary forest, while in the Selectively-logged forest it was less than half of the Primary forest estimate (Table 4). *C. ferox* density was an order of magnitude lower than *F. fossana* in the Primary and Selectively-logged rainforests, but not significantly different between these forests ( $\alpha = 0.05$ ). In the Fragmented <2.5 km forest, we concluded only that *C. ferox* density may be greater than zero as one individual was detected at two camera stations in the largest rainforest fragment (192 ha) in that grid, or zero if the animal was a transient.

### 3.4. Carnivore Occupancy

Our fully parameterized models fit the data ( $P > 0.05$ ), thus we maintain an overdispersion factor of 1.0. The detection probabilities and occupancies for native and exotic carnivores were influenced by both landscape- and camera-level variables (Table 5). In the contiguous rainforest grids, we found *C. ferox* and *G. fasciata* detection probability increased the further a camera station was from the matrix (*Distmatrix*; Table 5 and Table 6). *C. ferox* was also detected less often on smaller secondary trails compared to maintained trails (*Trail*). *G. fasciata* detections were negatively influenced by increasing trap success of *C. familiaris* (*Dog*). We found *F. fossana* detection probability increased with the use of lure (*Lure*). *C. familiaris* detections were positively associated with local people trap success (*Locals*). In the fragmented rainforests, our results indicate that detection probability for native carnivores varied by grid (*Grid*), with higher detection at the protected Fragments >15 km (Table 5 and Table 6). Exotic carnivore detection probability within the fragmented rainforests varied significantly, with higher

detections within the matrix compared to rainforest fragments (*ForestType*), increasing detections with local people trap success (*Locals*), and increasing detections with the use of lure (*Lure*; Table 5 and Table 6).

In the contiguous rainforests, *G. fasciata* occupancy was higher on average in the Primary forest due to larger basal area compared to the Selectively-logged forest (Table 7, Fig. 2). In comparison, our data showed that *G. fasciata* occupancy in the fragmented rainforests was determined by fragment size (Table 5); fragments greater than 50 ha had a probability of occupancy >95% (Table 7, Fig. 2). *G. fasciata* was never detected outside the rainforest fragments. In the contiguous rainforests, our data reveal no clear habitat association for *C. ferox* or differences in occupancy in the Primary or Selectively-logged forests (Table 5 and Table 6). We could not model occupancy for either *F. fossana* or *G. e. elegans* due to their high naïve occupancy in the contiguous rainforests (Table 8). However, in the fragmented forests we found *G. e. elegans* had a higher occupancy within the fragments compared to the matrix (*ForestType*) and was negatively affected by increasing *F. catus/silvestris* trap success (Table 7 and Fig. 3). *C. familiaris* occupancy in the contiguous rainforests was negatively affected by increasing distance to the closest village from camera stations (*DistVillage*; Table 5 and Table 7). On average, *C. familiaris* occupancy was lower at the contiguous rainforest than the fragmented rainforest and was highest in the Fragments <2.5 km (Table 8). *V. indica* and *F. catus/silvestris* occupancy was not different between fragmented forests. While both these exotic carnivores used the rainforest fragments and matrix, *V. indica* had a significantly higher occupancy within the matrix (*ForestType*; Table 7 and Table 8). We could not evaluate *E. goudotii* occupancy in the contiguous rainforest or *C. ferox* at the Fragmented <2.5 km forest due to poor detection probability (Table 8).

### 3.5. RNP and Madagascar Carnivore Populations

RNP may protect a total population of 516 to 1,193 individual *F. fossana*, but only 39 adult *C. ferox*. We determined from our average adult *C. ferox* rainforest density that  $\geq 9.5 \text{ km}^2$  of primary rainforest was necessary for a single adult, while  $\geq 5.5 \text{ km}^2$  of dry forest was necessary according to estimates from the west (Hawkins and Racey 2005). Across Madagascar, we estimated a total population of 8,626 adult *C. ferox* with 4,476 rainforest animals belonging to 32 populations and 4,150 dry forest animals belonging to 38 populations. Ninety-five percent of the total rainforest population was contained in two forest complexes (Fig. 4), separated immediately north of Lac Alaotra Biological Reserve (UTM: 900815E, 8074030S). The northeast and central-east rainforest complexes could support 2,638 and 1,627 *C. ferox* adults, respectively. Dry forests were more fragmented with 95% of the total population divided into nine separate populations. Two dry forest complexes could support  $>300$  adult *C. ferox*, a central-west and north-west population, estimated at 2,877 and 456, respectively. Considering the protected forest cover only, we estimated an island-wide protected *C. ferox* population of only 2,635 adults (780 Dry forest, 1,855 Rainforest). The protected areas of Masaola-Makira rainforest and Zahamena-Mantadia-Vohidrazana rainforest complex were the only areas identified as potentially holding  $>300$  adult *C. ferox*. At Masaola-Makira, Madagascar's largest protected area, we estimated  $5,445 \text{ km}^2$  of primary forest, thus a potential protected population of 572 adult *C. ferox*.

## 4. Discussion:

Carnivores are globally threatened by habitat loss, fragmentation, and degradation (Karanth and Chellam 2009). Malagasy carnivores are no exception. Our data suggest that within Madagascar's southeastern rainforests, forest loss/fragmentation/degradation, selective-logging and exotic carnivore presence have significant negative implications for the conservation of native carnivores. Congruent with other carnivore community studies (Crooks 2002; Michalski and Peres 2005), rainforest fragmentation has altered the species composition of Malagasy carnivores, such that contiguous rainforests hold a higher number of native and lower number of exotic carnivore species compared to fragmented rainforests. Fragmentation sensitivity appears to differ by species as observed in other studies (Crooks 2002); the larger body-sized *Euplerinae* species (*C. ferox*, *E. goudotii*, *F. fossana*) were absent or nearly so from the fragmented rainforests, suggesting greater sensitivity compared to the smaller-bodied *Galidiinae* species (*G. e. elegans*, *G. fasciata*) which occupied fragmented forests. The single *C. ferox* detected within the largest fragment (192 ha) in the Fragments <2.5 km site may have been a transient animal; the low number of recaptures suggests this animal did not occupy the area, at least in the warm-dry season we sampled. Although we were 56 trap nights (2.15 actual nights with the 26 camera stations we deployed) short of a 95% probability of a single detection of *C. ferox* in the Fragments >15 km (assuming the same capture frequency at the Fragments <2.5 km), we are confident this animal was absent, as a local ecological knowledge study conducted in the area found no local people to have observed *C. ferox* in recent years (2004-2009; Kotschwar 2010).

Selective-logging is known to have complex and often species-specific effects on mammals (Bicknell and Peres 2010; Meijaard et al. 2005; Paviolo et al. 2009). Among Asian civets, logging can have both positive and negative consequences within this diverse group, with



logging increasing the distribution of some civets, while negatively affecting the abundance of others (Meijaard and Sheil 2008). Despite our Selectively-logged forest having reduced basal area and tree density and an altered canopy cover compared to the Primary forest, we found no difference in the carnivore community composition between these areas. Either selective-logging prior to 1991 had not altered the carnivore composition, or contiguous unlogged forest facilitated recolonization in the last two decades.

Similar to findings on tigers (*Panthera tigris*; Rayan and Mohamad 2009), our structurally-altered Selectively-logged rainforest had the same density of *C. ferox* as compared to the Primary forest. We hypothesize that *C. ferox*'s flexible diet, which may explain why this species occupies diverse forests across Madagascar, may also allow *C. ferox* to tolerate a certain level of forest disturbance (Robert et al. 2003). In agreement with previous findings that *C. ferox* rainforest density is lower than dry forest density (Gerber et al. 2010), our average adult-only rainforest density (0.105 km<sup>-2</sup>) was also lower than the adult-only dry forest density (0.18 km<sup>-2</sup>; Hawkins and Racey, 2005). This lower rainforest density may reflect a combination of more patchily distributed resources common in rainforests (Turner 1996), lower primate prey biomass compared to Madagascar's dry forests (Ganzhorn et al. 2003) or lower prey accessibility related to the more complex habitat structure (Balme et al. 2007).

*F. fossana* appear particularly sensitive to forest disturbance. While we found *F. fossana* absent from both fragmented rainforests <2.5 km and >15 km from intact primary forest, they are also unlikely to occupy Madagascar's open human-dominated landscape (Kotschwar 2010) and have been described as intolerant to degraded forests (Kerridge et al. 2003). Some evidence suggests *F. fossana* are able to use fragments <2.5 km from intact forest (Dehgan 2003). Dehgan

(2003) visually observed *F. fossana* at three fragments 93, 745 and 1,368 m (200, 2.5, and 30 ha, respectively) from the intact rainforest, but not at his farthest fragment at 2,438 m (31 ha).

These losses of *F. fossana* with forest fragmentation and reduced densities with selective logging are similar to studies of rainforest civets in Borneo and Malaysia (Colón 2002; Heydon and Bulloh 1996). Carnivore density is generally positively correlated with prey biomass (Carbone and Gittleman 2002), thus observed decreases in carnivore density with selective-logging may be explained by reduced prey species richness and/or abundance. Forest logging in Madagascar's rainforests has been shown to reduce amphibian abundance and diversity (Vallan 2002; Vallan et al. 2004), simplify aquatic macroinvertebrate communities (Benstead and Pringle 2004), and affect native small-mammals (Lehtonen et al. 2001), all of which may impact *F. fossana* populations. Selective-logging is also thought to have a disproportionate effect on terrestrial species with narrow diets that are primarily frugivorous, carnivorous, or insectivorous (Meijaard et al. 2008). Although *F. fossana* diet has generally been described as omnivorous, there is some evidence that this species may exhibit seasonal diet specialization on insectivores in the warm-wet season and vertebrates in the cold-dry season (Goodman et al. 2003). This potential seasonal specialization may make them more vulnerable to selective-logging-induced alterations of prey communities.

The two native carnivores found to occupy fragmented rainforest were the *Galidiinae* mongooses, *G. e. elegans* and *G. fasciata*. While *G. e. elegans* has been known to use rainforest fragments (Goodman 2003a), *G. fasciata*'s presence is more surprising, given their local rarity in the primary rainforest (Goodman 2003b). Despite both species presence in fragments, they were both still constrained by disturbances, as *G. fasciata* was constrained to the larger fragments and *G. e. elegans* constrained by increasing levels of activity by the exotic *F. catus/silvestris*. *F.*

*catus/silvestris*' broad distribution across Madagascar, their negative impact on *G. e. elegans*, and their documented predation upon diurnal lemurs (Brockman et al. 2008) make them a considerable conservation threat to endemic wildlife.

We found at least one exotic carnivore in each rainforest site, with *C. familiaris* being the most ubiquitous. In the contiguous rainforest, *C. familiaris*' use of the forests was negatively related to the distance to the closest village, such that beyond 4 km from a village *C. familiaris* is unlikely to use intact forest. Considering the many villages surrounding RNP, we predicted that 15% and 65% of RNP has greater than 50% and 5% probability of use by *C. familiaris*, respectively. This is a great concern as *C. familiaris* are expected to affect medium and small carnivores through interference competition and are known to serve as disease vectors (Vanak and Gompper 2009). In the dry forests, *C. familiaris* and *F. catus/silvestris* have been implicated in the transmission of a number of diseases to *C. ferox* (Dollar 2006). Even when forests are protected from direct forest loss, disease transmission from domestic or exotic animals remains a critical threat to native wildlife, with significant negative effects on the survival and persistence of many species (Deem et al. 2001).

The exotic *V. indica* is thought to occur widely throughout Madagascar, mostly within disturbed habitats (Dollar 2006). While there is evidence this species occasionally uses the edges of intact rainforest (Gerber et al. 2010), as well as occurs outside the forest, their absence from the contiguous rainforests suggests they cannot permanently occupy intact rainforests. In contrast, in the fragmented forests, *V. indica* was found using the matrix more than the rainforest, which is consistent with habitat use in their native range (Chen et al. 2009). However, any use of the fragments poses the possibility of competition with the native mongooses that also occupy these fragments.

## 5. Conservation Implications:

Rainforest species are generally considered sensitive to fragmentation effects (Turner 1996), thus it may be expected that Madagascar's increasingly fragmented forests (Harper et al. 2007) pose a threat to the conservation of rainforest carnivores. With species persistence in a fragmented landscape often due to the ability to tolerate matrix conditions (Turner 1996), the Malagasy rainforest carnivores' intolerance to the open human-dominated landscape (This study; Kotschwar 2010) necessitates protection and management of forests for native carnivore persistence. Given the documented negative effects of fragmentation in particular on *F. fossana*, its populations throughout Madagascar are likely to vary greatly in size and be highly isolated. Additionally, human hunting of *F. fossana* and *C. ferox* may significantly reduce numbers of these species outside protected areas, as both are known to be consumed (Golden 2009; Kerridge et al. 2003).

Although our island-wide *C. ferox* population extrapolation is imperfect, we found it a useful exercise to enhance understanding of the potential population sizes and isolation of this threatened carnivore and known lemur predator. There is a great need in the rainforest and dry forest to increase the sizes of protected areas to maintain even moderate protected populations of *C. ferox*. This is especially true for dry forests, as the largest protected dry forest area was Kirindy Metea National Park, with 839 km<sup>2</sup> of primary forest, thus a potential population of only 151 adult *C. ferox*. To protect *C. ferox* populations, expansion of protected areas may not need to be in the form of national parks and thus exclusion of local people, but minimally a protection of *C. ferox* from human predation and maintenance of forest structure. In addition to expanding protected areas, establishing forested corridors among fragments and protected areas could

encourage and maintain movements of potentially isolated carnivore populations. Two areas in the eastern rainforest which should be a high priority for forest restoration include 1) the gap between the two eastern rainforest complexes, which were only linked by a series of small (<25 ha) fragments, and 2) the area 16 km north of RNP (UTM: 751529E, 7689031S) which had a gap of approximately 4.5 km between forest fragments. Corridors could benefit carnivore movement, as well as increase forest connectivity as a means to ameliorate the effects of vegetation shifts predicted by climate change (Hannah et al. 2008). However, re-establishment of carnivores in fragments, especially *C. ferox*, may create a risk to lemur population persistence (Irwin et al. 2009; Kotschwar 2010).

Our findings indicate that degraded rainforest fragments are of limited conservation value in supporting an intact endemic Malagasy carnivore community compared to primary and selectively-logged contiguous rainforest. However, degraded fragments may be of significant value in maintaining connectedness of carnivore populations across the landscape. We recommend protecting intact primary rainforest to conserve Madagascar's endemic carnivore populations, protecting fragments to maintain connectedness of the forest landscape, and continuing to study how local people and carnivores coexist in forests that provide forest products and are of carnivore conservation value.

In order to significantly improve our understanding of *C. ferox* and its populations, future research should investigate the 1) minimum fragment size required for occupancy, 2) movement dynamics within and between contiguous and fragmented areas, and 3) density variation within and between all forest types, especially in the spiny forests where no quantitative data exists. The spiny forests cover 20,267 km<sup>2</sup>; if *C. ferox* occupied this unique habitat at even a moderate

density, it would significantly increase our population estimates and would be of great conservation value to this species' long-term survival.

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Table 1. Photographic-sampling grids at four rainforest sites in Madagascar and summary capture/recapture data of the individually-identifiable *Cryptoprocta ferox* and *Fossa fossana*. Sampling occurred from May-December, 2008 and October-December, 2009.

Rainforest Grid	Mean Camera Spacing (m ± SD) (No. Camera Stations)	Season	Sampling Dates	Total Trap Nights <sup>a</sup>	<i>C. ferox</i> Adults: male-female (total recaptures) <sup>b</sup>	<i>F. fossana</i> Individuals: male-female (total recaptures) <sup>b</sup>
Primary	513 ± 93 (27)	Cold-Dry	08/12/08 – 10/09/08	1446	3-3, (75)	16-17, (644)
Selectively-Logged	567 ± 94 (26)	Cold-Dry	06/09/08 – 08/09/08	1417	2-2, (37)	11-11, (428)
Fragmented <2.5 km	558 ± 128 (31)	Warm-Dry	10/15/09 – 12/07/09	1379	1-0, (1)	0-0, (0)
Fragmented >15 km	584 ± 86 (27)	Warm-Dry	10/20/08 – 12/11/08	1323	0-0, (0)	0-0, (0)

<sup>a</sup>Trap nights are total sampling effort where at least one of two remote cameras were functioning at a station per 24-hour period

<sup>b</sup>Total recaptures are for the spatially-explicit capture-recapture model, where individuals can be recaptured at multiple stations on a single sampling occasion

Table 2. Grid-level vegetation structure  $\pm$  SE at four rainforest sites with increasing levels of disturbance in southeastern Madagascar. Sampling occurred from May-December, 2008 and October-December, 2009. Different letters associated with vegetation variables across sites indicate sites differ significantly in that variable (experiment-wise  $\alpha = 0.05$ ).

Vegetation Structure	Primary (N= 27)	Selectively-logged (N=26)	Fragmented <2.5 km <sup>a</sup> (N=27)	Fragmented >15 km <sup>a</sup> (N=13)
Tree Density ( $\geq 10$ cm D <sub>130</sub> stems/ha)	1612 $\pm$ 27 A	622 $\pm$ 17 B	337 $\pm$ 11 C	500 $\pm$ 11 BC
Basal Area (m <sup>2</sup> /ha, stems $\geq 10$ cm D <sub>130</sub> )	102 $\pm$ 13 A	24 $\pm$ 2 B	8 $\pm$ 4 C	13 $\pm$ 3 C
Down/Dead Cover % ( $\geq 15$ cm D <sub>130</sub> )	5 $\pm$ 2 A	4 $\pm$ 0.5 A	2 $\pm$ 0.3 B	0.6 $\pm$ 0.6 C
Ground Cover % ( 0-0.5 m)	70 $\pm$ 4 A	91 $\pm$ 1 B	57 $\pm$ 4 A	91 $\pm$ 3 B
Shrub Cover % (0.5-5 m)	87 $\pm$ 4 AB	94 $\pm$ 2 A	78 $\pm$ 4 B	85 $\pm$ 3 AB
Low-Tree Canopy Cover % (0-5 m)	5 $\pm$ 2 A	11 $\pm$ 0.9 B	45 $\pm$ 4 C	16 $\pm$ 2 B
Mid-Tree Canopy Cover % (5-15 m)	58 $\pm$ 5 A	86 $\pm$ 2 B	27 $\pm$ 4 C	31 $\pm$ 4 C
High-Tree Canopy Cover % ( $\geq 15$ m)	66 $\pm$ 4 A	38 $\pm$ 4 B	6 $\pm$ 2 C	4 $\pm$ 2 C

<sup>a</sup> Rainforest habitat only was quantified in these two fragmented forest sites which are respectively <2.5 and > 15 km from the contiguous rainforest

Table 3. Model selection (model likelihood >0.125) using a maximum-likelihood spatially-explicit capture-recapture model to estimate density of the fossa (*Cryptoprocta ferox*) and Malagasy civet (*Fossa fossana*) in a Primary and Selectively-logged contiguous rainforest grid within Madagascar's eastern rainforests. Sampling occurred from May-December, 2008 and October-December, 2009.

