International Journal of Primatology

Patterns in predator-primate distribution, relative activity, and co-occupancy across fragmented and contiguous forests in northeastern, Madagascar.

--Manuscript Draft--

Manuscript Number:	
Full Title:	Patterns in predator-primate distribution, relative activity, and co-occupancy across fragmented and contiguous forests in northeastern, Madagascar.
Article Type:	SI: Camera Trapping
Keywords:	Exotic predators, Fosa, Interaction occupancy model, Lemur, Multi-species occupancy, predator-prey dynamics
Corresponding Author:	Zach Farris, MS Virginia Tech Blacksburg, VA UNITED STATES
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	Virginia Tech
Corresponding Author's Secondary Institution:	
First Author:	Zach Farris, MS
First Author Secondary Information:	
Order of Authors:	Zach Farris, MS
	Sarah Karpanty, PhD
	Felix Ratelolahy
	Marcella J. Kelly, PhD
Order of Authors Secondary Information:	
Manuscript Region of Origin:	MADAGASCAR
Abstract:	Predator-primate interactions remain under studied. Much of our knowledge on predator-primate dynamics has resulted from indirect investigations of these interactions; however, novel approaches are needed to better understand the spatial relationships between predators and primates across changing landscapes. We combined photographic surveys of predators with line transect sampling of lemurs across contiguous and fragmented forests to: 1) compare relative activity of predators and lemurs in each forest type; 2) estimate occupancy and detection for predators and lemurs across the landscape; 3) estimate predator-primate co-occupancy or interactions across each forest type; and 4) assess which variables influence occupancy, detection, and co-occupancy across the landscape. In fragmented forest sites we found strong decreases in endemic carnivore and lemur activity, increases in exotic carnivore and human (Local) activity, and increases in positive association ('attraction') between Locals and lemurs, as well as domestic dog and lemurs. Domestic dog-lemur interactions changed from no association or negative association ('avoidance') in contiguous forest to positive ('attraction') in fragmented forest. Finally, distance to forest edge and distance to nearby villages proved important in predicting predator occupancy and detection. These results highlight the growing threat to endemic carnivores and lemurs with increases in habitat loss and fragmentation throughout Madagascar. This study demonstrates, for the first time, the effectiveness of these novel techniques to investigate how multi-predator species impact primate species across contiguous and fragmented forests.

Cover Letter

Department of Fisheries and Wildlife Sciences
College of Natural Resources

Mail Code 0321, Blacksburg, Virginia 24061

(540) 231-5573 Fax: (540) 231-7580

WCS
PROGRAMME MADAGASCAR

August 18, 2013

To Whom It May Concern:

We would like to express our gratitude for your willingness to review and manuscript and consider it for publication in the International Journal of Primatology. We acknowledge that the data presented in the manuscript have not been published previously and are not under consideration for publication elsewhere. Furthermore, the co-authors on this paper (Sarah Karpanty, Marcella Kelly, and Felix Ratelolahy) acknowledge their participation in collecting data for this project and writing this manuscript. Additionally, each co-author has approved the final version of this manuscript and its consideration for publication in International Journal of Primatology. Finally, as addressed within the manuscript we received permission from the appropriate authorities at Virginia Tech and the Malagasy government to conduct this research and publish our findings.

Once again we appreciate your willingness to consider this manuscript for publication in your journal. Please do not hesitate to let us know if there is any additional information needed from us.

Sincerely,

Zach J. Farris, Virginia Tech

Sarah Karpanty, Virginia Tech

Marcella Kelly, Virginia Tech

Felix Ratelolahy, Wildlife Conservation Society Madagascar Program

Patterns in predator-primate distribution, relative activity, and co-occupancy across fragmented and contiguous forests in northeastern, Madagascar.

Authors: Zach J. Farris, Sarah M. Karpanty, Felix Ratelolahy, and Marcella J. Kelly

Institution: Virginia Tech

Address: 100 Cheatham Hall, Virginia Tech, Blacksburg, VA 24061-0321

Corresponding author: Zach J. Farris

Contact info: 124 Cheatham Hall, Virginia Tech, Blacksburg, VA 24061-0321

zjfarris@vt.edu, (501) 358-9649

Abstract:

Predator-primate interactions remain under studied. Much of our knowledge on predator-primate dynamics has resulted from indirect investigations of these interactions; however, novel approaches are needed to better understand the spatial relationships between predators and primates across changing landscapes. We combined photographic surveys of predators with line transect sampling of lemurs across contiguous and fragmented forests to: 1) compare relative activity of predators and lemurs in each forest type; 2) estimate occupancy and detection for predators and lemurs across the landscape; 3) estimate predator-primate co-occupancy or interactions across each forest type; and 4) assess which variables influence occupancy, detection, and co-occupancy across the landscape. In fragmented forest sites we found strong decreases in endemic carnivore and lemur activity, increases in exotic carnivore and human (Local) activity, and increases in positive association (‘attraction’) between Locals and lemurs,

as well as domestic dog and lemurs. Domestic dog-lemur interactions changed from no association or negative association (‘avoidance’) in contiguous forest to positive (‘attraction’) in fragmented forest. Finally, distance to forest edge and distance to nearby villages proved important in predicting predator occupancy and detection. These results highlight the growing threat to endemic carnivores and lemurs with increases in habitat loss and fragmentation throughout Madagascar. This study demonstrates, for the first time, the effectiveness of these novel techniques to investigate how multi-predator species impact primate species across contiguous and fragmented forests.

Keywords:

Exotic predators, Fosa, Interaction occupancy model, Lemur, Multi-species occupancy, predator-prey dynamics.

Introduction

Predator-primate interactions remain under studied as a result of the challenges associated with investigating these relationships. Predation by carnivores and other predators has been shown to influence primate behavior, population dynamics, spatial distribution, and group size (Terborgh and Janson 1986; Isbell 1994; Hill and Lee 1998; Miller 2002; Zuberbühler and Jenny 2002; Goodman 2003; Shultz et al. 2004; Colquhoun 2006; Karpanty 2006; Hart 2007; Miller and Treves 2007; Irwin et al. 2009; Willems and Hill 2009). In addition to the direct effects of predators on primate survival, it is equally important to quantify the indirect, non-lethal interactions, and/or risk effects associated with anti-predator behavior as these interactions may also be significant (Lima 1998; Creel 2011). Investigation of these non-lethal interactions and anti-predator behaviors, as well as lethal interactions and direct mortality is challenging and often relies on indirect investigation, such as vocalization or playback studies [non-lethal interactions] (Karpanty and Wright 2007; Rahlfs and Fichtel 2010; Schel and Zuberbühler 2012), as well as diet analysis of carnivore scat and investigation of prey remains [lethal interactions] (Isbell 1994; Hart 2007; Henschel et al. 2011; Morino 2011; Braczkowski et al. 2012; Burnham et al. 2013; Jooste et al. 2013). Indeed, much of our knowledge on predator-primate dynamics has resulted from such indirect investigations and, while these studies remain important in understanding predator-primate interactions, novel approaches are needed to better understand the spatial relationships, and variation in those relations, between predators and primates across changing landscapes.

The on-going patterns in forest loss and fragmentation throughout primate habitat worldwide makes it especially urgent to understand the spatial interactions of predators and primates and how the altering of landscapes impacts these interactions. Researchers have shown

how forest loss and fragmentation negatively impact a host of primate species in various regions of the world (Johns and Skorupa 1987; Onderdonk and Chapman 2000; Ganzhorn et al. 2003; Gilbert 2003; Harcourt and Doherty 2005; Arroyo-Rodríguez and Dias 2010; Boyle and Smith 2010; Yanuar and Chivers 2010; Schwitzer et al. 2011; Estrada et al. 2012; Kankam and Sicotte 2013). Additionally, habitat loss and fragmentation further intensify extinction risk for numerous primate species via ecological factors such as environmental stochasticity and catastrophic events (Lande 1998). As a result, an understanding of how native and exotic predators impact primate populations in disturbed and fragmented forests is critical for conservation and management of these populations. For example, predation by Fosa (*Cryptoprocta ferox*), Madagascar's top carnivore, was found to lead to the extirpation of sifakas from disturbed, fragmented forest sites in Madagascar and the consumption of primates by *C. ferox* (relative to other prey) is believed to increase in forest fragments (Irwin et al. 2009). While research exists on the impacts of habitat loss and fragmentation on both predators and primates worldwide, an attempt to link carnivore and primate interactions across fragmented and contiguous forests is still lacking. The combination of camera trapping and line-transect sampling presents a unique approach to investigate these interactions so as to further our knowledge of how predator-primate dynamics are impacted by fragmentation.

Our objectives were to quantify the spatial distribution and occupancy of lemurs and predators in both contiguous and fragmented forests across the Masoala-Makira landscape in northeastern Madagascar, and to assess patterns of co-occupancy between predators and their potential lemur prey. Specifically we: 1) Compare the relative activity and/or trap success of predators and lemurs between contiguous and fragmented forest sites; 2) Determine the landscape and habitat variables impacting predator and lemur occupancy and detection across the

landscape; 3) Quantify the distributional relationship (co-occupancy) between predator-lemur occupancy in contiguous and fragmented forest sites; and 4) Assess the level of convergence among variables impacting predator-lemur occupancy, detection, and co-occupancy. Through these analyses we provide valuable insight on the spatial interactions (i.e. random assemblages vs. species attraction/avoidance) among predators and lemurs, and the variables influencing these relationships.

Methods

Study site

We surveyed predators and lemurs using photographic surveys and line transects in two contiguous and two fragmented forest study sites across the Masoala-Makira landscape (Figure 1) from August 2010 to November 2012, including three surveys of one of our contiguous forest sites (Table 1). There are six species of endemic carnivore (Eupleridae), three species of exotic carnivore, and 22 species of lemur that are known to occur across the Masoala-Makira landscape [Appendix I] (Garbutt 2007; Farris 2012). Madagascar's endemic carnivores have generalist diets (Garbutt 2007); however, the following endemic and exotic carnivores are known lemur predators (Goodman 2003) and will be the focus for this manuscript: Fosa (*Cryptoprocta ferox*), Ring-tail vontsira (*Galidia elegans*), Domestic dog (*Canis familiaris*), and Feral cats (*Felis silvestris catus*). In addition, poaching of carnivores and lemurs has been shown to be a serious threat for this region (Golden 2009) and, as a result, humans (non-researchers; hereafter 'Locals') have been included in our analyses as well.

The two contiguous forest study sites, Anjanaharibe (AJB) and Mangabe (MGB), were located inside the Makira Natural Park (NP), which is a combination of a 372,470 ha park and

351,037 ha community managed buffer zone. Makira NP, overseen by Wildlife Conservation Society Madagascar Program and Madagascar's Ministry of Environment and Forests (MEF), is the newest and the largest protected area in Madagascar; it protects the largest remaining tract of contiguous rainforest in Madagascar and is thought to contain the highest levels of biodiversity in Madagascar (Kremen 2003; Holmes 2007). The AJB and MGB study sites are located within contiguous forest and consist of intact, primary rainforest with varying degrees of degraded, secondary rainforest present near the forest edge (Figure 1). MGB is bisected by a heavily traveled local trail that connects the western and eastern portions of Makira NP. The Farankarina study site (FRK) was located inside the Farankarina forest reserve, a 1,650 ha reserve overseen by the Antongil Conservation organization in collaboration with Madagascar's MEF. This reserve is separated by at least 5 km from intact forest (Figure 1) and consists of primary, undisturbed rainforest in the southern portion of the protected area (~350 ha) and highly degraded forest with extensive forest loss in the northern portion of the protected area (~2,350 ha). Our final site (Lohan'sanjinja, SLJ) was located 9.3 km from the nearest protected area and no community management system existed for this site. This site consists of a narrow strip of highly degraded forest (~1.3 km wide) with extensive forest loss and a collection of forest patches connecting it to intact forest in the north (Figure 1).