Species	Rainforest Grid	Models <sup>a</sup>	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>	Model Likelihood	k	Deviance
<i>Cryptoprocta ferox</i>	Primary	HalfNormal g <sub>0</sub> (sex) σ(.)	865.61	0.00	0.446	1.00	3	839.27
		HalfNormal g <sub>0</sub> (h) σ(.)	865.66	0.05	0.435	0.98	3	839.32
		HalfNormal g <sub>0</sub> (.) σ(.)	868.42	2.81	0.109	0.25	2	842.08
	Selectively-Logged	NegExp g <sub>0</sub> (h) σ(h)	438.14	0.00	0.713	1.00	4	465.41
		NegExp g <sub>0</sub> (Sex) σ(Sex)	442.02	3.88	0.102	0.14	4	469.29
<i>Fossa fossana</i>	Primary	Hazard Rate g <sub>0</sub> (sex) σ(h)	3858.47	0.00	0.99	1.00	6	3782.57
	Selectively-Logged	NegExp g <sub>0</sub> (sex+lure) σ(h)	2479.68	0.00	0.99	1.00	6	2426.87

<sup>a</sup>Distance functions: Hazard Rate, Half-Normal, Negative-Exponential;  $g_0$  is the detection probability when a single trap is located at the center of an animal's home range;  $\sigma$  is the spatial scale detection probability away from the center of the home range; Sex is males versus females; Lure is chicken meat used as a scent-lure and unavailable for consumption by carnivores;  $h$  is individual heterogeneity

Table 4. Density estimates of the fossa (*Cryptoprocta ferox*) and Malagasy civet (*Fossa fossana*) in four rainforest areas within Madagascar with statistical significance (95% confidence interval of two means overlap less than half the average margin of error) indicated with different capital letters ( $\alpha = 0.05$ ). Sampling occurred from May-December, 2008 and October-December, 2009.

	<i>Cryptoprocta ferox</i>	<i>Fossa fossana</i>
Rainforest Grid	Density $\pm$ SE (adults/km <sup>2</sup> )	Density $\pm$ SE (individuals/km <sup>2</sup> )
Primary	0.12 $\pm$ 0.05 A	3.19 $\pm$ 0.55 C
Selectively-Logged	0.09 $\pm$ 0.04 A	1.38 $\pm$ 0.22 D
Fragmented <2.5 km	$\geq 0^a$	0 B
Fragmented >15 km	0 B	0 B

<sup>a</sup>One animal was detected, which precluded estimation

Table 5. Model selection (model likelihood >0.125) of occupancy and detection probability for native and exotic rainforest carnivores in southeastern Madagascar at two contiguous (Primary and Selective-logged) and two fragmented (< 2.5 and > 15 km from contiguous forest) sampling grids. Sampling occurred from May-December, 2008 and October-December, 2009.

Rainforest Grid	Species	Models <sup>a</sup>	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>	Model Likelihood	k	-2*log likelihood
Contiguous	<i>Canis familiaris</i>	ψ(DistVillage) p(Locals)	235.92	0.00	0.61	1.00	4	227.92
		ψ(Grid + DistVillage),p(Locals)	237.65	1.73	0.26	0.42	5	227.65
	<i>Cryptoprocta ferox</i>	ψ(Grid+Locals) p(Trail + DistMatrix)	993.86	0.00	0.41	1.00	6	981.86
		ψ(Locals) p(Trail + DistMatrix)	995.92	2.06	0.15	0.36	5	985.92
		ψ(.) p(Trail + DistMatrix)	997.21	3.35	0.08	0.19	4	989.21
		ψ(Grid) p(Trail + DistMatrix)	998.02	4.16	0.05	0.13	5	988.02
	<i>Fossa fossana</i>	ψ(.) p(Lure)	3434.08	0.00	0.99	1.00	3	3428.08
	<i>Galidictis fasciata</i>	ψ(Grid + BasalArea) p(DistMatrix + Dogs)	528.36	0.00	0.92	1.00	6	515.21

Fragmented	<i>Canis familiaris</i>	$\psi(\text{Grid})$ p(Locals + ForestType + Lure)	1278.88	0.00	0.84	1.00	6	1266.88
		$\psi(\cdot)$ p(Locals + ForestType + Lure)	1282.34	3.46	0.15	0.18	5	1270.34
	<i>Felis catus/silvestris</i>	$\psi(\text{DD})$ p(Dog)	373.05	0.00	0.66	1.00	4	364.22
		$\psi(\text{Grid}+\text{DD})$ p(Dog)	375.29	2.24	0.22	0.33	5	364.01
	<i>Galidia elegans</i>	$\psi(\text{ForestType}) + \text{Cat}$ p(Grid)	973.43	0.00	0.85	1.00	5	962.25
	<i>elegans</i>							
	<i>Galidictis fasciata</i>	$\psi(\text{Area})$ p(Grid)	456.53	0.00	0.99	1.00	4	447.76
	<i>Viverricula indica</i>	$\psi(\text{ForestType} + \text{Locals})$ p(ForestType)	541.85	0.00	0.40	1.00	5	531.85
		$\psi(\text{ForestType})$ p(ForestType)	542.93	1.08	0.23	0.58	4	534.93
		$\psi(\text{ForestType} + \text{Cat})$ p(ForestType)	544.33	2.48	0.12	0.29	5	534.33
		$\psi(\text{ForestType} + \text{Dog})$ p(ForestType)	544.72	2.87	0.10	0.24	5	534.72

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<sup>a</sup> $\psi$  : occupancy, p: detection probability, Area: rainforest fragment area, BasalArea: basal area, Cat: *Felis catus/silvestris* trap success,

DD: down and dead cover, DistMatrix: closest distance to non-rainforest, DistVillage: distance to closest village, Dog: *Canis*

*familiaris* trap success, ForestType: difference at fragmented grids between rainforest habitat and matrix, Grid: difference between

contiguous rainforest grids or fragmented rainforest grids, Locals: local human trap success, Lure: effect of using lure versus not using at only Selectively-logged and Fragments <2.5 km grids, Trail: maintained trails versus small trails



Table 6. Occupancy analyses of detection probability (p) regression coefficients ( $\beta$  (SE)) for the top models of endemic and exotic carnivores at two fragmented and two contiguous rainforest grids within Madagascar's eastern forests. Sampling occurred from May-December, 2008 and October-December, 2009.

Rainforest Grids	Parameter <sup>a</sup>	<i>Canis familiaris</i>	<i>Cryptoprocta ferox<sup>b</sup></i>	<i>Felis catus/silvestris<sup>c</sup></i>	<i>Fossa fossana<sup>c</sup></i>	<i>Galidia elegans elegans<sup>d</sup></i>	<i>Galidictis fasciata</i>	<i>Viverricula indica<sup>c</sup></i>
Contiguous	Intercept	<b>-3.90 (0.31)</b>	<b>-2.57 (0.10)</b>	-	<b>1.44 (0.09)</b>	-	<b>-4.02 (0.24)</b>	-
	DistMatrix	-	<b>0.43 (0.10)</b>	-	-	-	<b>1.19 (0.23)</b>	-
	Dog	-	-	-	-	-	<b>-1.16 (0.38)</b>	-
	Locals	<b>0.60 (0.18)</b>	-	-	-	-	-	-
	Lure	-	-	-	<b>0.90 (0.10)</b>	-	-	-
	Trail	-	<b>-1.62 (0.30)</b>	-	-	-	-	-
Fragmented	Intercept	<b>-3.07 (0.18)</b>	-	<b>-3.63 (0.19)</b>	-	<b>-1.77 (0.09)</b>	<b>-2.67 (0.15)</b>	<b>-3.66 (0.31)</b>
	Dog	-	-	<b>0.81 (2.44)</b>	-	-	-	-
	ForestType	<b>0.95 (0.16)</b>	-	-	-	-	-	<b>0.96 (0.36)</b>
	Grid	-	-	-	-	<b>-1.90 (0.27)</b>	<b>-1.91 (0.43)</b>	-

Locals	<b>0.43 (0.05)</b>	-	-	-	-	-	-
Lure	<b>0.68 (0.20)</b>	-	-	-	-	-	-

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<sup>a</sup>Dash(-) indicates the parameter is not applicable and bold indicates the estimate is statistically different than zero. DistMatrix: closest distance to non-rainforest, Dog: *Canis familiaris* trap success, ForestType: difference at fragmented grids between rainforest habitat (1) and matrix (0), Grid: difference between fragmented rainforest grids (Fragments >15 km (0) and Fragments <2.5 km (1)) or contiguous rainforest grids (Primary (0) and Selectively-Logged (1)), Locals: local human trap success, Lure: effect of using lure versus not using at only Selectively-logged and Fragments <2.5 km grids, Trail: maintained (0) trails versus small secondary trails (1)

<sup>b</sup>*C. ferox* was detected at one of the fragmented grids, but poor recaptures precluded modeling

<sup>c</sup>Species was not detected at either the fragmented or the contiguous rainforests

<sup>d</sup>*G. e. elegans* was detected at both contiguous forests, but naïve occupancy equals one at those grids, thus precluded modeling

Table 7. Occupancy analyses ( $\psi$ ) regression coefficients ( $\beta$  (SE)) for the top models of each carnivore species at two fragmented and contiguous rainforest grids within Madagascar's eastern forests. Sampling occurred from May-December, 2008 and October-December, 2009.

Rainforest Grids	Parameter <sup>a</sup>	<i>Canis familiaris</i>	<i>Cryptoprocta ferox<sup>b</sup></i>	<i>Felis catus/silvestris<sup>c</sup></i>	<i>Fossa fossana<sup>c</sup></i>	<i>Galidia elegans elegans<sup>d</sup></i>	<i>Galidictis fasciata</i>	<i>Viverricula indica<sup>c</sup></i>
Contiguous	Intercept	-0.91 (0.51)	1.85 (1.43)	-	<b>3.95 (1.10)</b>	-	-0.17 (0.42)	-
	BasalArea	-	-	-	-	-	<b>0.99 (0.38)</b>	-
	DistVillage	<b>-1.21 (0.54)</b>	-	-	-	-	-	-
	Grid	-	2.33 (1.27)	-	-	-	-0.10 (0.45)	-
	Locals	-	3.15 (2.62)	-	-	-	-	-
Fragments	Intercept	0.188 (0.40)	-	1.30 (1.17)	-	1.19 (0.72)	<b>6.34 (3.13)</b>	0.28 (1.42)
	Area	-	-	-	-	-	<b>12.05 (4.74)</b>	-
	Cat	-	-	-	-	<b>-1.84 (0.80)</b>	-	-
	DD	-	-	4.17 (2.17)	-	-	-	-
	ForestType	-	-	-	-	<b>-2.71 (1.09)</b>	-	<b>2.63 (1.06)</b>

Grid	<b>1.18 (0.44)</b>	-	-	-	-	-	-
Locals	-	-	-	-	-	-	5.86 (8.37)

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<sup>a</sup>Dash (-) indicates the parameter is not applicable and bold indicates the estimate is statistically different than zero. Area: rainforest fragment area, BasalArea: basal area, Cat: *Felis catus/silvestris* trap success, DD: down and dead cover, DistVillage: distance to closest village, ForestType: difference at fragmented grids between rainforest habitat (1) and matrix (0), Grid: difference between fragmented rainforest grids (Fragments >15 km (0) and Fragments <2.5 km (1)) or contiguous rainforest grids (Priamry (0) and Selectively-Logged (1)), Locals: local human trap success

<sup>b</sup>*C. ferox* was detected at the fragmented sites, but with no recaptures at only two sites precluded occupancy estimation

<sup>c</sup>Species was not detected at either the contiguous or fragmented sites

<sup>d</sup>*G. e. elegans* was detected at both contiguous forests, but naïve occupancy equals one at those grids, thus precluded modeling

Table 8. Model-averaged occupancy (SE) of native and exotic carnivores in two contiguous and two fragmented rainforest sites within Madagascar's eastern forests. Sampling occurred from May-December, 2008 and October-December, 2009.

	Contiguous Rainforest Grids		Fragmented Rainforest Grids			
	Primary	Selectively-Logged	<2.5 km from Primary Rainforest	Matrix	>15 km from Primary Rainforest	Matrix
<i>Canis familiaris</i>	0.27 (0.08)	0.39 (0.10)	0.87 (0.07)	0.87 (0.07)	0.67 (0.06)	0.67 (0.06)
<i>Cryptoprocta ferox</i>	0.93 (0.05)	0.72 (0.08)	0.069 <sup>a</sup>	0.00	0.00	0.00
<i>Eupleres goudotii</i>	0.07 <sup>a</sup>	0.31 <sup>a</sup>	0.00	0.00	0.00	0.00
<i>Fossa fossana</i>	0.98 (0.02)	0.98 (0.02)	0.00	0.00	0.00	0.00
<i>Galidia elegans elegans</i>	1.00 <sup>a</sup>	1.00 <sup>a</sup>	0.77 (0.10)	0.19 (0.12)	0.77 (0.10)	0.19 (0.12)
<i>Galidictis fasciata</i>	0.57 (0.13)	0.23 (0.10)	0.67 (0.09)	0.04 (0.04)	0.67 (0.09)	0.04 (0.04)
<i>Felis catus/silvestris</i>	0.00	0.00	0.64 (0.12)	0.64 (0.12)	0.41 (0.09)	0.41 (0.09)
<i>Viverricula indica</i>	0.00	0.00	0.57 (0.08)	0.94 (0.04)	0.57 (0.08)	0.94 (0.04)

<sup>a</sup>Naïve occupancy, due to limited dataset

<sup>b</sup>Naïve occupancy equals one at those grids, thus precluded modeling

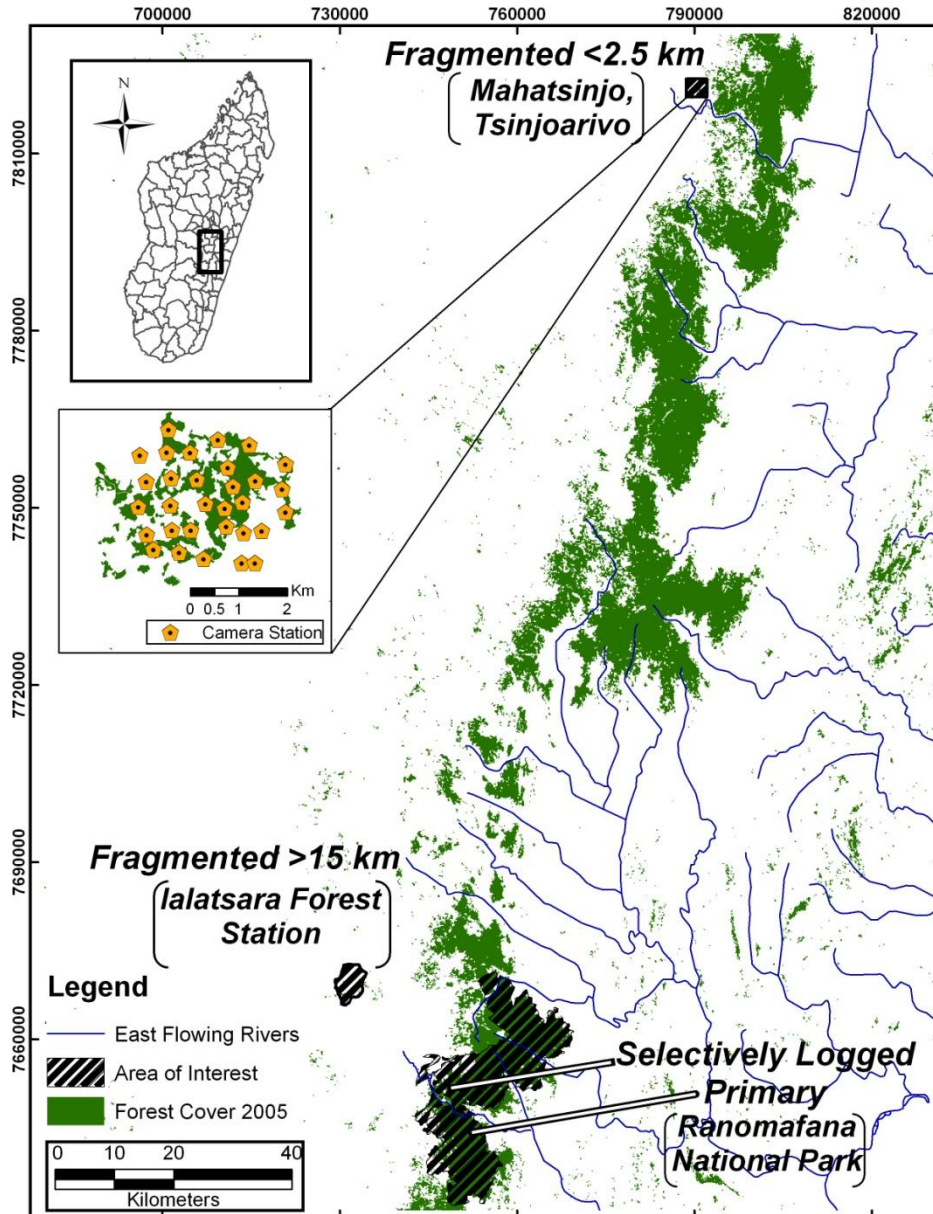


Figure 1. Carnivores were sampled at four photographic-sampling sites within Madagascar's eastern rainforests from May-December, 2008 and October-December, 2009. Top insert map shows political provinces and location on the island of Madagascar, while the bottom insert map shows the camera station sampling layout among rainforest fragments at Mahatsinjo, Tsinjoarivo as an example. Rainforest extent from Conservation International, 2010.

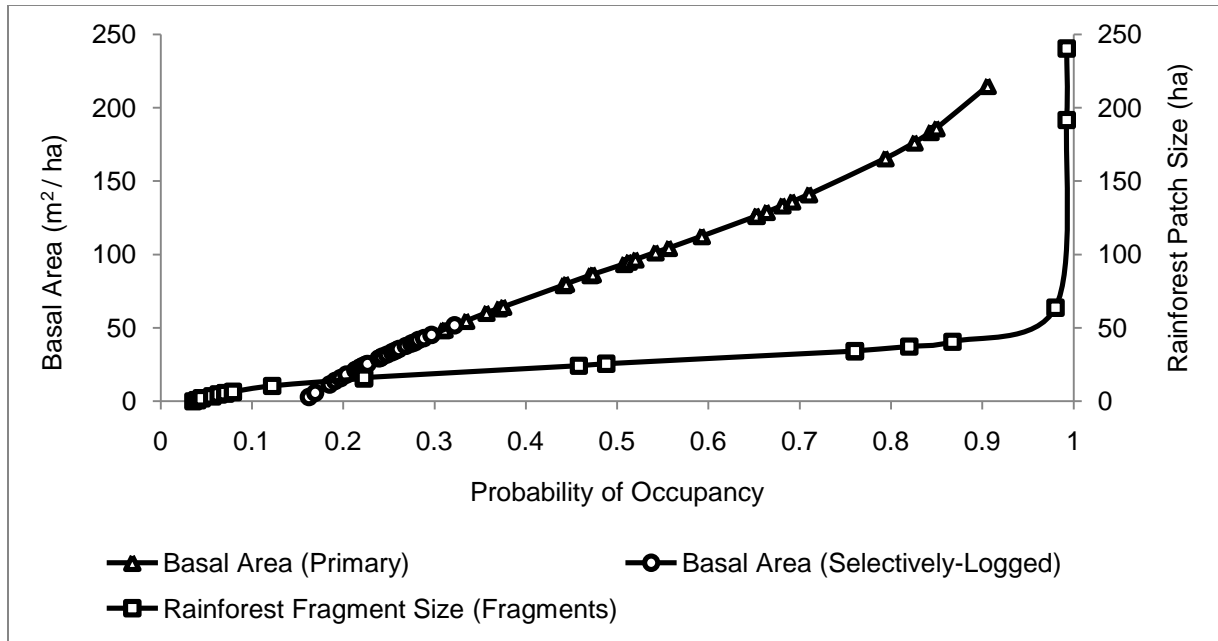


Figure 2. Broad-striped mongoose (*Galidictis fasciata*) occupancy variation by basal area in contiguous rainforests within Ranomafana National Park and occupancy variation by fragment size in fragmented rainforests (<2.5 km and >15 km from intact contiguous rainforest), sampled within Madagascar's eastern forests from May-December, 2008 and October-December, 2009.