Field Methods

Predator surveys

At all four study sites we established a camera-trapping grid consisting of 23 to 25 camera stations spaced approximately 500 m apart to photographically sample wildlife (Table 1). We used both digital (Moultrie D40, Reconyx PC85 and Cuddeback IR) and film-loaded camera-

traps (DeerCam DC300) which were operational 24 hour/day, positioned about 20–30 cm off the ground, and placed on opposing sides of existing human trails (0.5-2.0 m wide) and game trails (< 0.5 m wide). We checked cameras every 5–10 days to change batteries and memory cards. We used no bait or lure at camera stations to attract wildlife.

Lemur surveys

We established three, 2 km long lemur transects at each of the four study sites. These transects were located along the existing human and game trails used for our photographic surveys of predators. At each study site we surveyed lemur transects five-six times diurnally, between 07:00 and 11:00, and five-six times nocturnally, between 18:30 and 0:00. For all lemur observations we recorded species, date, time, number in group, distance to center of group, height, detection cue, behavior, and weather conditions.

Landscape and Habitat Sampling

To understand how landscape and habitat metrics impact predator-primate occupancy, detection, and co-occupancy we used Landsat satellite imagery (2006 and 2009) with habitat classifications and masking provided by the Wildlife Conservation Society Madagascar program to measure the distance of each camera station to the nearest forest edge and to the nearest village. To sample vegetation at each camera station we walked a 50 m transect in three directions (0, 120, and 240 degrees) starting at the camera station and classified the canopy height and percent cover every 10 meters at each transect. At 25 m and 50 m on each transect we used the point-quarter method (Pollard 1971) to measure tree density and basal area. Finally, at 20 m and 40 m we measured understory cover at three levels (0-0.5 m, 0.5-1.0 m, and 1.0-2.0 m) along a 20 m transect running perpendicular to the established habitat transect.

Analyses

Predator Trap Success and Lemur Activity

We defined a 'capture event' for predators as all photographs of a particular species within a 30 minute time period. For carnivores and Locals we used capture events to construct daily detection histories consisting of 0's (not detected) and 1's (detected) for each species at each camera station. To provide a measure of relative activity for each predator species, we calculated trap success (TS) by dividing the number of capture events by total number of trap nights, minus malfunctions, multiplied by 100. We defined a trap night as a 24 hour period in which at least one of the two cameras at a given camera station was functioning properly. For lemurs we defined a 'capture event' as all observations of a given species occurring within 25 m of one another for a particular survey. This 25 m spacing was used to ensure groups were not double counted and to ensure spatial independence for captures of solitary lemur species. Any lemur capture occurring within 250 m of the camera station (based on the 500 m spacing between camera stations) was considered as a detection (1) for that particular camera station. For each study site we used lemur transect surveys to construct detection histories (0's and 1's) for each lemur species. To compare lemur activity across stations and study sites, we divided the number of captures by number of transect surveys for each study site.

Single-season, single-species occupancy

Occupancy estimation provides an estimate of species occurrence across a study area using detection/non-detection data from various survey techniques while accounting for spatial variation and variation in detection probabilities (Bailey et al. 2004; Thompson 2004; Gerber et al. In Review). In particular, single-season, single-species occupancy estimation provides an

estimate of the proportion of an area that is 'used' (occupied) by a target species over a single specified sampling period, or season, in which the population and/or site is closed to changes in the state of occupancy (MacKenzie 2006; Gerber et al. In Review). The collection of detections (1s) and non-detections (0s) over a given season generates a detection history for the target species which is used to estimate two population parameters: occupancy and detection probability (MacKenzie 2006). This technique provides a better estimate of the proportion of an area occupied by the target species than using presence-absence only data (detection not incorporated) because it accounts for: 1) imperfect detection ($p < 1.0$); 2) detection that varies by species; and 3) detection that varies by habitat (MacKenzie et al. 2002). In addition, this modeling approach allows for the inclusion of covariates to determine how numerous variables influence occupancy and/or detection of the target species.

To investigate how predator and lemur occupancy and detection vary across the landscape we combined detection histories across all four study sites (AJB, MGB, FRK, SLJ) and analyzed single-season, single-species occupancy models with covariates in program PRESENCE (Hines 2006). We used only one survey of the AJB study site (1AJB 2010 survey) to estimate single-season, single-species lemur and predator occupancy given that covariate values were identical, not independent, across all three surveys of this site. To estimate occupancy for lemurs we constructed a detection history using camera stations that overlapped with lemur transects, which provided 11-13 camera stations per study site and 48 overall. To estimate occupancy for predators we constructed a detection history using the location of all individual camera stations, which provided 20-25 camera stations per study site and 95 overall. Detection histories for both predators and lemurs were collapsed down to 6-day intervals (encounter occasions) to improve maximum likelihood convergence. We hypothesized that the

following variables would be important for explaining predator and/or lemur occupancy and detection and, as a result, used them as covariates in our models: distance to forest edge, distance to nearest village, canopy height, percent canopy cover, tree density, basal area, understory cover, Locals trap success, *Canis familiaris* trap success, *Felis silvestris catus* trap success, *Cryptoprocta ferox* trap success, and *Galidia elegans* trap success. To improve maximum likelihood convergence with covariates all variables with values > 2.0 were Z-scored.