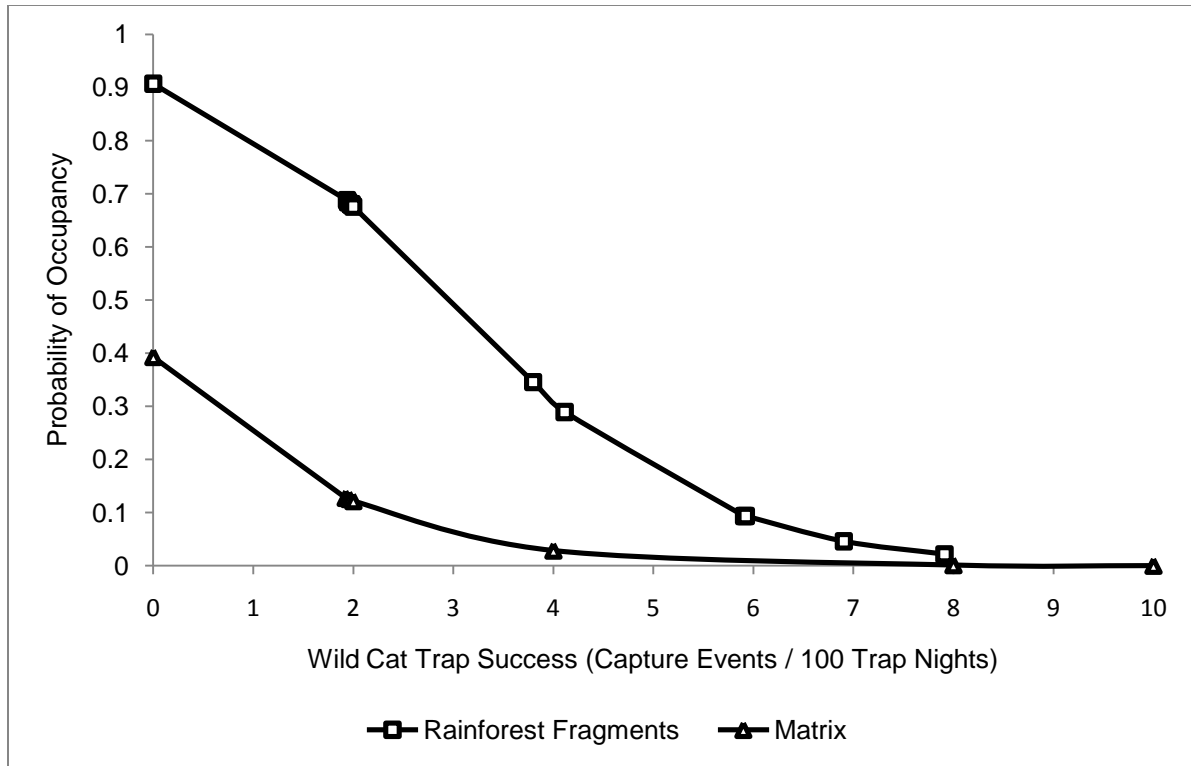


Figure 3. Ring-tailed mongoose (*Galidia elegans elegans*) occupancy variation within rainforest fragments and surrounding matrix (open human-dominated habitat) and the effect of exotic-wild cats (*Felis catus/silvestris*). Sampling occurred within Madagascar's eastern forests from May-December, 2008 and October-December, 2009.



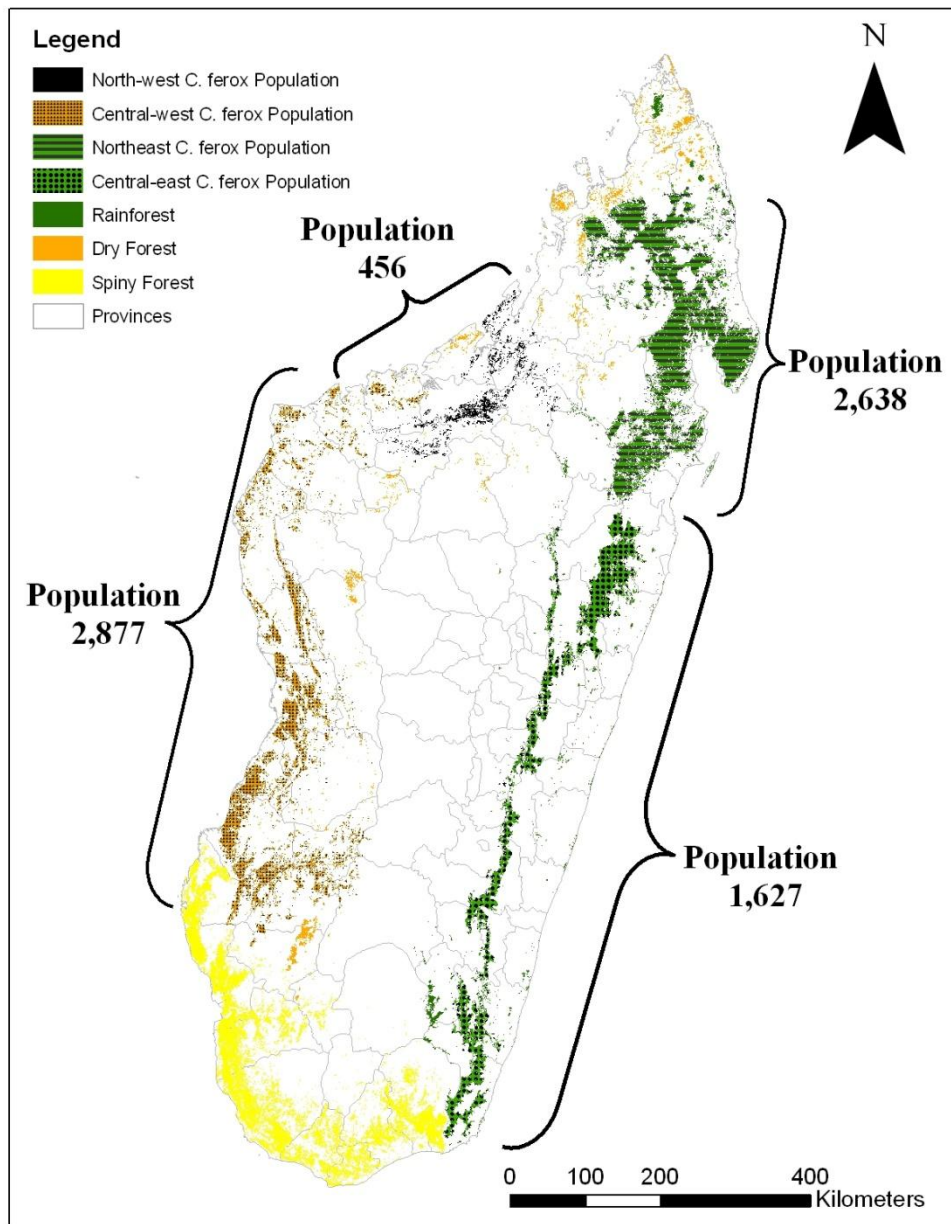


Figure 4. Madagascar's primary forest cover (2005) and estimated fossa (*Cryptoprocta ferox*) populations >300 adults. Ninety-five percent of the total rainforest population is contained in two forest complexes, while 80% of the total dry forest population is contained in two forest complexes. Forest fragments were joined into a single population when forested areas large enough to hold  $\geq 1$  fossa were <4.9 km from each other.

## Chapter 4 - Temporal activity patterns of Malagasy rainforest carnivores

### Abstract:

Understanding the temporal activity patterns of animals can provide meaningful insight into behavioral responses to habitat disturbance and mechanisms of co-existence among sympatric species. We used photographic-sampling to quantify the temporal activity patterns of Madagascar's native carnivores (*Cryptoprocta ferox*, *Fossa fossana*, *Galidia elegans elegans*, *Galidictis fasciata*, *Eupleres goudotii*), exotic carnivores (*Viverricula indica*, *Canis familiaris*, *Felis catus*, *Felis silvestris*) and local people within the eastern rainforests. We sampled carnivores in two contiguous (Primary and Selectively-logged) and two fragmented rainforests (Fragments <2.5 km and >15 km from intact primary rainforest). To avoid issues of non-independence of consecutive photographs, we defined an activity-sample as the median time of all photographs of the same species or individual taken within a 0.5 hour period and applied a kernel density estimator to quantify activity patterns. We compared the overlap in the daily activity patterns among all species and assessed how each individual species used dawn, day, dusk, and night time periods with respect to their availability in the diel cycle. Malagasy carnivores had diverse activity patterns (diurnal, nocturnal, crepuscular) with varied temporal activity overlap (5.8 to 88.8%) among species. Species with greater temporal overlap differed from each other in other aspects of their ecology, such as diet, in accordance with predictions from niche theory. Rainforest site and season had little effect on the diurnal *G. elegans elegans* or the nocturnal *G. fasciata*, which were detected at all sites. *C. ferox* in the contiguous rainforest selected the crepuscular hours greater than would be expected by the availability of this time period in the diel cycle, but overall the activity pattern of this species could be described as cathemeral. As a major lemur predator, understanding *C. ferox* activity patterns will

help to better understand lemur predation risk and the evolution of anti-predator behaviors, specifically cathemerality of many lemur species at risk of predation by *C. ferox*. The temporal overlap of exotic carnivores with native carnivores is of significant conservation concern due to the potential for both direct resource competition and disease transmission.

### **Introduction:**

The distribution of a species' activity through time is an important niche-dimension that has profound implications for its ecology and evolution (Kronfeld-Schor and Dayan 2003; Pianka 1973). How species use time is inextricably linked to morphological and physiological adaptations (Aschoff et al. 1982; Hayward and Slotow 2009). For example, most carnivores have vision that is highly adaptable for activity throughout the diel-cycle (Kavanau and Ramos 1975), so it is not surprising that many carnivores also exhibit a high degree of plasticity in temporal activity patterns (Gittleman 1986; Zielinski 2007). Carnivore temporal activity has been shown to be influenced by prey availability (Zielinski et al. 1983), daily or seasonal temperature variation (Lourens and Nel 1990; Zub et al. 2009), human activity (Beckmann and Berger 2003; Griffiths and Schaik 1993; Kolowski et al. 2007), interspecific competition (Hayward and Slotow 2009; Hunter and Caro 2008; Romero-Muñoz et al. 2010), and intra-guild predation (Palomares and Caro 1999).

While the activity patterns of many carnivores appear temporally flexible, we know little about how carnivores may alter their activity patterns in response to new disturbances and ecological changes, such as those caused by forest loss and fragmentation (Beckmann and Berger 2003). If an animal's temporal activity is at all constrained by phylogeny (Roll and Kronfeld-Schor 2006), it may be unable to adapt in ecological time to a changing environment. Impacts of

habitat loss are often evaluated with regard to altering species richness and abundance. However, to fully understand ecological processes at the population level, we also need knowledge of the impact on individual's behavior (i.e. activity patterns) and ecological relationships (Norris et al. 2010; Presley et al. 2009; Sutherland and Dolman 1994).

The cue to which many animals maintain their activity patterns is the day/night cycle (Kronfeld-Schor and Dayan 2003), which is of course unaltered by habitat change. Day-length (or night-length) can act as an ecological constraint that limits an animal's time to perform its essential activities (Hill et al. 2003). However, not all mammals exhibit simple unimodal activity, as either diurnal or nocturnal. More complex or multimodal patterns, such as crepuscular activity (bimodal peaks in activity at dawn and dusk), are common among carnivores (Gittleman 1986). Cathemerality, which is defined by an evenness of activity throughout the diel-cycle, or when significant activity occurs during both the day and night (Tattersall 2006), is also common across mammalian taxa (Curtis et al. 2006; Halle and Stenseth 2000; Schaik and Griffiths 1996). Crepuscular and cathemeral activity patterns may allow individuals to adjust to habitat alterations or new disturbance events (i.e. human activity) compared to strict diurnal/nocturnal patterns which constrain an individual to activity just during those limited hours (Hill et al. 2003).

Like many carnivores, the activity patterns of Madagascar's rainforest carnivores are still poorly understood. Of the nine extant endemic carnivore species within the endemic family *Eupleridae* (Goodman and Helgen 2010; Yoder et al. 2003), five are known to occupy the southeastern rainforests (broad striped mongoose *Galidictis fasciata*, fossa *Cryptoprocta ferox*, Malagasy civet *Fossa fossana*, ring-tailed mongoose *Galidia elegans elegans*, small-toothed civet *Eupleres goudotii*; Gerber et al. 2010). Malagasy carnivore activity patterns have only

generally been described (Albignac 1972; Dollar 1999; Hawkins 1998). As these Malagasy rainforest carnivores co-occur at the local scale (i.e. at a sampling station; B. Gerber, unpublished data), temporal activity separation may be an important factor in their co-existence. Additionally, *C. ferox* and *G. e. elegans* are known lemur predators, which suggests their activity patterns may have direct implications for lemur predation risk and the evolution of anti-predator behaviors, including lemur activity patterns (Colquhoun 2006; Karpanty and Wright 2007).

Our objectives were to sample Madagascar's endemic rainforest carnivores, exotic carnivores (domestic dog, *Canis familiaris*; exotic-wild cat, *Felis catus* and *Felis silvestris*, grouping the domestic and introduced African wildcat, *F. catus/silvestris*, as they are difficult to distinguish from each other; small-Indian civet *Viverricula indica*) and local people using non-invasive remote photographic-sampling to 1) quantify temporal activity patterns, 2) compare temporal activity overlap among native and exotic carnivores and local people across a continuum of increasingly disturbed rainforests, and 3) evaluate the selection or avoidance of the dawn, day, dusk, and night time-periods through the diel-cycle.

## **Materials and Methods:**

### **Study Areas:**

We worked in the southeastern rainforests of Madagascar at four study sites (Fig. 1). We sampled the contiguous rainforests at the Valohoaka-Vatoranana (Primary) and Sahamalaotra trail-systems (Selectively-logged) located in the boundaries of Ranomafana National Park (RNP). We also sampled two fragmented rainforests at Mahatsinjo, Tsinjoarivo (Fragments <2.5 km from intact rainforest) and Ialatsara Forest Station (Fragments >15 km from intact rainforest).

Our Primary rainforest site had little anthropogenic disturbance (Wright 1997), while our Selectively-logged rainforest experienced moderate logging pressure before RNP was established in 1991 (JC. Razafimahaimodison, Pers. Comm.). Our Fragments <2.5 km site was located 150 km north of RNP within a network of unprotected hilltop rainforest fragments <2.5 km from the large tract of contiguous primary rainforest. Fragments were surrounded by a human-dominated landscape of agriculture and naturally regenerating shrub. Our Fragments >15 km site was northwest of RNP, located in a protected fragmented rainforest >15 km from the main tract of contiguous primary rainforest. Fragments were surrounded by shrub, exotic pine and eucalyptus, open areas recently burned, and minimal agriculture. In both fragmented sites, forest edges were hard transitions to open habitat, caused by human activities such as burning, grazing, and farming. Local people used both fragmented study areas for travel and forest products, but only at the Fragments <2.5 km site did people live between the fragments. Sampling took place over a period of two years from May-December, 2008 (Primary, Selectively-logged, and Fragments >15 km) and October-December, 2009 (Fragments <2.5 km). The two contiguous rainforests at RNP were sampled in the cold-dry season (April-October) and the two fragmented grids in the warm-dry season (November-February, Tecot 2008). A five year average (2005-2009) min-max daily temperature was 13-20 °C at RNP during the cold-dry season. The temperature during the warm-dry season sampling at the Fragments >15 km and Fragments <2.5 km sites were 15-24°C and 12-26°C, respectively. The five year average (2005-2009) daily rainfall  $\pm$  SD was  $6.2 \pm 11.4$  mm at RNP during the cold-dry season. The average rainfall  $\pm$  SD during the warm-dry season sampling at the Fragments >15 km and Fragments <2.5 km sites were  $5.1 \pm 8.4$  mm and  $7.4 \pm 14.0$  mm, respectively.

## Sampling:

We used a random starting point to establish a systematic grid of passive-infrared camera stations along established trail-systems to photographically sample carnivores at each rainforest site. We deployed 26 to 31 camera stations for at least 52 days in each site. The average spacing  $\pm$  SD among adjacent stations was  $555 \pm 100$  m. Camera stations consisted of two independently-operating passive infrared cameras, mounted on opposite sides of a trail. This allowed a photographic-capture of both flanks of every animal, thus improving individual identification in recaptures for *C. ferox* and *F. fossana*, which are individually-identifiable (Gerber et al. 2010). We attached cameras 20 cm above the ground and set them to be active for 24 hours/day. Camera types included Deercam DC300's (DeerCam, Park Falls, USA) which were set to a 1-min delay between consecutive photographs and Reconyx PC85's (Reconyx, Inc. Holmen, Wisconsin), which were set with no time delay. Each photograph recorded the date and time of the sample. We used chicken meat as a scent-lure to effectively sample these rare/elusive species at all sites. However, in the Selectively-logged and Fragments <2.5 km sites, we sampled for approximately half the time with and half without scent-lure to evaluate the effect on carnivore activity patterns. We checked camera stations every three to five days to ensure continued operation, replacing batteries, scent-lure, film, and memory cards when necessary.

## Data Analyses:

### *Temporal Activity Pattern Distribution and Overlap*

We defined an activity-sample as the median time of all photographs of the same species or individual (*C. ferox* and *F. fossana*) detected at a camera station within a 0.5 hour period, thus

avoiding non-independence of consecutive photographs (O'Brien et al. 2003; Ridout and Linkie 2009). To assess whether this effectively reduced the temporal dependency of activity samples within our datasets, we calculated the median time between consecutive samples of individuals within a rainforest site, or consecutive samples of individually-unidentifiable species at each camera station. To evaluate the effect of scent-lure on carnivore activity, we tested if species activity distributions (over total diel-cycle) from data collected with and without lure were different using the non-parametric circular Mardia-Watson-Wheeler statistical test (MWW; Batschelet 1981). Analyses using this test were restricted to datasets with  $\geq 10$  activity samples (Fisher 1993). We considered  $P < 0.1$  as significant.