For each lemur and predator species, we first generated a list of *a priori* models. To assess model fit we used a Pearson's goodness-of-fit test (P = 0.05) and to assess over-dispersion we used a measure of c-hat. For any species investigated, if the model did not fit the observed data (based on our goodness-of-fit test and/or showed evidence of severe over-dispersion, c-hat value > 3.0) occupancy was not estimated, unless otherwise noted. To determine the highest ranking covariates and top ranking models, based on AIC score, as well as competing models, based on ΔAIC < 2.0, we used model selection. In addition, upon analyzing all *a priori* models we also generated 1-3 *post hoc* models based on the highest ranking covariates for occupancy and detection. For each target species we reported the highest ranking model (based on AIC values which rank models based on parsimony, a tradeoff between over- and under-fitting the data), and reported an estimate of occupancy and detection with standard error.

Two-species Interaction Models: Predators-Lemurs

In addition to the single-season, single-species occupancy modeling the two-species interaction (co-occupancy) modeling approach provides a unique framework to investigate biological interactions among species, including competitive exclusion, predator-prey interactions, and community assemblages (MacKenzie et al. 2004). These co-occupancy models

1) take into account imperfect detection of all target species; 2) estimate the occupancy of two or more species; and 3) determine if the presence of one species impacts the occupancy or detection of the other (MacKenzie 2006). More specifically these models use a maximum likelihood approach that "enables the magnitude of interspecific interactions in probabilities of occurrence to be estimated directly, while accounting explicitly for imperfect detectability" (MacKenzie et al. 2004). When using a co-occupancy model for two species at any given study site we have four possible states of occupancy: 1) occupied by both predator A and lemur B; 2) occupied by predator A only; 3) occupied by lemur B only; or 4) occupied by neither species (MacKenzie et al. 2004). The probability of a given location *i* belonging to one of the four possible states is found with the equation from MacKenzie et al. (2004):

$$\varphi_i = [\ \widehat{\Psi}_i^{AB} \quad \widehat{\Psi}_i^{A} - \widehat{\Psi}_i^{AB} \quad \widehat{\Psi}_i^{B} - \widehat{\Psi}_i^{AB} \quad 1 - \widehat{\Psi}_i^{A} - \widehat{\Psi}_i^{B} + \widehat{\Psi}_i^{AB}\ ]$$

The co-occupancy model provides nine estimable parameters (Table 2) based on these four possible states. In addition, a "species interaction factor" ['SIF'] (MacKenzie et al. 2004), can be calculated using: $\hat{\gamma} = \widehat{\Psi}^{AB}/(\widehat{\Psi}^{A}\,\widehat{\Psi}^{B})$, where $\widehat{\Psi}^{AB}$ is the probability of both predator A and lemur B being present at a given site (Table 2). The SIF, "the ratio of how much more or less likely the species are to co-occur at a site compared to what would be expected if they co-occurred independently" (MacKenzie 2006), provides a measure of interaction to determine if two target species co-occur independently ($\hat{\gamma}$ = 1.0), if co-occurrence is less than it would be if independent ($\hat{\gamma}$ < 1.0, 'avoidance'), or if co-occurrence is greater than it would be if independent ($\hat{\gamma}$ > 1.0, 'attraction'). The nine estimable parameters and SIF variable allow for the investigation of three key hypotheses: 1) level of co-occurrence between two target species; 2) independence

of detecting the species; and 3) whether detection of each species depends upon the presence of the other species (MacKenzie et al. 2004; MacKenzie 2006).

To evaluate whether the presence of a particular predator species influenced the occurrence of a particular lemur species we used a single-season, two-species interaction occupancy model (MacKenzie et al. 2004; MacKenzie 2006) and modeled these interactions in Program PRESENCE (Hines 2006). We combined all surveys of contiguous forest (*1AJB, 2AJB, 3AJB, MGB*), as well as all surveys of fragmented forest (*SLJ, FRK*) to provide a comparison of interactions across these two forest types. We could only use lemur transects which overlapped with camera stations. As a result, we used a total of 23 camera stations in fragmented forest and 72 stations in contiguous forest to estimate predator-primate co-occupancy. We investigated the interaction, based on the SIF variable, between each combination of predator and lemur species. A formal comparison of models is required to assess whether two species occur independently of one another [SIF ≠ 1.0] (MacKenzie 2006). To accomplish this assessment of independence we created two models for each predator-lemur species comparison: 1) a 'full model' in which occupancy of species A and B, as well as SIF are estimated; and 2) a 'reduced model' in which occupancy of A and B are estimated and SIF is fixed to 1.0 (independent). Two species were said to be independent when the difference in the ΔAIC value between these two models was >2.0 (MacKenzie 2006). Any predator-lemur comparison in which the two species were not independent (ΔAIC < 2.0) were not reported. We consider an interaction supported if the full model is supported over the reduced model according to the AIC, and the CIs for the SIF do not overlap 1.0 (independence).

Ethical Note

255 This non-invasive research project complied with protocols approved by the Institutional
256 Animal Care Committee of Virginia Tech and adhered to the legal requirements of Madagascar's
257 Ministry of the Environment and Forests (permit N^{o} 128/11 and 128/12).

258 Results

259 Our photographic and line transect surveys documented a total of six endemic carnivores,
260 two exotic carnivores, and 12 lemur species (Appendix I); however, for this manuscript we focus
261 solely on confirmed lemur predators and lemur species having adequate captures for our two-
262 species interaction occupancy models (White-fronted Brown lemur *Eulemur albifrons*, Eastern
263 Wooly lemur *Avahi laniger*, and Eastern Mouse lemur *Microcebus rufus*).