We then tested for individual, sex, and rainforest site effects on activity patterns. For the individually-identifiable *C. ferox* and *F. fossana*, we first tested for differences among individual's activity distributions within a site using MWW. If no differences were observed among individuals, we pooled datasets at each site and tested for differences among sites and sexes. For all other carnivores and local people, we were unable to test for individual variation and thus recognize the pooling of activity samples at each site is possibly pseudoreplication, depending on if there was individual variation in activity patterns (Aebischer et al. 1993). However, we still used these pooled data to test for differences of species' activity distributions among sites using MWW.

For all species, we pooled datasets when activity distributions were not different across forest sites or forest sites and sex. We then used Rao's test of uniformity on these pooled/un-pooled species' activity distributions to evaluate whether species exhibit a uniform or cathemeral activity pattern throughout the diel cycle using the R package Circular (R Development Core Team 2010). The Rao's test was preferred over Rayleigh's or Kuiper's V Test as it is more



powerful when the data is multimodal (Mardia and Jupp 2000), as is common with carnivores (Gittleman 1986). If distributions were non-uniform, we calculated the directional median and standard error of activity in the diel cycle.

To quantify the overall activity pattern of each species and overlap among sympatric species, we utilized a kernel density analysis (Ridout and Linkie 2009). Following Ridout and Linkie (2009) we attempted to minimize bias with small or large sample sizes by employing two kernel estimators; we used their equation 3.1 (page 325) with a smoothing parameter of 1.25 when sample sizes were  $\leq 50$  and their equation 3.3 (page 325) with a smoothing parameter of 1.00 when sample sizes were  $\geq 50$ .

#### *Relative Preference and Selection/Avoidance of Time Periods in the Diel-Cycle*

To determine the relative preference of, and selection and/or avoidance of, different periods of the diel-cycle by carnivores and local people, we categorized the diel-cycle based on sunrise/sunset times at each rainforest site into dawn, day, dusk, and night. We defined the crepuscular hours of dawn and dusk as  $\pm 1$  hour before and after sunrise and sunset. For *C. ferox* and *F. fossana*, from which we could identify the sexes, we used a generalized multinomial model with a logit link (PROC LOGISTIC; SAS Institute Inc.) to test whether the proportion of use among dawn, day, dusk and night differed by site and sex. For other species for which we could not identify the sexes, we tested whether the proportion of use among dawn, day, dusk, and night differed by site using a likelihood-ratio chi-square test in a contingency table (Zar 1998). If we found differences, we used partial chi-square cell values to interpret the contribution of individual cells to overall significance. When we found no differences among forest sites or forest sites and sex, we pooled datasets.

We used the subsequent datasets to examine whether Malagasy carnivores and local people select or avoid dawn, day, dusk and night, given their availability. For *C. ferox* and *F. fossana*, we were able to use the individual as the sampling unit and employed compositional analyses (Aebischer et al. 1993). Although we could not identify individuals of *G. e. elegans*, we still used compositional analyses using camera stations as the sampling unit. Camera stations are likely to capture some variation among individuals, and serve as a proxy for individual, within the forest sites as home ranges for this species are likely small compared to camera station spacing (Dunham 1998). Additionally, sample sizes of *G. e. elegans* activity samples were adequate at camera stations which made this feasible. We used the kernel density analysis to derive the proportions of use among temporal classes from individuals and camera stations with  $\geq 10$  activity samples from the kernel probability distributions. We were unable to use the camera station as a sampling unit for other individually-unidentifiable species due to too few activity samples per camera station.

Compositional analysis calculates the difference in log-ratios of proportions of used and available temporal classes for each individual. We used a randomization procedure with 1000 iterations to overcome issues when log-ratio differences were not multivariate normal and calculated Wilks' lambda ( $\lambda$ ), a multivariate analog to the t-test (Mardia et al. 1979), to test if temporal activity classes were used randomly. If temporal classes were used non-randomly ( $P < 0.1$ ), this implied that the species selected or avoided certain temporal classes and we then performed a series of pair-wise comparisons to determine relative preference (Aebischer et al. 1993).

For all other species (*C. familiaris*, *E. goudotii*, *F. catus/silvestris*, *G. fasciata*, *V. indica*, local people), we determined selection/avoidance of temporal classes using Bailey's

simultaneous confidence intervals constructed around the proportional use of temporal classes (Cherry 1996). As before, we are unable to account for individual variation and recognize this is possibly pseudoreplication (Aebischer et al. 1993). We used the kernel density analysis to derive the proportions of use among temporal classes from datasets with  $\geq 10$  activity samples from the kernel probability distributions. A Bonferroni correction was used to control for the non-independence of multi-comparisons, thus we increased the Type II error to fix the experiment-wise error rate at  $P < 0.1$  (Byers et al. 1984; Cherry 1996). When the available temporal class was below the lower confidence limit interval, the time class was selected. When the available proportion was higher than the upper confidence limit interval, the time class was avoided. Otherwise, the time class was used in proportion to its availability. When there were no observations in a given temporal class and the availability was large, we assumed the species avoided this time period. These analyses cannot account for relative preference, thus there are no rankings of temporal classes for the individually-unidentifiable species.

## **Results:**

We collected activity data on all five native southeastern rainforest carnivores, three exotic carnivores, and local people at our four study sites (Table 1). Species presence and number of activity samples at the forest sites varied, and the limited datasets ( $\leq 10$  activity samples) of *C. ferox* at Fragments  $< 2.5$  km, and *C. familiaris* and *E. goudotii* at the Primary rainforests, precluded certain species comparisons across all sites.

We identified fifteen *C. ferox* individuals in total, but only three individuals each at the Primary and Selectively-logged forests had  $\geq 10$  observations per individual for analyses. We identified fifty-five *F. fossana* individuals total at the Primary and Selectively-logged sites, of

which thirty-one could be used for analyses. *F. fossana* were absent from the two fragmented forest sites. The median time between consecutive photographs of *C. ferox* and *F. fossana* individuals at a forest site was greater than 17.5 hours. The median time between consecutive photographs of individually-unidentifiable species at a camera station was greater than 19 hours, except at the Primary site where *G. e elegans* was observed a median time of every seven hours. We found no differences between activity distributions of native or exotic carnivores when sampled with or without scent-lure at either the Selectively-logged or Fragments <2.5 km rainforests where we conducted this comparison; at the other two sites lure was used for the entire sampling period (Table 2).

For *C. ferox* and *F. fossana*, we found no differences among individual animal's activity distributions within sites (*C. ferox* individuals: Primary,  $W = 6.90$ ,  $P = 0.14$ , Selectively-logged,  $W = 5.46$ ,  $P = 0.24$ ; *F. fossana* individuals: Primary,  $W = 39.86$ ,  $P = 0.11$ , Selectively-logged,  $W = 17.97$ ,  $P = 0.59$ ) and thus pooled individuals at each site. Comparing the activity distributions of each species across sites, we found significant differences for *C. familiaris*, *F. fossana*, *G. e. elegans*, *V. indica* and local people (Table 1). For example, the median time of *C. familiaris*' diel-activity was similar at the fragmented sites, but occurred much earlier in the day at the Selectively-logged site (Table 3). While temporal activity patterns for *F. fossana*, *G. e. elegans*, *V. indica*, and local people were different among some of the sites, the actual median time of use was not greatly different. Of all species, only *F. catus/silvestris* demonstrated a uniform or cathemeral activity pattern throughout the diel cycle (Table 3). We found species-specific and site-specific temporal activity patterns and thus overlap varied by species and sites compared (Table 4, Figure 2). Temporal activity patterns were remarkably similar between the Primary and Selectively-logged sites, e.g., between *C. ferox* and *F. fossana* there was only a difference of

0.6% in their overlap. Across all four forest sites, the temporal activity overlap of *G. e. elegans* and local people remained high at 75-88%.

We found that activity during the dawn, day, dusk, and night time periods for *G. e. elegans*, *V. indica*, and local people differed significantly across sites (Table 5). For *G. e. elegans*, we found less than expected use of dawn and greater use of dusk at the Selectively-logged site (Fig. 3) compared to the other sites; activity in this dusk time period accounted for 70% of the total chi-square value (Dawn  $\chi^2 = 6.19$ , Dusk  $\chi^2 = 18.36$ , and Total  $\chi^2 = 34.94$ ). There were no differences in activity use of the different time periods across the other sites, thus we pooled the data at the Primary, Fragments <2.5 and >15 km sites for *G. e. elegans* ( $\chi^2 = 5.55$ ,  $df = 6$ ,  $P = 0.67$ ). For local people, we found less than expected use of dawn at the Primary site and greater use of dawn at the Fragments <2.5 km site compared to the other sites, which accounted for 49% of the total chi-square value (Primary  $\chi^2$  of Dawn = 4.12, Fragments <2.5 km  $\chi^2 = 3.69$ , and Total  $\chi^2 = 15.87$ ). There were no differences in activity use of temporal classes across the other sites, thus we pooled the Selectively-logged and Fragments <2.5 km sites ( $\chi^2 = 0.34$ ,  $df = 2$ ,  $P = 0.844$ ) for local people. All other species showed no differences in use of different time periods across sites, thus we pooled their datasets across all forest sites in which they were detected.

*C. ferox*, *F. fossana*, and *G. e. elegans* exhibited non-random use of dawn, day, dusk and night (Table 6). *C. ferox* preferred the crepuscular hours, with no significant difference between activity at dawn and dusk. *C. ferox* were active during the day and night, but daytime hours were used less than the other time classes (Table 6, Figure 3). We found *F. fossana* to be predominantly nocturnal, but they also used the crepuscular hours. At all sites, *G. e. elegans* was highly diurnal. We found *G. fasciata* to be highly nocturnal, with use of the crepuscular hours in

proportion to their availability and no activity during the day (Figure 4). As for the exotic *V. indica*, we found them to use the night and dusk significantly more than available, while avoiding the daytime.

## **Discussion:**

Understanding species' temporal activity patterns and how those patterns may vary across seasons, habitats, or other changing ecological conditions provides important insight into mechanisms of species coexistence and details of ecological relationships between those coexisting species. How animals use time can also be important in understanding and predicting how species can persist within a changing landscape (Kronfeld-Schor and Dayan 2003; Norris et al. 2010). In particular, changing landscapes due to habitat loss and fragmentation are often accompanied by changing patterns of human use or altered abundances of other species that may impact activity patterns of all species in that system. This may be especially important in understanding predator persistence, as their activity patterns can be strongly influenced by human activity (Griffiths and Schaik 1993) and relationships among sympatric competitors (Schoener 1974).

We quantified the temporal activity patterns of the Malagasy rainforest carnivores across a gradient of disturbed rainforests to gain insight into the temporal structure of carnivore communities and how a changing landscape may influence their persistence. Our photographic-sampling grids provided an efficient means to sample the entire carnivore community activity in contrast to radiotelemetry which is often limited to few individuals of a single or few species. Despite predictions that lure or bait could influence species temporal activity (Schlexer 2008), we found that scent-lure at camera stations had no effect on the activity patterns of native or

exotic carnivores at the contiguous and fragmented rainforests. To account for with the non-independence of consecutive photographs, our 30-min interval adequately removed temporal dependence between consecutive photographs and thus reduced any systematic bias within our analyses.

Our detailed evaluation of Malagasy rainforest carnivore activity was generally consistent with natural history accounts, but also provided new insights. For example, we provide the first systematic, detailed evaluation of *C. ferox*'s temporal activity patterns. This is of particular importance to discussions concerning lemur behavior as one explanation for cathemerality in some lemur species (e.g. *Eulemur fulvus rufus*, red-fronted brown lemur) is that it developed as an anti-predator strategy, such that lemurs are temporally cryptic and thus unavailable to the assumed 'cathemeral' *C. ferox* (Colquhoun 2006). While *C. ferox* has previously been described as nocturnal, crepuscular, and cathemeral in different studies (Albignac 1972; Albignac 1973; Dollar 1999), we found them to prefer crepuscular activity (using both dawn and dusk greater than would be expected given their availability in the diel cycle) and secondly to select night over the daytime. However, it is notable that 23.6% of all *C. ferox* activity occurred during the daytime. Whether *C. ferox* activity can be described as cathemeral is expressly contingent on the definition of cathemerality (Tattersal 2006). If cathemerality is defined as uniform activity throughout the diel-cycle, *C. ferox* cannot be characterized as cathemeral from our findings. However, if cathemerality is significant activity during the day and night, then our findings would classify *C. ferox* as cathemeral under this less strict definition (Tattersall 2006).

To effectively evaluate whether lemur cathemerality may be an anti-predator tactic against the crepuscular or cathemeral *C. ferox*, it is necessary to understand how *C. ferox* predation rates on lemurs vary throughout the entire diel-cycle, which is currently unknown. To

hypothesize that temporal crypticity is an effective means to reduce predation risk assumes the predator synchronizes their activity pattern to match their prey, which is not always the case. Predator temporal activity will often generally correspond to the time period when prey are most vulnerable, which is a function of detectability and catchability (Zielinski 2007). Predators that forage primarily by sight and sound use prey activity as a foraging cue, such that we would expect predators to track their prey's temporal activity to maximize predation potential. However, if a predator primarily locates and can access inactive (cryptic or resting) prey, for example by olfaction, we would expect the predator's activity to be asynchronous with that of the prey. *C. ferox*'s unique morphology precludes any meaningful prediction as to which of the preceding scenarios is more likely as they possess strong olfactory, visual, and auditory acuity with a large rhinarium similar to *Viverrids*, a tapetum lucidum common to many carnivores, and large rounded ears which resemble species of *Felidae* (Kohncke and Leonhardt 1986).

Interestingly, cathemeral lemurs often exhibit a peak activity at the crepuscular hours (Donati and Borgognini-Tarli 2006), which if *C. ferox* are cueing in on prey activity would suggest a high predation risk for cathemeral lemurs given our findings of crepuscular activity patterns by *C. ferox*. Predation risk is no doubt a strong selective force on prey behavior, however, the relationship between lemur predation risk and *C. ferox* and lemur temporal activity patterns is likely more complex than simple temporal activity avoidance through crypticity. More extensive diet studies of *C. ferox* are needed to understand if cathemeral lemurs are more or less at risk of predation by this carnivore than would be expected if diet selection were random. We also hypothesize that if lemurs are intending to be temporally cryptic as to reduce predation risk by *C. ferox*, a random activity pattern should be preferred.



In addition to providing new data for debates concerning carnivore-lemur interactions, our quantification of native Malagasy carnivore activity patterns showed a lack of any major effects of habitat and season on temporal activity patterns. Among the Malagasy carnivores, there was a wide diversity in the diel-activity patterns (diurnal, nocturnal, and crepuscular) and selection of dawn, day, dusk and night time periods. Temporal overlap varied considerably between species, ranging from 5.8 to 88.8%.

Niche theory provides a meaningful framework to understand these varying degrees of temporal overlap, as we expect a high degree of overlap in one niche component should be associated with a low degree of overlap in one or more niche dimensions (Schoener 1974). As similarly-sized carnivores often have high dietary overlap, it is informative to explore patterns of temporal niche overlap and separation by comparing similar body-sized carnivores (Donadio and Buskirk 2006; Woodward and Hildrew 2002). For example, the activity of the two small mongoose species, *G.e. elegans* and *G. fasciata* overlapped only 7.5 to 16.1% across all rainforests, while the two medium-sized civets *F. fossana* and *E. goudotii* activity overlapped 88.6%. In addition to body-size, natural history observation suggest the mongoose species share a similar diet (Goodman and Benstead 2003), which may explain why these two co-occurring rainforest carnivores have such divergent temporal activity patterns. In contrast, the two civets have high temporal activity pattern overlap, but may be segregated by habitat and diet specializations; *E. goudottii* appears to be strongly associated with wetland habitats and has a unique dietary specialization on earthworms and insects (Albignac 1973, 1974) while *F. fossana* may be more of a generalist in both habitat use and diet (Kerridge et al. 2003). The larger body size of *C. ferox* may preclude it from foraging competition with the other sympatric carnivores,

thus explaining the high overlap in temporal activity patterns (30 to 88.8%) with the other carnivores.

Reducing temporal activity overlap, and overlap in other niche dimensions, among carnivores can be important in reducing competition and especially intraguild predation, which in some populations can account for 89% of mortality and actually suppress the victim population (Donadio and Buskirk 2006; Kamler et al. 2003; Palomares and Caro 1999). There is currently no evidence to suggest whether Malagasy rainforest carnivores exhibit intraguild predation. However, intraguild predation is common among other carnivore communities, with predation highest among vertebrate predators that share some dietary overlap, and when the larger animal is 2 to 5.4 times greater in body size than the smaller animal (Donadio and Buskirk 2006). Among Malagasy rainforest carnivores, we would thus predict a high potential for antagonistic behavior and possibly killing between *C. ferox* → *F. fossana* and *F. fossana* → *G. fasciata*. Intraguild predation of *G. fasciata* by *F. fossana* is one explanation for *G. fasciata*'s general rarity in contiguous rainforest where *F. fossana* is ubiquitous, while at fragmented rainforests *F. fossana* is absent and *G. fasciata* is observed frequently (this thesis, Chapter 3; Goodman and Benstead 2003).

Malagasy carnivores showed no marked changes in their temporal activity that could be attributed to fragmentation effects, selective logging, season, or human and exotic carnivore activity. This is consistent with findings from other studies which have shown subtle changes in activity pattern due to human activity, resource availability, or habitat disturbance (Ngoprasert et al. 2007; Norris et al. 2010; Presley et al. 2009; Zielinski 1988); marked changes, such as an animal shifting its activity from primarily diurnal to nocturnal appears rare (Griffiths and Schaik 1993; Kitchen et al. 2000). Of the native Malagasy carnivores, *G. e. elegans* and *F. fossana* both

showed only minor differences in their diel activity patterns across sites, maintaining their overall respective diurnal (median range, 10:39-12:21) and nocturnal activity (median range, 23:29-23:37) patterns regardless of rainforest site. Among all species, the activity patterns of *C. familiaris* and local people varied the most across sites. Local people consistently maintained a diurnal activity pattern, but demonstrated varied patterns of activity within the day, especially in how they selected or avoided the crepuscular hours. While this variation is likely a result of the different distances local people lived relative to the rainforest sites, their changing activity patterns may affect the behavior of carnivore species differently, especially for the diurnal *G. e. elegans* or the crepuscular *C. ferox*.

Temporal activity overlap between species does not have to be large to incur costs of competition, especially interactions between native and exotic carnivores, which have no shared evolutionary history. For example, at the fragmented rainforests, we previously found a increasing *F. catus/silvestris* trap success correlated with declining occupancy of *G. e. elegans* within rainforest fragments and the surrounding matrix (this thesis, Chapter 3), despite their moderate activity overlap (37-53%). The direct interaction between *C. ferox* and *C. familiaris* in terms of activity overlap was less than 50%, however, this is likely enough potential contact for disease transmission (Whiteman et al. 2007). Lastly, the overlap in activity patterns between the introduced *V. indica* and the native *G. fasciata* increased from 56% at the Fragments <2.5 km site to 86% at the Fragments >15 km site suggesting that the effects of fragmentation on activity pattern overlap may vary depending on distance to contiguous forest and other undescribed factors (i.e. number of households and people). More study is needed to determine if this increased temporal overlap may adversely affect the ability of *G. fasciata* to persist in the landscape for the long-term.

Our ability to explore changes in Malagasy carnivores' temporal activity due to habitat alteration and the activity of local people and exotic carnivores was limited by the absence of *F. fossana*, *E. goudotii*, and *C. ferox* from our fragmented forest study areas. The absence of these carnivores begs the questions as to what degree temporal activity overlap with exotic carnivores and local people, as well as limited plasticity in activity patterns, prohibits these carnivores from occupying fragmented rainforests. To direct effective conservation action and encourage carnivore persistence in a disturbed landscape, we need disentangle the dietary-spatial-temporal constraints that are limiting carnivore populations within Madagascar's human-dominated landscape.

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Table 1. The number of photographic-activity samples for Malagasy carnivores, exotic carnivores, and local people from four rainforest sites, sampled in two seasons within Madagascar's eastern rainforests. Also, a non-parametric circular test of differences among activity distributions (continuous time) across all sites and a pair-wise analysis when the overall test indicated a significant difference; sites were not included when sample sizes were < 10.

Species <sup>a</sup>	Primary /	Selectively- Logged /	Fragments <2.5 km /	Fragments >15 km /	Dataset <sup>b</sup>	Global	
	Cold-Dry	Cold-Dry	Warm-Dry	Warm-Dry		Mardia-Watson-Wheeler Test W	P
<i>Canis familiaris</i>	7	17 A	169 B	97 B	Site	18.98	< 0.001
<i>Cryptoprocta ferox</i>	91	51	2	0	Sex / Site	1.84 / 0.69	0.40 / 0.71
<i>Eupleres goudotii</i>	2	16	0	0	Site	NA	NA
<i>Fossa fossana</i>	780 A	460 B	0	0	Sex / Site	3.64 / 27.76	0.80 / 0.002
<i>Felis catus/silvestris</i>	0	0	23	16	Site	4.53	0.10
<i>Galidia elegans elegans</i>	1554 AB	427 A	28 AC	185 BC	Site	10.03	0.04
<i>Galidictis fasciata</i>	52	10	10	27	Site	1.23	0.98
<i>Viverricula indica</i>	0	0	22 A	49 B	Site	7.64	0.02
Local People	75 AB	149 A	434 C	58 BC	Site	52.42	< 0.001

<sup>a</sup>An activity sample was the median time of all photographs of the same species or individual (*C. ferox* and *F. fossana*) detected at a camera station within a 0.5 hour period. The same letter within a species indicates the activity distributions are not statistically different, experiment-wise  $P < 0.1$ .

<sup>b</sup>Species activity distributions were tested for differences across sites or sites and sexes. *C. ferox* and *F. fossana* were the only species for which sexes could be identified

Table 2. Comparison of activity distributions of Malagasy and exotic carnivores before and after the use of scent-lure to detect carnivores at photographic sampling stations. Sampling occurred within Madagascar's eastern rainforest from May-August, 2008 and October-December, 2009 at a Selectively-logged and fragmented rainforest <2.5 km from intact primary rainforest, respectively.

Species	Rainforest Site	Mardia-Watson-Wheeler Test	Temporal Overlap (% $\pm$ SE) <sup>a</sup>
<i>Canis familiaris</i>	Fragments <2.5 km	W = 2.68, P = 0.26	82.47 $\pm$ 0.06
<i>Cryptoprocta ferox</i>	Selectively-Logged	W = 1.52, P = 0.47	83.43 $\pm$ 0.09
<i>Fossa fossana</i>	Selectively-Logged	W = 0.38, P = 0.83	95.51 $\pm$ 0.02
<i>Felis catus/silvestris</i>	Fragments <2.5 km	W = 1.35, P = 0.51	72.08 $\pm$ 0.11
<i>Galidia elegans elegans</i>	Selectively-Logged	W = 3.63, P = 0.16	81.75 $\pm$ 0.06
<i>Galidia elegans elegans</i>	Fragments <2.5 km	W = 1.54, P = 0.46	84.62 $\pm$ 0.12
<i>Viverricula indica</i>	Fragments <2.5 km	W = 3.34, P = 0.19	71.72 $\pm$ 0.15

<sup>a</sup> Temporal overlap of activity data collected with and without using lure by applying a kernel density analyses

Table 3. Test of uniform activity distributions of Malagasy carnivores, exotic carnivores, and local people throughout the diel-cycle. Photographic-activity samples were collected at four rainforest sites within Madagascar's eastern rainforests, sampled from May-December, 2008 and October-December, 2009; data were pooled if activity distributions among sites were not statistically different.

Species	Rainforest Sites <sup>a</sup>	Rao's Test of Uniformity	Median Direction of Activity $\pm$ SE <sup>b</sup>
<i>Canis familiaris</i>	SL	U = 227.221, P < 0.01	08:30 $\pm$ 00:48
	Fragments <2.5 km	U = 153.974, P < 0.01	16:18 $\pm$ 01:01
	Fragments >15 km	U = 144.026, P < 0.10	18:37 $\pm$ 02:09
<i>Cryptoprocta ferox</i>	Primary + SL	U = 145.250, P < 0.05	23:34 $\pm$ 00:51
<i>Eupleres goudotii</i>	Primary + SL	U = 175.750, P < 0.01	01:41 $\pm$ 01:04
<i>Felis catus/silvestris</i>	Fragments <2.5 + >15 km	U = 148.750, P > 0.10	NA
<i>Fossa fossana</i>	Primary	U = 202.418, P < 0.01	23:37 $\pm$ 00:07
	SL	U = 203.856, P < 0.01	23:29 $\pm$ 00:11
<i>Galidia elegans</i>	Primary	U = 208.263, P < 0.01	11:19 $\pm$ 00:05
<i>elegans</i>	SL	U = 214.189, P < 0.01	12:21 $\pm$ 00:09
	Fragments <2.5 km	U = 202.929, P < 0.01	10:47 $\pm$ 00:35
	Fragments >15 km	U = 200.568, P < 0.01	10:39 $\pm$ 00:17
<i>Galidictis fasciata</i>	Primary + SL + Fragments		
	<2.5 + >15 km	U = 210.091, P < 0.01	23:31 $\pm$ 00:18
<i>Viverricula indica</i>	Fragments <2.5 km	U = 197.795, P < 0.01	01:40 $\pm$ 00:46
	Fragments >15 km	U = 206.515, P < 0.01	23:18 $\pm$ 00:30

Local people	Primary	U = 221.700, P < 0.01	13:06 ± 00:22
	SL	U = 213.678, P < 0.01	11:40 ± 00:13
	Fragments <2.5 km	U = 194.220, P < 0.01	11:17 ± 00:12
	Fragments >15 km	U = 194.031, P < 0.01	10:03 ± 00:32

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<sup>a</sup>Primary: little anthropogenic disturbance, SL: selectively-logged prior to 1991, Fragments <2.5 km and Fragments >15 km: fragmented rainforest and their distance from intact primary rainforest

<sup>b</sup>The median time, or central location, in the 24-hr period of all observations.



Table 4. Percentage of temporal overlap ( $\% \pm \text{SE}$ ) across four rainforest sites within Madagascar's eastern rainforests by species pairs using kernel density analyses. Photographic activity-sampling occurred from May-December, 2008 and October-December, 2009. A) Primary (top triangle) and Selectively-logged (bottom triangle) rainforest sites, B) Fragments <2.5 km from intact forest (top triangle) and Fragments >15 km from intact forest (bottom triangle).

A)

Species temporal overlap at the Primary rainforest site

Species temporal overlap at the Selectively-logged rainforest site t	<i>C.ferox</i>	X	71.17 ± 3.97	32.67 ± 4.06	64.84 ± 5.04	LSS	NA	LSS	NA	28.72 ± 4.01
	<i>F. fossana</i>	70.62 ± 5.31	X	5.80 ± 0.55	88.82 ± 3.97	LSS	NA	LSS	NA	5.39 ± 1.93
	<i>G. e. elegans</i>	30.07 ± 5.05	8.21 ± 0.85	X	7.47 ± 0.63	LSS	NA	LSS	NA	74.86 ± 4.72
	<i>G. fasciata</i>	63.21 ± 2.24	81.95 ± 15.92	13.71 ± 3.07	X	LSS	NA	LSS	NA	5.83 ± 1.58
	<i>E. goudotii</i>	77.03 ± 10.21	88.61 ± 9.72	22.00 ± 5.62	78.34 ± 15.24	X	LSS	LSS	LSS	LSS
	<i>V. indica</i>	NA	NA	NA	NA	NA	X	NA	NA	NA
	<i>C. familiaris</i>	43.18 ± 7.14	20.20 ± 5.01	49.84 ± 7.55	18.73 ± 7.25	25.25 ± 8.01	NA	X	NA	LSS
	<i>F. catus/silvestris</i>	NA	NA	NA	NA	NA	NA	NA	X	NA
	Local People	30.00 ± 5.00	8.77 ± 1.34	88.17 ± 3.07	4.19 ± 1.16	18.78 ± 4.07	NA	52.21 ± 8.46	NA	X

<sup>a</sup>LSS: low sample size <10 activity samples, NA: species did not co-occur

B)

Species temporal overlap at the Fragments <2.5 km rainforest site

		<i>Cryptoprocta</i>	<i>Fossa</i>	<i>Galidia</i>	<i>Galidictis</i>	<i>Eupleres</i>	<i>Viverricula</i>	<i>Canis</i>	<i>Felis catus/</i>	Local
		<i>ferox</i>	<i>fossana</i>	<i>elegans</i>	<i>fasciata</i>	<i>goudotii</i>	<i>indica</i>	<i>familiaris</i>	<i>silvestris</i>	People
Species temporal overlap at the Fragments >15 km rainforest site	<i>C.ferox</i>	X	NA	NA	NA	NA	NA	NA	NA	NA
	<i>F. fossana</i>	NA	X	NA	NA	NA	NA	NA	NA	NA
	<i>G. e. elegans</i>	NA	NA	X	13.72 ± 3.59	NA	10.81 ± 2.75	54.49 ± 5.44	52.79 ± 9.7	77.78 ± 6.77
	<i>G. fasciata</i>	NA	NA	16.07 ± 3.2	X	NA	56.00 ± 14.67	37.80 ± 8.79	55.33 ± 9.52	5.19 ± 1.11
	<i>E. goudotii</i>	NA	NA	NA	NA	X	NA	NA	NA	NA
	<i>V. indica</i>	NA	NA	13.12 ± 1.82	85.70 ± 7.95	NA	X	36.76 ± 7.30	45.12 ± 9.93	8.86 ± 1.56
	<i>C. familiaris</i>	NA	NA	55.14 ± 4.18	51.79 ± 5.69	NA	54.28 ± 5.21	X	75.38 ± 7.31	60.22 ± 2.87
	<i>F. catus/ silvestris</i>	NA	NA	37.19 ± 7.25	60.00 ± 11.37	NA	71.12 ± 11.06	70.88 ± 6.66	X	52.51 ± 8.06
	Local People	NA	NA	83.69 ± 6.16	13.63 ± 3.37	NA	13.27 ± 3.24	50.36 ± 5.22	36.45 ± 7.95	X

<sup>a</sup>LSS: low sample size <10 activity samples, NA: species did not co-occur

Table 5. Chi-square test results for differences between activity periods (Dawn, Day, Dusk, Night) of Malagasy carnivores and local people across four rainforest sites and sexes.

Photographic activity-sampling occurred within Madagascar's eastern rainforests from May-December, 2008 and October-December, 2009.

Species	Datasets <sup>a</sup>	X <sup>2</sup>	df	P <sup>b</sup>
<i>Canis familiaris</i>	Site (SL, Frag <2.5 km, Frag >15 km)	27.32	6	<0.001
<i>Cryptoprocta ferox</i>	Site (Primary and SL) x Sex (Male-Female)	2.54	3	0.47
<i>Eupleres goudotii</i>	Site (Primary, SL)	NA	NA	NA
<i>Felis catus/silvestris</i>	Site (Frag <2.5 km, Frag >15 km)	1.70	3	0.42
<i>Fossa fossana</i>	Site (Primary and SL) x Sex (Male-Female)	0.39	3	0.94
<i>Galidia elegans elegans</i>	Site (Primary, SL, Frag <2.5 km, Frag >15 km)	35.20	9	<0.001
<i>Galidictis fasciata</i>	Site (Primary, SL, Frag <2.5 km, Frag >15 km) <sup>c</sup>	5.42	6	0.49
Local People	Site (Primary, SL, Frag <2.5 km, Frag >15 km)	26.47	9	0.02
<i>Viverricula indica</i>	Site (Frag <2.5 km, Frag >15 km) <sup>c</sup>	0.08	3	0.96

<sup>a</sup>Primary: little anthropogenic disturbance, SL: selectively-logged prior to 1991, Frag <2.5 km and Frag >15 km: fragmented rainforest and their distance from intact primary rainforest. *C. ferox* and *F. fossana* were the only species the sexes were identifiable, thus activity differences were evaluated across sites and sexes

<sup>c</sup>Removed day category due to no observations

Table 6. Compositional analyses of three Malagasy carnivores sampled across four rainforest sites, sample size, test of random use of dawn, day, night, and dusk, and the ranking of selection in order of relative preference. Photographic activity-sampling occurred within Madagascar's eastern rainforests from May-December, 2008 and October-December, 2009.

Species <sup>a</sup>	N <sup>b</sup>	Wilk's $\lambda$	Randomized P	Ranking of Temporal Activity Classes <sup>c</sup>
<i>Cryptoprocta ferox</i>	6	0.0032	0.0314	Dusk>Dawn>>>Night>>>Day
<i>Fossa fossana</i>	31	0.0422	0.0001	Night>>>Dusk>Dawn>>>Day
<i>Galidia e. elegans</i> (SL)	17	0.0194	0.0010	Day>>>Dusk>Dawn>>>Night
<i>Galidia e. elegans</i> (Primary + Frag <2.5 + >15 km)	34	0.0428	0.0010	Day>>>Dawn>>>Dusk>>>Night

<sup>a</sup> *Galidia elegans elegans* Primary: little anthropogenic disturbance, SL: selectively-logged prior to 1991, Frag <2.5 km and Frag >15 km: fragmented rainforest sites and their distance from intact primary rainforest

<sup>b</sup> Number of individuals, except *G. e. elegans* where camera stations were used as the sampling unit

<sup>c</sup> Relative preference of time classes, ranked from the most preferred to the least, > indicates a non-significant difference between two classes while >>> indicates a significant difference ( $P < 0.1$ )

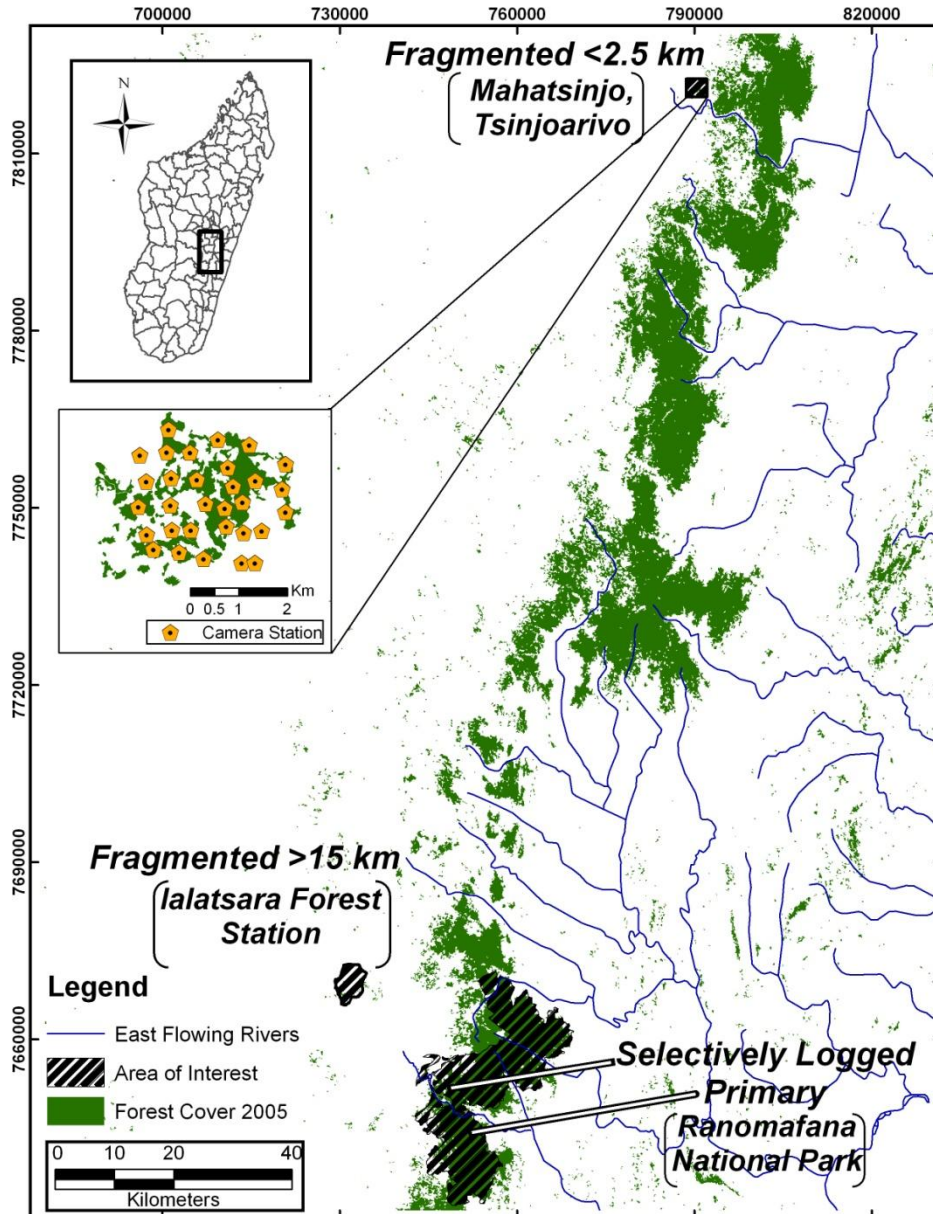
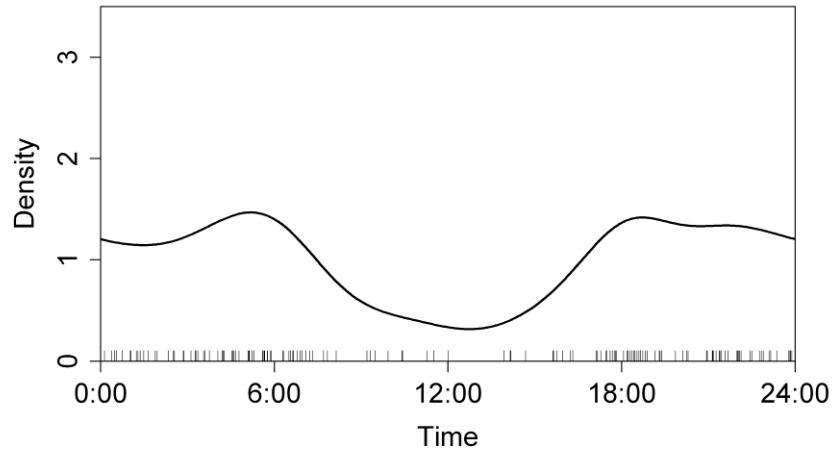
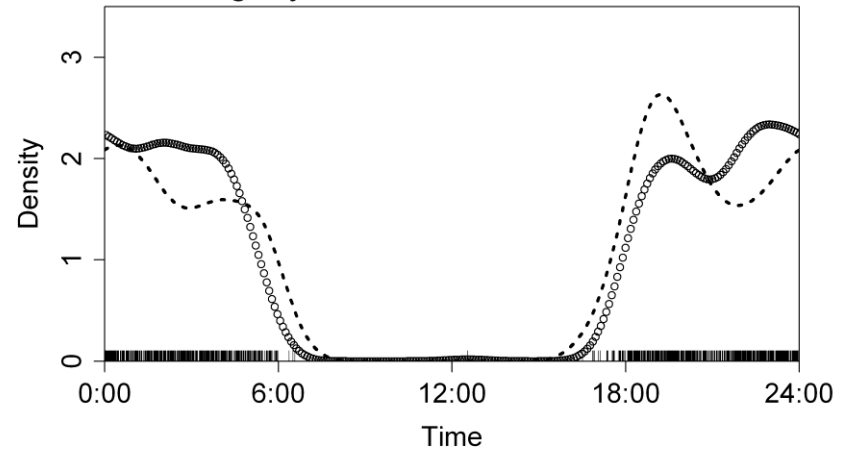


Figure 1. Carnivores were sampled at four photographic-sampling sites within Madagascar's eastern rainforests from May-December, 2008 and October-December, 2009. Top insert map shows political provinces and location on the island of Madagascar, while the bottom insert map shows the camera station sampling layout among rainforest fragments at Mahatsinjo, Tsinjoarivo as an example. Rainforest extent from Conservation International, 2010.