264 Our results highlight the difference in predator and lemur trap success or relative activity
265 between contiguous and fragmented forests across the Masoala-Makira landscape. In particular,
266 we found endemic carnivore trap success was higher across contiguous forest while exotic
267 carnivore and Locals trap success was higher in fragmented forest sites (Table 3). Despite the
268 higher rates in exotic carnivore and Locals trap success for fragmented forests we found the
269 MGB contiguous study site had the highest trap success for both *Canis familiaris* and Locals
270 compared to all other sites (Table 3). *Felis silvestris catus* were not detected at any fragmented
271 forest site but were present in all surveys of contiguous forest. For lemurs, *Avahi laniger* and
272 *Microcebus rufus* relative activity (number of captures per transect) was highest in the
273 fragmented FRK site (0.72 and 1.61, respectively) while *Eulemur albifrons* activity was highest
274 during the 1AJB survey (Table 3).

275 We found understory cover had the greatest impact (both positive and negative depending
276 on the species) on the majority of our endemic and exotic carnivore occupancy and detection

probabilities overall (Table 4). We also found distance to village and distance to forest edge were important variables for occupancy and survey period (time) was important for detection. We found that Locals trap success was positively associated with *C. familiaris* occupancy and *C. familiaris* trap success had a strong positive association with Locals occupancy based on beta values. Locals showed the most wide-ranging occurrence across the landscape ($\widehat{\Psi}$ = 0.82 ± SE 0.06) while *Felis silvestris catus* showed the most limited occurrence ($\widehat{\Psi}$ = 0.30 ± SE 0.08) for predators (Table 4). For *Avahi laniger* we found occupancy and detection to be most influenced by Locals trap success and *Cryptoprocta ferox* trap success (respectively). For *Microcebus rufus* we found canopy height had the greatest influence on occupancy (Table 4). Both *Avahi laniger* ($\widehat{\Psi}$ = 0.90 ± SE 0.09) and *Microcebus rufus* ($\widehat{\Psi}$ = 0.53 ± SE 0.14) had high occupancy across the landscape (Table 4). We were unable to provide estimates of *Eulemur albifrons* occupancy and detection as a result of the limited number of captures for this lemur species.

As a result of the limited number of lemur surveys in relation to photographic surveys of predator species, lemur 'captures' were low which provided difficulty allowing our co-occupancy models to converge when estimating detection probabilities for these species. To address this problem we fixed the detection rate at the value determined in our single-season, single-species occupancy analyses. Using these resulting detection probabilities in the two-species interaction occupancy models allowed the models to converge and provide estimates of the species interaction factor (SIF) between species.

Our two-species interaction model results indicate a strong contrast in predator-primate co-occupancy in contiguous versus fragmented forest sites. In fragmented forest we found evidence of species 'attraction' (SIF > 1.0) among all Locals and lemur pairings, *Canis familiaris*

and lemur pairings, and all *Galidia elegans* and lemur pairings. *Cryptoprocta ferox* was the only species without evidence of 'attraction' with lemur species in fragmented forest. *Canis familiaris* was the only species to move from no association (SIF = 1.0) or 'avoidance' (SIF < 1.0) in contiguous forest to 'attraction' (SIF > 1.0) in fragmented forest with all three lemur species (Table 5). Additionally, we found *Canis familiaris* and *Avahi laniger* had the greatest change in species interaction factor from 'avoidance' in contiguous (SIF = 0.61 ± SE 0.14; Figure 2a) to 'attraction' in fragmented forest (SIF = 1.24 ± SE 0.14; Figure 2b, Table 5). We found evidence for 'attraction' between Locals and *Microcebus rufus* in contiguous forest (SIF = 1.24 ± SE 0.15; Table 5; Figure 3a) yet strong 'avoidance' between *Canis familiaris* and *Microcebus rufus* (SIF = 0.16 ± SE 0.13; Figure 3b) and between *Galidia elegans* and *M. rufus* in contiguous forest (SIF = 0.16 ± SE 0.16; Table 5; Figure 3c). *Cryptoprocta ferox* had no evidence of 'attraction' with any lemur species in contiguous or fragmented forest; however, this top endemic carnivore showed evidence of 'avoidance' with *Eulemur albifrons* in fragmented forest (SIF = 0.46 ± SE 0.23; Table 5).

Of all lemur species *Microcebus rufus* had the greatest number of potential interactions (non-independent occurrence or SIF ≠ 1.0) with predators (Table 5, Figure 3). In fact, 89% (n = 9) of all *Microcebus rufus*-predator comparisons provided evidence of potential interaction ('attraction' or 'avoidance') relationship, whereas only 50% (n = 8) of *Avahi laniger*-predator and 50% (n = 6) of *Eulemur albifrons*-predator comparisons provided evidence of a potential ('attraction' or 'avoidance') relationship.

Discussion

The challenges associated with collecting data on elusive predators and primates have resulted in a death of information on predator-primate interactions. Our research demonstrates the effectiveness of a novel, non-invasive technique of combining photographic surveys with line transect sampling to investigate these complex interactions. More specifically, this study reveals a reliable, cost-effective approach to investigate: 1) how predator and primate activity and occurrence differ from contiguous to fragmented forest; 2) which variables influence predator and primate occupancy across the landscape; and 3) the potential interactions of predators and their primate prey and how these interactions change across contiguous and fragmented forest.

Change in Relative Activity or Trap Success: Contiguous to Fragmented Forest

Our analyses highlight the differences in trapping rates and distribution of endemic and exotic carnivores, as well as Locals between contiguous and fragmented forests. *Canis familiaris* and Locals trap success were more widespread across fragmented forest sites. This increase in distribution and activity in forests that are becoming more fragmented and patchy is believed to be the cause for the majority of positive associations observed between lemur species and *Canis familiaris* and Locals in our analysis. Despite the widespread activity for both *Canis familiaris* and Locals across fragmented forests across the Masoala-Makira landscape, surprisingly *Felis silvestris catus* were not detected in any fragmented study sites but were present in all surveys of contiguous forest. Interestingly, recent studies by Gerber et al. (2010; 2012) from the south-eastern Ranomafana NP differ from results presented here on *Felis silvestris catus*. Gerber et al. (2012) found a strong increase in *Felis silvestris catus* occupancy in fragmented forest. However, occupancy estimates of *Canis familiaris* and Locals were similar between the two studies. Additional work is needed to understand the variables influencing the presence and/or absence of

342 *Felis silvestris catus*, a confirmed lemur predator, across eastern rainforest habitat in
343 Madagascar.