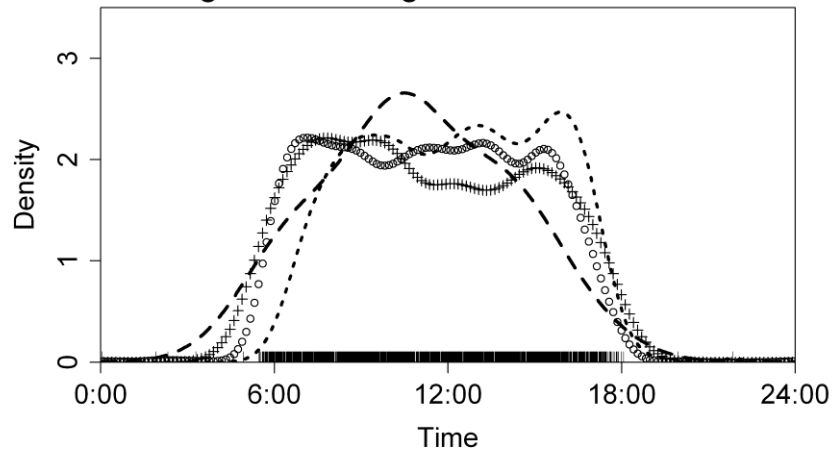
a) *Cryptoprocta ferox*,  
Fossa



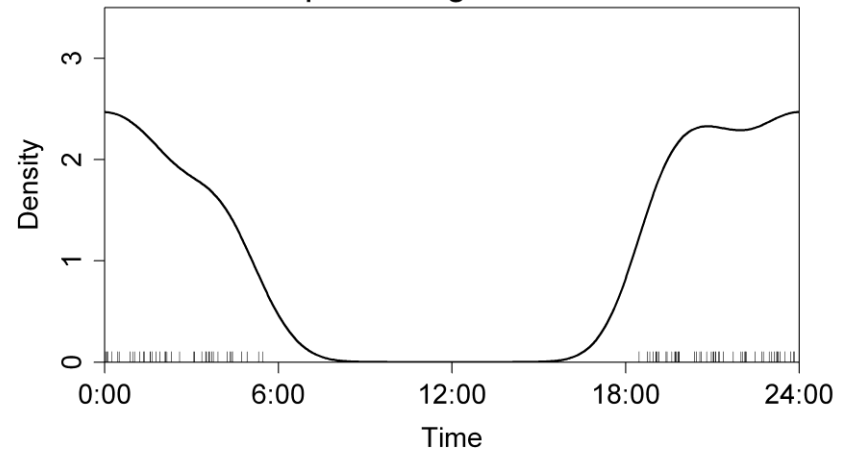
b) *Fossa fossana*,  
Malagasy Civet



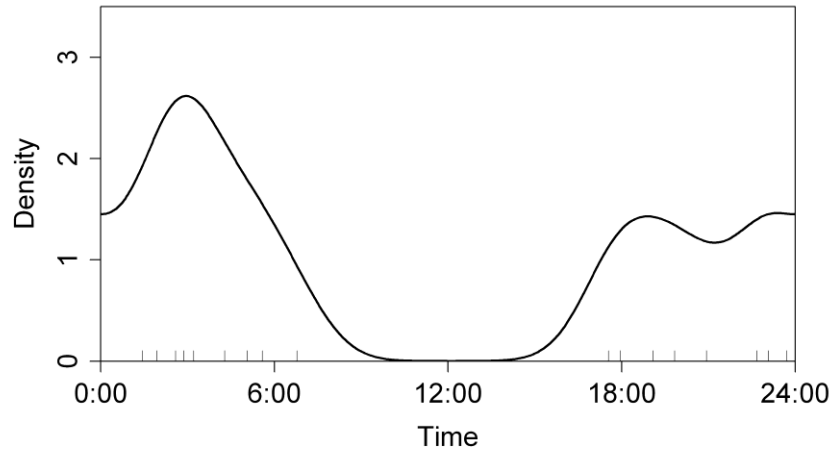
c) *Galidia elegans elegans*,  
Ring-tailed Mongoose



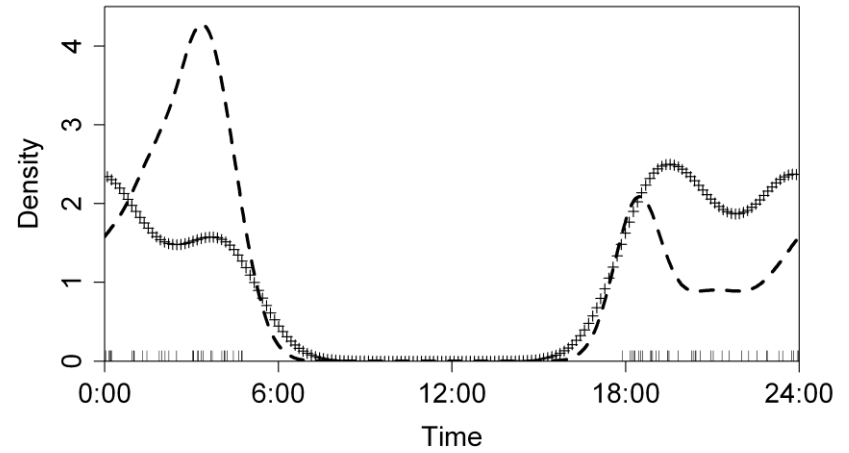
d) *Galidictis fasciata*,  
Broad-striped Mongoose



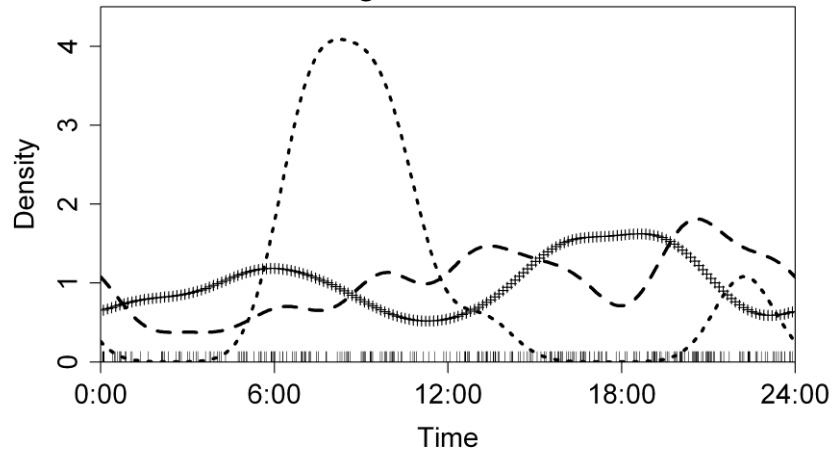
e) *Eupleres goudotii*,  
Small-toothed Civet



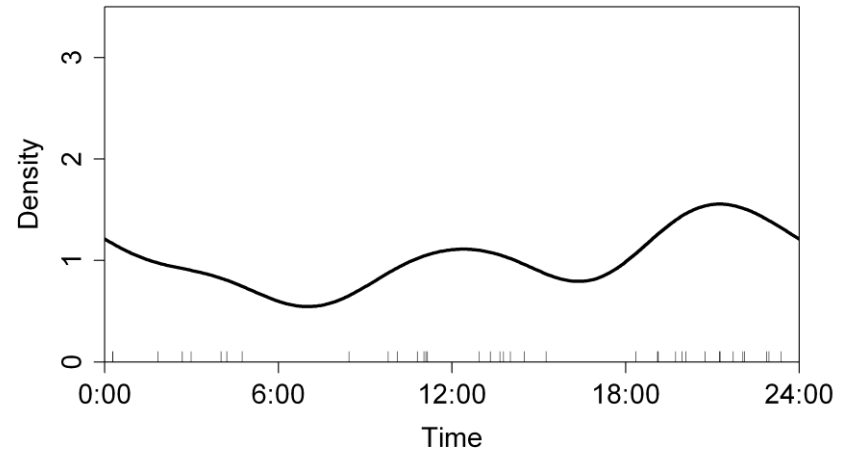
f) *Viverricula indica*,  
Small Indian Civet



g) *Canis familiaris*,  
Domestic Dog



h) *Felis catus/silvestris*,  
Exotic-Wild Cat



*i) Local People*

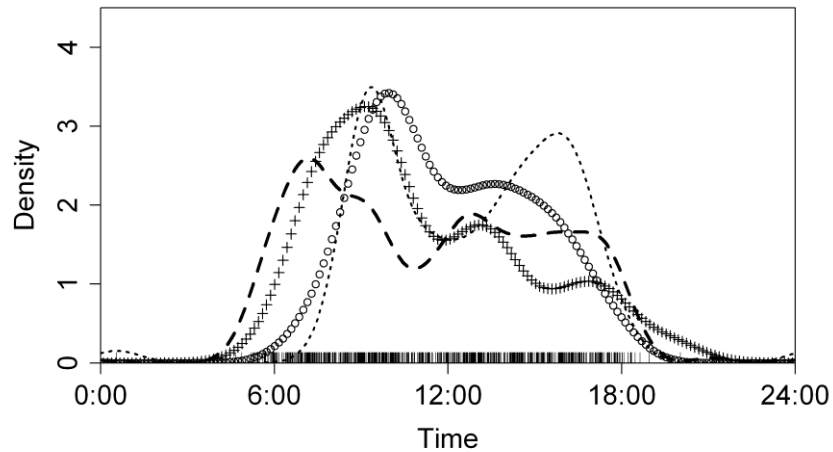


Figure 2. Temporal activity of Malagasy rainforest carnivores, exotic carnivores, and local people. Species activity samples were collected at four rainforest sites within Madagascar's eastern forests; data were pooled across sites when activity distributions were not different. Solid (—) lines indicate the use of all data from all relevant sites for each species, circles (○) indicate data from the Primary site, dotted (···) lines indicate data from the Selectively-logged site, dashed (---) lines indicate data from Fragments <2.5 km site, and plus signs (+) indicate data from the Fragments >15 km site. Tick marks on the x-axis represent all activity samples for each species. Y-axis is not consistent among all graphs.



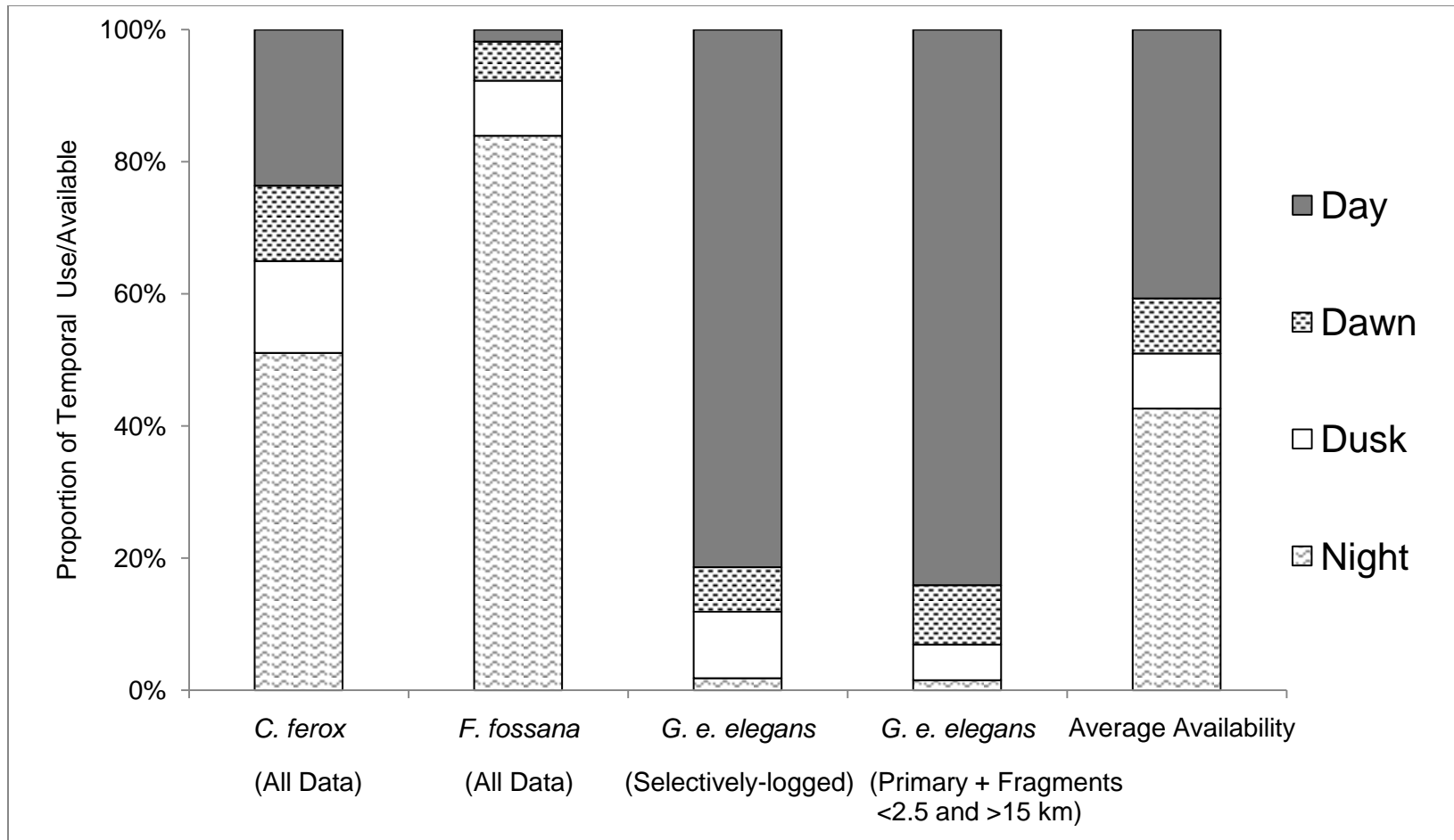
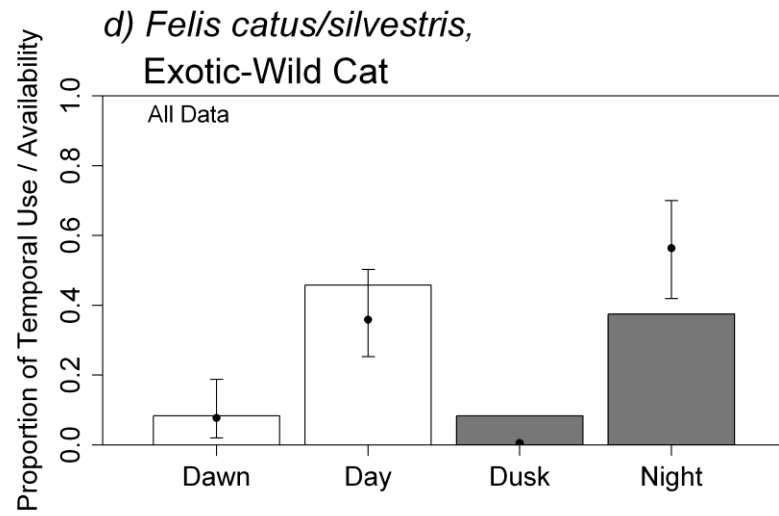
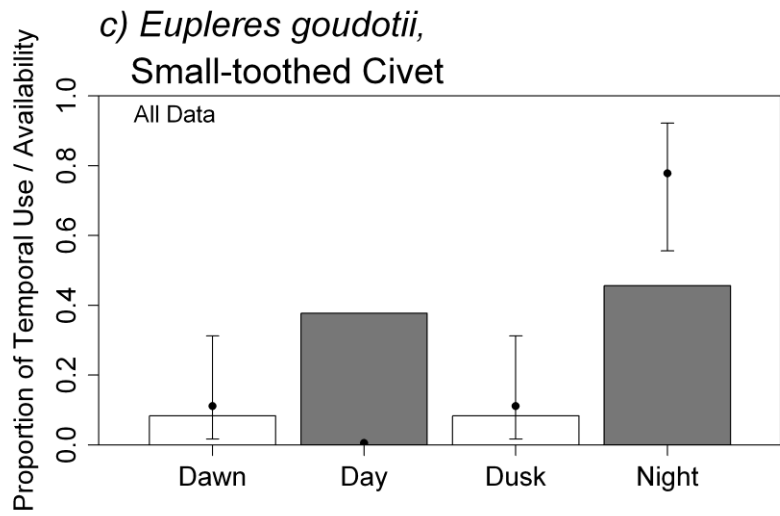
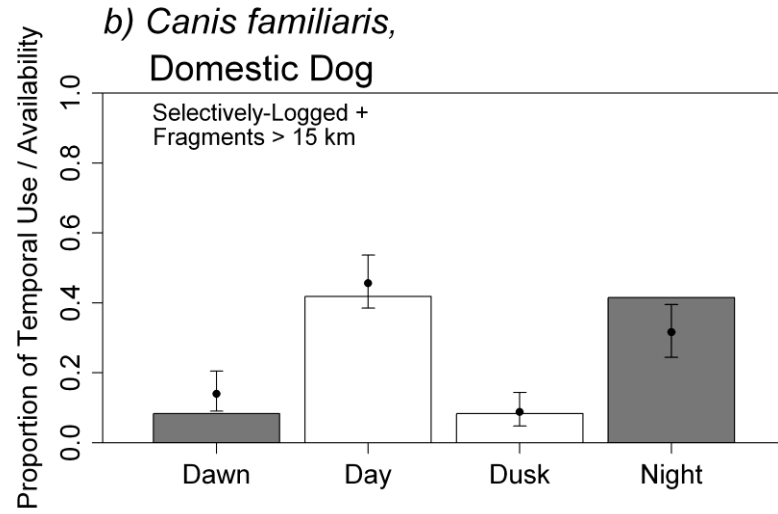
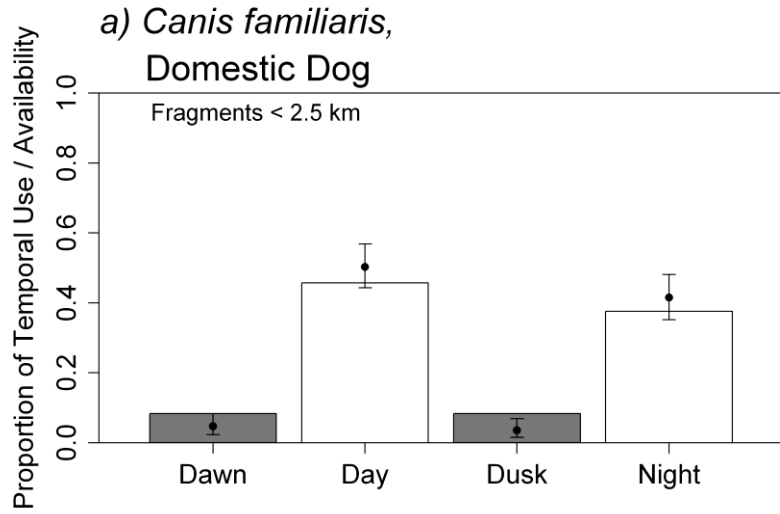
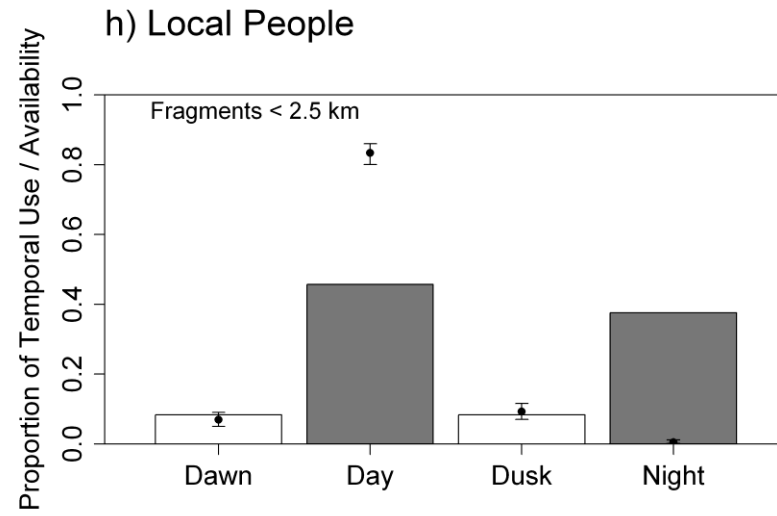
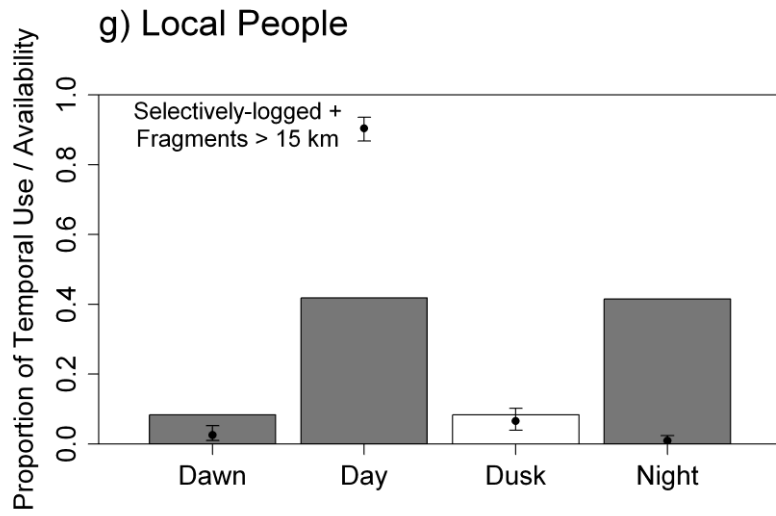
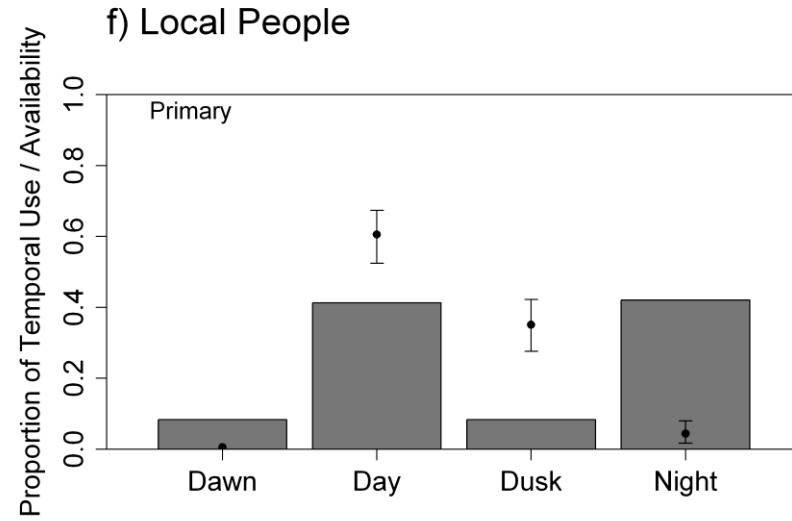
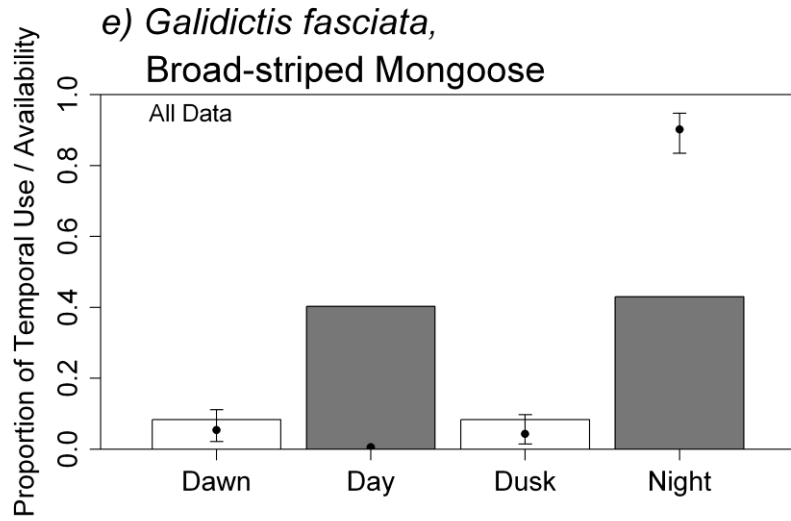


Figure 3. Proportional activity of Malagasy carnivores used for compositional analyses and average availability of the temporal classes. Species activity samples were collected at four rainforest sites within Madagascar’s eastern forests, which were pooled when the proportional use of activity time classes across sites were not different. Photographic activity-sampling occurred from May-December, 2008 and October-December, 200





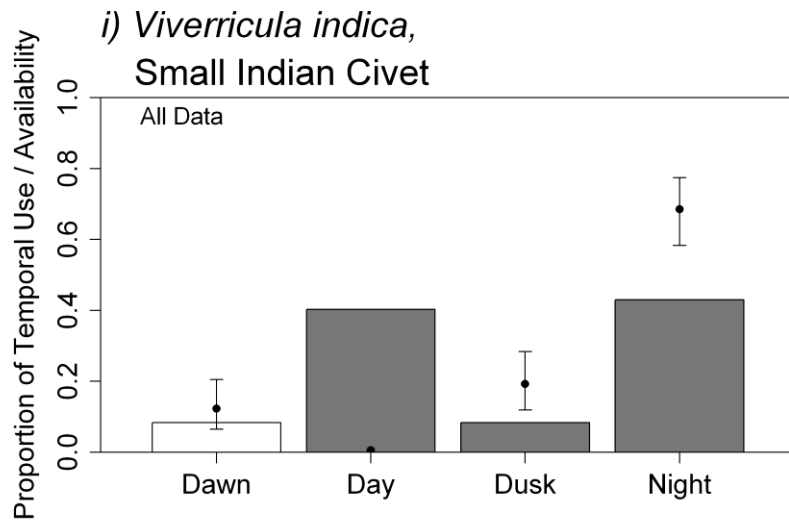


Figure 4. Selection and/or avoidance of dawn, day, dusk, and night by *Galidictis fasciata*, exotic carnivores, and local people. Species activity samples were sampled at four rainforest sites across Madagascar, which were pooled when the activity proportions of time classes were not different across sites. The bars indicate the available time for each time class, while the circular-points indicate the proportion of activity-use and confidence interval in each time class; dark grey bars indicate the time class was selected (lower confidence limit of activity-use is above availability) or avoided (upper confidence limit of activity-use is below availability), while white bars indicate use was in proportion to availability (confidence limits include availability). When there were no observations in a temporal class and the availability was large, we assumed the species avoided this time period.

# Appendix A: Native/Exotic Carnivore Species Accounts for Southeastern Madagascar

## Native Carnivores

Fossa (*Cryptoprocta ferox*):

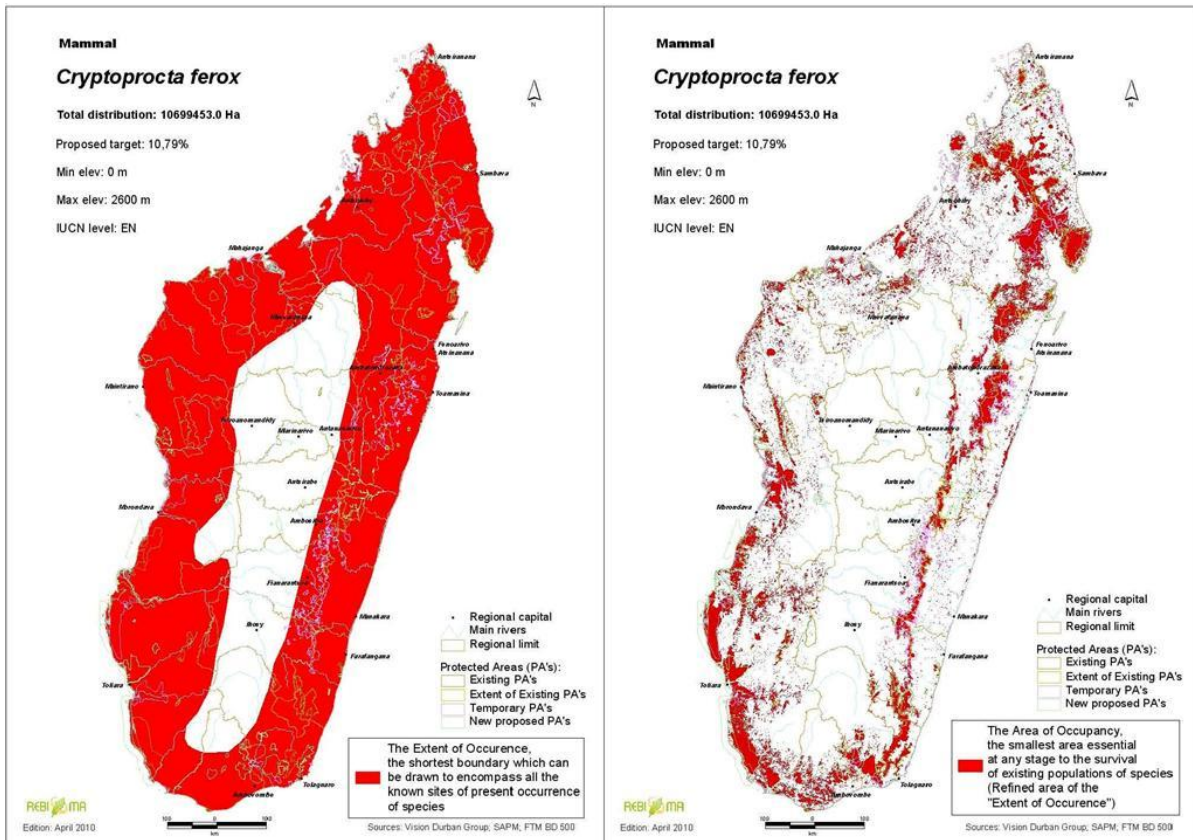


Figure 1. Rebioma (<http://www.rebioma.net>) fossa (*Cryptoprocta ferox*) extent of occurrence and area of occupancy.

*C. ferox* is Madagascar's largest extant, endemic terrestrial species. In one study at Kirindy forest (dry forest), *C. ferox* averaged a total length of 1.4 m and adult males weighed  $7.4 \pm 1.2$  kg while adult females weighed  $6.1 \pm 0.6$  kg (Hawkins and Racey 2005). In separate study from the dry forests of Ankarafantsika and Kirindy Mitea National Parks, adult males weighed  $7.44 \pm 1.97$  kg and adult females  $6.38 \pm 1.05$  kg (Dollar 2006). A single adult male captured in the eastern rainforest weighed 8.1 kg (Dollar 1999). *C. ferox* have semi-retractable claws, reversible ankles, and a tail length equal to body length. Additionally, *C. ferox* use both plantigrade and digitigrade locomotion (Laborde 1986; Laborde 1986; Laborde 1987). Juvenile female *C. ferox* between the age of one and two have been found to have temporary masculinization, where they develop an enlarged, spinescent clitoris, supported by an os clitoridis, and a pigmented secretion on the ventral fur that in adults only occurs with males. This may serve to reduce harassment by male or female conspecifics (Hawkins et al. 2002).

*C. ferox*'s current geographic extent covers most forest types on Madagascar, including areas above the tree line (Goodman et al. 1997; Hawkins 2003). In the western dry forests, *C. ferox* has a mean homerange of  $14.8 \text{ km}^2$  and a density of  $0.24$  individuals/ $\text{km}^2$  and  $0.18$  adults/ $\text{km}^2$  (Hawkins and Racey 2005). In comparison, the pilot study to this thesis estimated *C. ferox* rainforest at  $0.17 \pm 0.06$  individuals/ $\text{km}^2$  (Gerber et al. 2010). The temporal activity pattern of *C. ferox* has been generally characterized in natural history accounts as crepuscular and nocturnal (Albignac 1972; Albignac 1975). Two males tracked via radiotelemetry in the eastern rainforest showed limited activity during the daylight hours, high activity at night, and a peak at dawn and pre-dusk (Dollar 1999). Temporal activity analyses of *C. ferox* in the dry forests using radiotelemetry showed no seasonal differences in activity patterns and some activity during the daylight hours, but most activity was concentrated at night (Hawkins 1998).

Whether or not the diet of *C. ferox* varies across forest types is still unknown. However, they have been recorded to prey on diverse species, including rodents, lipotyphlans, lemurs, birds, amphibians, reptiles, and insects (Dollar et al. 2007; Hawkins and Racey 2008). In the dry forests, greater than 50% of *C. ferox*'s diet can be made up of lemurs (Hawkins and Racey 2008). One study in the montane forests at Montagne d'Ambre National Park found that *C. ferox* diet was made up of 40% lemur biomass, however, when considering numbers of individuals, rodents made up the majority of consumed prey items (Rasolonandrasana 1994). Lemur species known to be preyed upon by *C. ferox* include a large range of small (*Microcebus sp.*) to large bodied lemurs (*Propithecus sp.*; Goodman et al. 1997; Goodman 2003c; Karpanty and Wright 2007). While *C. ferox* predation pressure on lemurs is likely to vary across forest types (Goodman 2003c), the impact can be considerable, including documented cases in which fossa predation resulted in the breakup of social groups or extirpation of lemur species from both contiguous and fragmented forests (Irwin et al. 2009). In one study, the frequency of prey consumed by *C. ferox* was correlated with the relative abundance of prey, suggesting *C. ferox* are opportunistic predators (Hawkins and Racey 2008). This flexible diet is likely what allows *C. ferox* to have such a broad distribution among vegetation types in Madagascar (Goodman 2003).

Malagasy Small-toothed Civet (*Eupleres goudotii*):

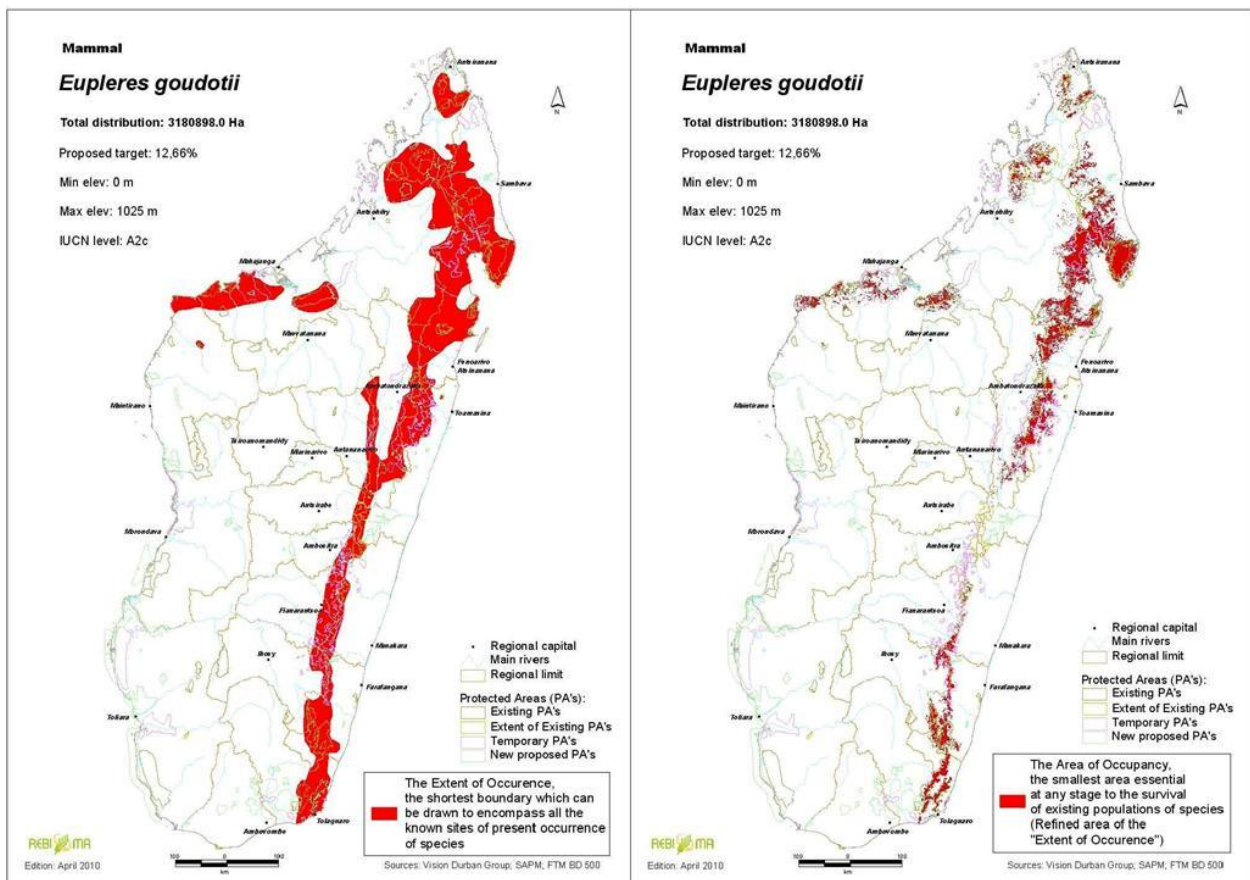


Figure 2. Rebioma (<http://www.rebioma.net>) Small-toothed civet (*Eupleres goudotii*) extent of occurrence and area of occupancy.