344 For lemurs the difference in activity between contiguous and fragmented forest is less
345 striking. The high activity of lemur species at the FRK site, however, likely results from the
346 presence of primary rainforest cover in the southern, protected area of the Farankarina reserve as
347 lemur observations for this portion of the site were considerably higher. In addition, this study
348 incorporates only the three most common lemur species observed. We found a strong decrease in
349 total lemur species richness from contiguous to fragmented forest, including an absence of all
350 diurnal species (excluding *Eulemur albifrons*) in all fragmented forest sites surveyed (Farris,
351 Unpublished data). This outcome is alarming given the on-going patterns of forest loss and
352 fragmentation throughout Madagascar. To better understand the effects of fragmentation and
353 forest loss on lemur species across this region a more thorough density estimation analysis across
354 each forest type, which incorporates numerous landscape and habitat covariates, is needed.

355 *Single-Season, Single-Species Occupancy Across the Landscape*

356 Our low numbers of captures, primarily for lemurs, prevented the comparison of
357 contiguous and fragmented forests using occupancy estimation with covariates; however, our
358 single-season, single-species occupancy and detection estimates across the landscape provide
359 insight into how each predator and lemur species are impacted by changes across the landscape.
360 The extremely high occupancy for both Locals and *Canis familiaris* across the landscape is an
361 alarming sign and demands attention of conservationists and managers across this region. The
362 strong positive association between these two species is expected given the use of *Canis*
363 *familiaris* by Locals to perform various tasks such as zebu herding and hunting. The relatively

high occupancy of *Cryptoprocta ferox* across the landscape is similar to recent research conducted by Gerber et al. (2010; 2012) in south-eastern Madagascar on carnivores. Additional research is needed on the population dynamics and diet of this wide-ranging predator across this region to better understand its impact on lemur populations, particularly in fragmented forest sites.

In our single species, single season occupancy analyses, understory cover was the most important variable for the majority of our predator species; however, the relationship was weak in all instances. Though important for other predators understory cover was not in any top ranking models for *Cryptoprocta ferox* or Locals occupancy, but proved to be important for detection in both these species. The role of understory cover in predator occupancy and detection appears to be widespread and may be important for predicting predator occupancy across the landscape. The importance of distance to forest edge and to village for both endemic and exotic carnivore occupancy also draws attention to the on-going trends in fragmentation, edge effects, and human encroachment and their impacts on endemic and exotic wildlife species across eastern rainforest habitat. For example, the strong inverse relationship between distance to village and *Cryptoprocta ferox* occupancy may stem from the killing of *C. ferox* by farmers across the Masoala-Makira region due to the depredation of livestock by *C. ferox.* In fact, this mortality resulting from hunting is likely one of the biggest conservation concerns for *Cryptoprocta ferox* in this region of Madagascar. While data exists on bushmeat use and local consumption for this region (Golden 2009; Golden et al. 2011) human-wildlife conflict throughout Madagascar remains little studied and data on *Cryptoprocta ferox* home range and daily activity patterns are critical to further explore this impending threat.

386 For lemurs the high occupancy estimates and similarly high relative activity of both
387 *Avahi laniger* and *Microcebus rufus* in fragmented forest appears to be indicative of their
388 widespread presence across eastern rainforest habitat (Garbutt 2007). Further, *Microcebus rufus*
389 showed an increase in detection nearer forest edge while *Avahi laniger* showed a positive
390 relationship with Locals activity. These results support the supposition that *Avahi laniger* and
391 *Microcebus rufus* may be more common in disturbed, secondary forest compared to primary
392 forest (Ganzhorn 1988;1995). The inability to provide estimates of occupancy for *Eulemur*
393 *albifrons* resulted from low capture rates in both contiguous and fragmented forest sites (Table
394 3). Longer transects and more repeat surveys of these transects may be required to obtain
395 adequate captures for this and other larger bodied, gregarious lemur species.

396 *Two-species Interaction Models: Contiguous and Fragmented Forests*

397 As a result of the limited number of captures for lemurs we were unable to incorporate
398 covariates into our two-species interaction models. However, examining single species, single
399 season occupancy with covariates allowed us to gain insight into variables that may be
400 influencing these predator-lemur interactions. For example the 'avoidance' between *Microcebus*
401 *rufus* and *Galidia elegans* may be habitat mediated and simply caused by *M. rufus*' positive
402 association with canopy height and *G. elegans* positive association with understory cover, two
403 habitat features that were not correlated at our study sites. *Galidia elegans* however, is known to
404 prey upon *Microcebus rufus* (Goodman 2003) and this 'avoidance' may result from the pressure
405 placed upon *M. rufus* by this endemic predator. Incorporating covariates into co-occupancy
406 models may be required to fully understand the role that both predation and habitat play in this
407 particular predator-primate interaction.