Currently, there are two species recognized as belonging to the genus *Eupleres*: *E. goudotii* and *E. major* (Goodman and Helgen 2010), which were previously identified as subspecies of *E. goudotii* (Albignac 1973). *E. goudotii* occupies the entire length of the eastern rainforest, including occupation of a mixture of spiny and gallery forest in the southeast (Goodman and Helgen 2010). In contrast, *E. major* is found in western Madagascar in the northwest Sambirano region and as far south as Baie de Baly National Park (Hawkins 1994; Goodman and Helgen 2010). *E. goudotii* is Madagascar's second largest carnivore, ranging in total body length from 455-650 mm and weighing 1.5-4.6 kg; the subspecies *E. major* is generally larger (Albignac 1973; Hawkins 1994). Prior to the cold-dry season (June-August) during which food is less plentiful, *E. goudotii* are known to store additional fat, especially in the tail. This extra weight has been thought to be used during the cold months for hibernation (Albignac 1973), however, this species has been observed to be active during this period (Dollar 1999). This species morphology is unique to Malagasy carnivores, having an elongated snout with small, fine, conical shaped dentition (Albignac 1972; Dollar 1999).

Almost no quantitative information is available regarding the ecology of *E. goudotii*. Their diet is poorly known, but they are believed to consume large quantities of earthworms, insects and some lizards, rodents, and birds. *E. goudotii* has been observed using its large non-retractable claws on their forepaws to excavate insects as well as dig burrows used for shelter (Albignac 1972; Albignac 1984). Their activity pattern is assumed to be nocturnal and/or crepuscular based on observations of captive individuals (Albignac 1972; Albignac 1974), however, they have been observed in the wild during daylight hours (Dollar 1999).

Malagasy Civet (*Fossa fossana*):

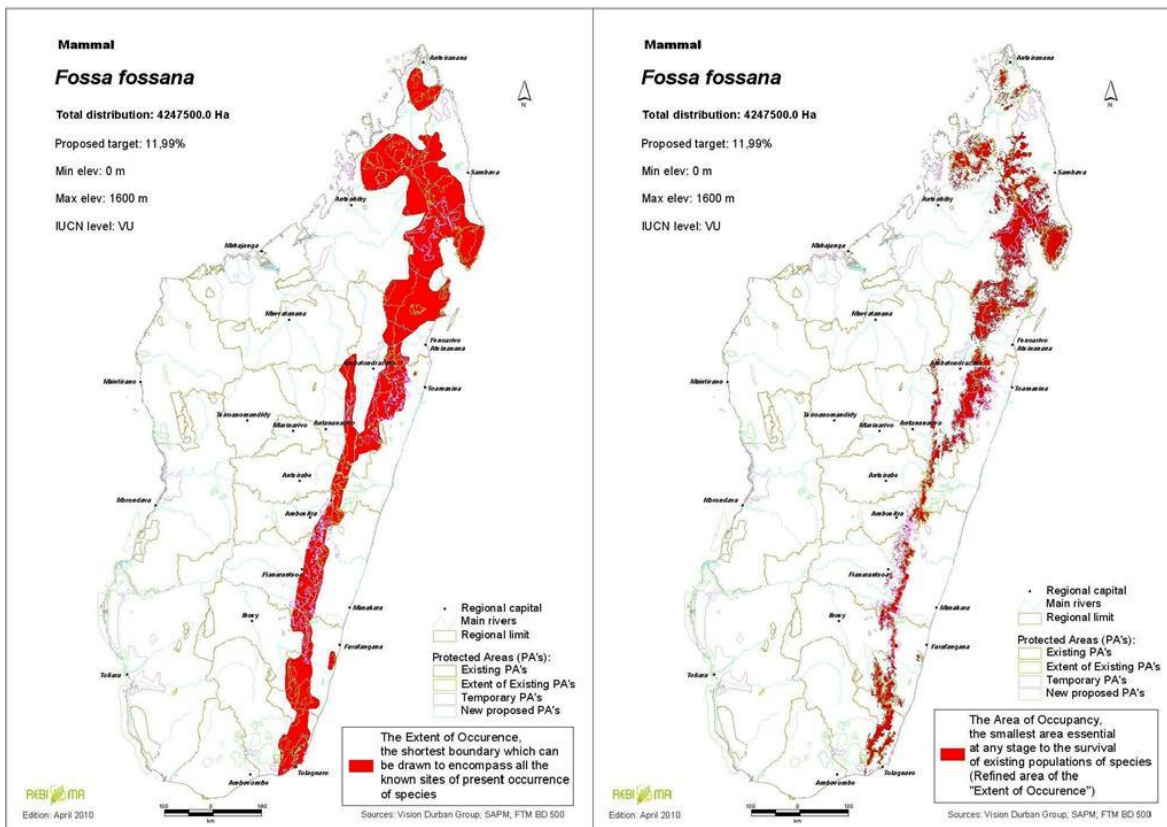


Figure 3. Rebioma (<http://www.rebioma.net>) Malagasy civet (*Fossa fossana*) extent of occurrence and area of occupancy.

*F. fossana* is Madagascar's third largest endemic carnivore, averaging a total length of 913 mm and weighing between 1.3-2.1 kg. There is no sexual dimorphism between sexes,

possibly due to their suspected pattern of monogamous pairing. Similar to *E. goudotii*, *F. fossana* is also known to store fat in its tail prior to the cold-dry months (Kerridge, Ralisoamalala et al. 2003). *F. fossana* are found in lowland and montane eastern rainforest and in the northwest Sambriano region. *F. fossana* are believed not to occur in secondary or disturbed habitats (Kerridge, Ralisoamalala et al. 2003), however, no data prior to this current study existed to support this conclusion. Currently, the only density estimate is from the pilot study to this thesis, which estimated *F. fossana* density in the rainforest at  $2.23 \pm 0.36$  individuals/km<sup>2</sup> (Gerber et al. 2010). Kerridge et al. (2003) used trapping and subsequent radiotelemetry data and estimated their homerange as between 0.073 and 0.552 km<sup>2</sup>. Although no density estimate was calculated in that study, Kerridge et al. (2003) remarked that 22 individuals were trapped in 2 km<sup>2</sup> of rainforest habitat (Kerridge et al. 2003).

*F. fossana* is considered nocturnal, however, no actual systematically-collected data to support this conclusion are available. From spool and line tracking and trapping efforts, *F. fossana* are thought to prefer wet areas, including streams and marshes (Kerridge et al. 2003). Presumed to be strictly terrestrial based on morphology, *F. fossana* are known to exhibit arboreal activity, however, it is unknown how often they exhibit this behavior (Albignac 1971; Goodman, Kerridge et al. 2003). *F. fossana* diet is diverse, including rodents, lipotyphlans, crustaceans, snakes, frogs, lizards, and many insect taxa (Rand 1935; Albignac 1971; Albignac 1973; Kerridge, Ralisoamalala et al. 2003). A single diet analysis from the eastern rainforest (Ranomafana National Park and Vevembe) indicated a high consumption of *Arthropoda* (60%), but also found evidence of numerous vertebrate prey (33%), including small-mammals, reptiles, and amphibians (Goodman et al. 2003). Lemur depredation has not been officially reported for *F. fossana*, but given its ability to climb trees, there is a potential for it to occur.

Broad-striped Mongoose (*Galidictis fasciata*):

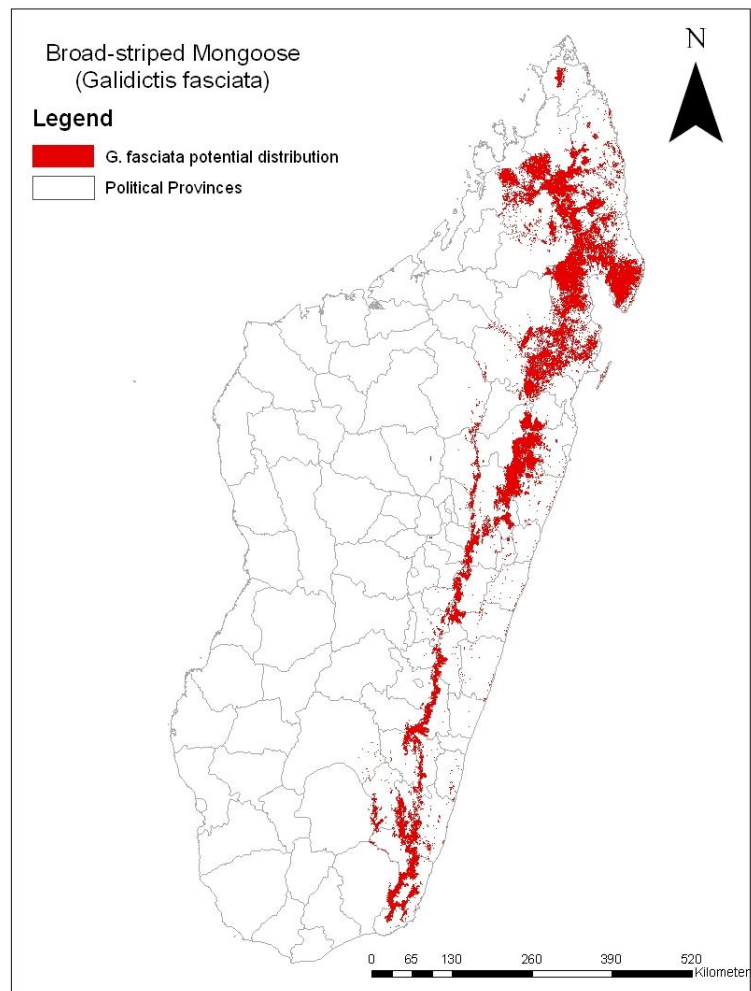


Figure 4. Broad-striped mongoose (*Galidictis fasciata*) extent of occurrence based on forest cover (2005).

There are two species recognized as *Galidictis*: *G. fasciata* occurs broadly throughout the eastern rainforests and *G. grandidieri* occurs in the southern spiny forests. *G. fasciata* averages  $857 \pm 50.4$  mm in total length and weighs  $640 \pm 105.4$  g. In contrast, *G. grandidieri* average total length is  $393.3 \pm 11.9$  mm and weighs  $1207.5 \pm 195.2$  g. Both species are thought to be nocturnal, but no systematically collected temporal activity data are known. *G. fasciata* is thought to be broadly distributed in low densities from lowland forests up to 1500 m elevation. There is currently no information on *Galidictis sp.* diet, but is believed to eat rodents, reptiles, and small amphibians (Goodman 2003).

Ring-tailed Mongoose (*Galidia elegans*):

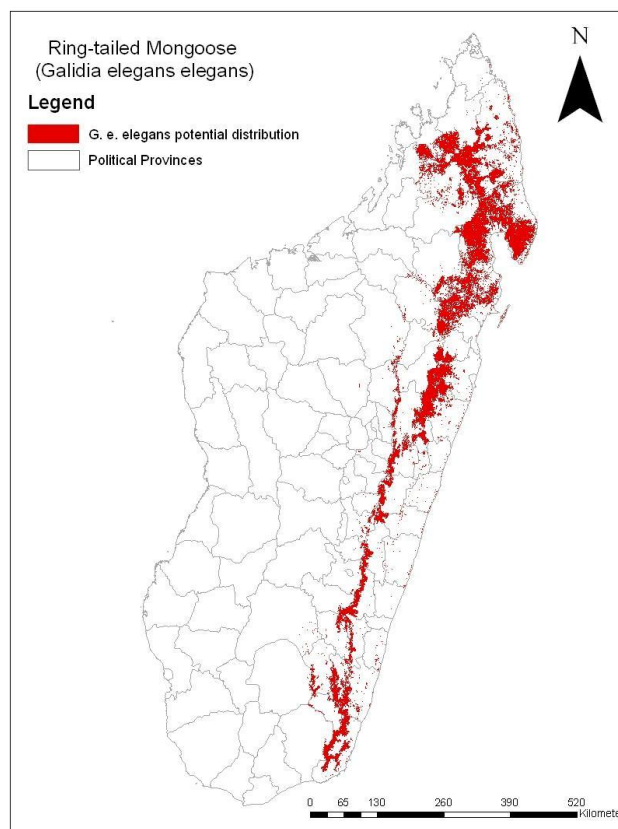


Figure 5. Ring-tailed mongoose (*Galidia elegans elegans*) extent of occurrence based on forest cover (2005).

*G. elegans* is the most conspicuous of the Malagasy carnivores due to its diurnal activity pattern and boldness for stealing chickens from villages and raiding research camps (Goodman

2003a). There are currently three recognized subspecies of *G. elegans*- *G.e. elegans* which occupy the entirety of the eastern rainforests, *G. e. dambrensis* which are isolated in the Sambirano region, and *G. e. occidentalis* which occur in the northern-western dry forests (Bennett et al. 2009). Within each region, *G. elegans* is thought to be fairly ubiquitous from sea level to tree line (Albignac 1984; Goodman and Pidgeon 1999; Goodman 2003). There have been occasional reports of *G. elegans* in the southern spiny forest (Goodman and Pidgeon 1999), including fossil remains (Muldoon et al. 2009), suggesting occupation, however, there is no verification of current and prolonged occurrence of the spiny forest.

*G. e. elegans* total length ranges from 560 to 670 mm and weighs from 760 to 1085 g (Dunham 1998). *G. elegans* morphology includes non-retractable claws which allow arboreal activity and membranes between the bases of all toes which assists in semi-aquatic activity while hunting. There are no absolute density estimates of *G. elegans*, but observations indicate they occur in high densities with home ranges of 20-25 ha (Goodman 2003). Dunham (1998) captured 12 individuals with 1,040 trap nights and estimated a density index of 37 individuals/km<sup>2</sup>. Radiotelemetry locations indicated that 11 animals shared approximately 20 ha.

Unlike other Malagasy carnivores, *G. elegans* is known to live in family groups that often consist of a single adult male and female, their most recent offspring, and occasionally an older juvenile offspring. *G. elegans*' diet has not been well studied, but is known to include numerous insect taxa, rodents, lipotyphlans, crayfish, lizards, snakes, and amphibians. In addition, *G. elegans* is a known lemur predator, having been observed preying upon *Cheirogaleus major* and *Microcebus rufus* (Goodman 2003c).

## Exotic Carnivores:

Domestic Dog (*Canis familiaris*):



Figure 6. Domestic Dog (*Canis familiaris*)

*C. familiaris* are common throughout Madagascar's villages and are viewed by local people as assisting in pest-control and security (Dollar 2006). It is common to find *C. familiaris* moving outside villages through native vegetation, including intact rainforest (Gerber et al. 2010), which may have significant consequences to native wildlife. *C. familiaris* are expected to affect medium and small carnivores through interference competition, as well as serve as disease vectors (Vanak and Gompper 2009). At Ankarafantsika *C. familiaris* has been implicated in transmitting several infectious diseases, including Canine Distemper and Canine Parvovirus, to *C. ferox* (Dollar 2006). In addition, there is increasing evidence that *C. familiaris* may be an important predator of large diurnal lemurs. They have been observed harassing, attacking, and attempting to kill *Propithecus verreauxi* at Beza Mahafaly Special Reserve. *P. verreauxi* respond to *C. familiaris* with typical ground-predator anti-predator behaviors, such as moving up in the canopy, visually scanning down, and alarm calling (Broackman et al. 2008).



The roles of *C. familiaris* as a predator of native wildlife, potential competitor with Malagasy carnivores, and disease vector are still poorly understood. The ubiquity of *C. familiaris* throughout Madagascar's villages as well as their activity within and around natural areas demands increasing research attention and creative solutions to ameliorate potentially harmful impacts of these domestic animals.

Wild/Feral Cat (*Felis sp.*):

A) *Felis catus*



B) *Felis silvestris*



Figure 7. Wild/Feral Cat (*Felis sp.*)

Based on general pelage patterns, Madagascar may contain two exotic species of the genus *Felis*: *Felis catus* and *Felis silvestris*. *F. catus* is known as the domesticated housecat, while *F. silvestris* is a wild cat that may have been introduced from mainland Africa. Genetic analyses of domesticated, feral, and wild cats are needed to better understand the phylogeny of this/these exotic carnivore(s). *Felis sp.* occurs throughout Madagascar within and near villages, as well as in native- and non-native vegetated habitats away from villages. Based on morphological and behavioral characteristics, local people and research often do make a distinction between wild cats (*F. silvestris?*) which occur outside of villages and domestic or feral (*F. catus?*) that may be more closely associated with villages (Dollar 2006; Brockman et al. 2008; Kotschwar, 2010). The wildcat may be a significant lemur predator, having been implicated in the predation of *Propithecus verreauxi* at Beza Mahafaly Special Reserve. *P. verreauxi* respond to *F. silvestris* typical ground-predator anti-predator behaviors, including moving up in the canopy and visually scanning downwards (Brockman et al. 2008).

There is currently no known data on the potential competition between *F. silvestris* and Madagascar's native carnivores. The use of natural areas by wildcats may also increase the risk of disease transmission to native carnivores. At Ankarafantsika, *F. silvestris* has been implicated in transmitting Feline Calicivirus to *C. ferox* (Dollar 2006). *F. silvestris*' potential impacts on both native carnivores and lemurs demands more attention, including conservation action that could limit their populations, especially within native habitats.

Small Indian Civet (*Viverricula indica*):



Figure 8. Small Indian Civet (*Viverricula indica*)

*V. indica* is an introduced carnivore to Madagascar, native to south Asia, where it occupies a mosaic of secondary and plantation forests with considerable edge habitat (Chen et al. 2009). This species was likely brought to Madagascar for the use of their scent glands to make perfumes, but have since established throughout the island. *V. indica* are most noticed in disturbed areas adjacent to villages, but have also been detected in degraded and fragmented forests, both in the eastern rainforest and western dry forests (Dollar 2006). There is some indication *V. indica* can use intact rainforest, as they have been detected on the edges of Ranomafana National Park (Gerber et al. 2010).

There is currently no known data on the potential competition between *V. indica* and Madagascar's native carnivores. *V. indica* is presumed to be able to predate upon small lemurs (Brockman et al. 2008), however, they are generally known to be scavengers that are not able to climb trees (Ewer 1973), such their impact on Madagascar's lemurs in terms of direct predation are likely negligible.

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**Appendix B: Relevant literature from the ISI Web of Science used to investigate common mark-recapture analyses.**

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