The interactions between *Canis familiaris* and lemurs may be the most concerning across this region. *Canis familiaris* shows a change from little co-occurrence to strong 'attraction' with all three lemur species moving from contiguous to fragmented forest (Table 5). In particular, the striking change in *Canis familiaris* and *Avahi laniger* co-occurrence from contiguous to fragmented forest presents an alarming trend. In addition to the increased activity and distribution of *Canis familiaris* in fragmented sites we also see strong increases in Locals activity and distribution and our single-season, single-species occupancy models suggest a strong 'attraction' between *Avahi laniger* occupancy and Locals trap success. Finally, we also find increased patchiness and reduction in forest habitat at these sites. These results indicate that the increase in trap success and widespread distribution of *Canis familiaris* and Locals, as well as the increased patchiness and limited habitat availability, are likely creating more encounters between these species, such as for *Canis familiaris* and *Avahi laniger* (Table 5). The impact on lemurs from these potential increased encounters across fragmented forest remains unknown, but we assume *Canis familiaris* and Local encounters will be damaging for all three lemur species. Surveys by our team of highly fragmented sites with exceptionally high trap rates of Locals and *Canis familiaris* have shown very low numbers and/or a complete absence of all lemur species (Farris, Unpublished data). Furthermore, the training of *Canis familiaris* by Locals to hunt various wildlife species, including lemurs, is common for this region (anecdotal accounts and personal observation) and co-occurrence may be linked to these hunting activities. Additional research on the use of *Canis familiaris* by Locals to hunt wildlife is needed to fully understand the pressure this places on lemur populations across this region. To our knowledge, this is the first attempt to model *Canis familiaris* and lemur interactions in Madagascar, or any *C. familiaris*-primate interactions in any region of the world. Additional long-term surveys of exotic

carnivores and co-occurring lemurs at these fragmented sites are needed to better understand this relationship and to improve conservation and management efforts throughout Madagascar.

The lack of *Felis silvestris catus* captures in fragmented forest in this study likely translates to minimal impact on lemur species; however, it does not diminish their influence on lemur species in contiguous forest. Our co-occupancy models indicate a strong 'avoidance' between *Felis silvestris catus* and *Microcebus rufus* in contiguous forest, despite both species having narrow distributions and low capture rates in these forest sites. During our surveys we obtained photographic evidence of *Felis silvestris catus* killing endemic rodents; however, we know of no available information on the rate of take or capture efficiency of various lemur species in the diet of either *Felis silvestris catus* or the more abundant and wide ranging *Canis familiaris*. A complete diet analysis of these two exotic carnivores, as well as a better understanding of the factors associated with their occupancy, is needed to understand the impact of these predators on endemic wildlife, particularly lemur species, throughout Madagascar.

We found no 'attraction' between *Cryptoprocta ferox* and any lemur species in either contiguous or fragmented forest despite the relatively high occupancy rate across the landscape for this top predator. This lack of association with lemur species likely results from the wide-ranging behavior of this endemic carnivore. Individual *Cryptoprocta ferox* (identified by unique markings from scars, ears, and tails) have been shown to use large areas encompassing an entire study site (camera grid) and all lemur transects (Farris, Unpublished data; Brian Gerber, Pers comm.). In recent years attention has been placed on the diet of *Cryptoprocta ferox* particularly as it relates to their hunting of lemurs, as they have been suggested to be lemur specialists (Wright et al. 1997); however, our results find no positive association between *Cryptoprocta ferox* and any of the three relatively small bodied lemur species compared in this study.

454 *Cryptoprocta ferox* did show evidence of 'avoidance' with *Eulemur albifrons* in fragmented
455 forest and this relationship could be the result of depredation by *C. ferox* on this lemur species.
456 Additional diet analyses of *Cryptoprocta ferox* from numerous habitat types across all seasons
457 are needed to explore this question further.

458 *Microcebus rufus* had the greatest number of co-occurrence relationships with predators
459 in our two-species interaction occupancy models. While this species has been shown to be wide-
460 ranging and common throughout eastern rainforest habitat (Garbutt 2007) our surveys found
461 their distribution to be limited, particularly in contiguous forest (Figure 3a-c). This narrow
462 distribution of *Microcebus rufus* captures may have influenced the number of 'avoidance'
463 interactions with the more wide-ranging predator species in our co-occupancy models. Our
464 single species models indicate that *Microcebus rufus* detection increases near forest edge.
465 Moreover, our models also show an increase in *Microcebus rufus* occupancy when canopy height
466 increases. Given that this lemur species, along with other nocturnal species, is detected using eye
467 shine from the tapetum lucidum when using a headlamp during nocturnal surveys, the low
468 number of captures and limited distribution for this species may result from our inability to spot
469 this species where understory is more dense. As a result, the number of captures and any
470 resulting co-occupancy between predators and *Microcebus rufus* may be underestimated by our
471 data due to potential observer bias. While our co-occupancy models provide valuable insight on
472 predator-primate interactions, the inclusion of habitat variables, and additional covariates, for
473 estimating species detection and co-detection would be an important improvement for
474 understanding the source of these interactions. Incorporating these covariates into the co-
475 occupancy models is important to understand the variables that may be influencing or causing
476 these co-occupancy and/or co-detection relationships (Waddle et al. 2010). Furthermore,

477 incorporating co-detection to understand how the presence of one species is impacting the other
478 may prove crucial to understanding the relationship between target species (Bailey et al. 2009).

479 While our work highlights a novel approach in combining camera trapping and line
480 transect for investigating predator-lemur interactions, our data collection was designed
481 specifically for the goal of estimating endemic and exotic carnivore population parameters from
482 camera traps (primarily density which requires large number of trap nights). However, future
483 studies designed to focus primarily on predator-primate dynamics could reduce the number of
484 trap nights for photographic surveys and place greater effort on increasing the number of primate
485 line-transect surveys across the site in order to improve maximum likelihood convergence, as
486 well as occupancy and detection estimation. Further, using only a single camera per camera
487 station and expanding both the camera grid and line-transects will allow for the estimation of
488 occupancy and detection over a broader area and include more covariate data for analyses. In
489 addition, a need for existing trails for camera placement exists (Maffei et al. 2004; Dillon and
490 Kelly 2007); however, the location of highly accessible and heavily travelled trails may bias
491 results, such as at the MGB site which had a heavily used trail that bisected the study site.
492 Furthermore, this high level of *Canis familiaris* and local activity at the MGB site may have also
493 impacted lemur observations as line-transects were placed along existing trails to overlap with
494 photographic sampling data. As a result, the placement of cameras and line-transects is a vital
495 part of study design for similar studies using these methods. We recommend increased sampling
496 to include more "sites" in order to simultaneously model habitat variables with the two-species
497 interaction model framework.

498 The importance of and potential use of these novel techniques to the field of primatology
499 is wide-ranging. The techniques presented in this paper allow for the investigation of multi-

predator species' impact on primate behavior and/or dynamics across numerous habitat types. Further, these non-invasive techniques can also assist researchers and managers in identifying factors (native and exotic) that are influencing the occupancy and detection of numerous rare, endangered, and/or elusive primate species. Finally, combining these new methods with other non-invasive methods (such as scat analysis) may provide a more reliable, robust investigation of predator-primate dynamics with significantly less researcher cost and effort, as well as less stress and/or harm to wildlife.

Acknowledgements

This research project was funded by the National Geographic Society-Waitts Grant, Virginia Tech Chapter of Sigma Xi, Idea Wild, Cleveland Metroparks Zoo, People's Trust for Endangered Species, European Association for Zoos and Aquariums, the Virginia Tech McGinnes Graduate Fellowship, as well as logistical and financial support from the Wildlife Conservation Society Madagascar Program. We thank our Malagasy field assistants (B.L. Donah, Marka'Helin, and R. Wilson) and Malagasy collaborators (C.B. Beandraina, B.A. Salofo, R.C. Christian, Didice, B. Papin, Rabeson, Tobey, Cressent, J. Fernando, and Sassid), our field volunteers (A. Evans, T. Nowlan, K. Miles, H. Doughty, K. Galbreath, J. Larson, C. Miller, and H. Davis) and data entry volunteers (S. Webster, C. Stachowiak, C. Carbaugh, T. Dandridge, S. McCarter, J. Cantor, R. Landry, E. Lower, S. Schneider, M. Martin, D. Kessler, A. Dicocco, C. Maynard, S. Lynn, T. Pangle, H. Boone, E. Ronis, K. Miller, S. Folkerts, J. Majors, M. Brown, S. Sawyer). We thank the Antananarivo and Maroantsetra staff of the Wildlife Conservation Society for their logistical support during all aspects of this work, the Antongil Conservation

522 staff for logistical aid at the Farankarina reserve, as well as the Madagascar Ministry of
523 Environment, Water, Forest, and Tourism for permitting this project. This manuscript benefited
524 from reviews by Brian Gerber and Asia Murphy.

Table 1. Sampling details for each photographic and lemur survey at each study site, including forest type, dates of survey, number of camera stations at each site, total trap nights, elevation range of photo stations in meters, and the average distance to the nearest village from the edge of the study site.

Study site	Forest Type	Survey Dates	# of Camera Stations	Trap Nights	Elevation (m)	Dist. to Nearest Village (km)
Anjanaharibe (1AJB)	Contiguous	Sept – Nov, 2010	25	1257	350-690	2.8
Anjanaharibe (2AJB)	Contiguous	Aug – Oct, 2011	24	1383	350-690	2.8
Anjanaharibe (3AJB)	Contiguous	Aug – Oct, 2012	24	1536	350-690	2.8
Mangabe (MGB)	Contiguous	Mar – May, 2011	24	1509	324-786	4.8
Lohan'sanjinja (SLJ)	Fragmented	Dec – Feb, 2010	24	1570	93-507	1.5
Farankarina (FRK)	Fragmented	Jun – Aug, 2011	23	1462	21-886	2.1

* Trap Nights = 24 hour period in which at least one of the two cameras at a given camera station is not malfunctioning x number of camera stations in study site

Table 2. Single season, two-species interaction occupancy model parameters (from MacKenzie et al. 2004).

Parameter	Description
Ψ_i^{AB}	Probability of both species being present at location *i*
Ψ_i^{A}	Probability of species A being present at location *i*, regardless of occupancy status of species B
Ψ_i^{B}	Probability of species B being present at location *i*, regardless of occupancy status of species A
p_{ij}^{A}	Probability of detecting species A during the *jth* survey of location *i*, given only species A is present
p_{ij}^{B}	Probability of detecting species B during the *jth* survey of location i, given only species B is present
r_{ij}^{AB}	Probability of detecting both species during the *jth* survey of location *i*, given both species are present
r_{ij}^{Ab}	Probability of detecting species A, but not B, during the *jth* survey of location *i*, given both species are present
r_{ij}^{aB}	Probability of detecting species B, but not A, during the *jth* survey of location *i*, given both species are present
r_{ij}^{ab}	Probability of detecting neither species during the *jth* survey of location *i*, given both species are present

Table 3. Trap success (SE) or relative activity of endemic carnivores, exotic carnivores, and Locals (non-researcher humans) and the number of detections per survey for each lemur species at each survey site. Trap success is calculated as total number of captures/trap nights, minus malfunctions, times 100 with a capture defined as all independent photos of a species within a 30-minute time period.

		Contiguous Forest Sites				Fragmented Forest Sites	
Scientific Name	Common Name	1AJB	2AJB	3AJB	MGB	SLJ	FRK
Cryptoprocta ferox	Fosa	2.2 (0.7)	1.3 (0.5)	1.6 (0.5)	6.5 (1.1)	1.8 (0.7)	1.0 (0.4)
Galidia elegans	Ring-tail vontsira	1.5 (0.4)	1.0 (0.3)	0.4 (0.2)	2.8 (1.3)	0.5 (0.2)	1.1 (0.3)
Canis familiaris	Domestic dog	1.0 (0.5)	1.1 (0.6)	0.7 (0.3)	21.4 (3.8)	19.4 (7.3)	13.5 (6.6)
Felis silvestris catus	Feral cat	0.2 (0.1)	0.3 (0.1)	2.0 (0.6)	1.3 (0.5)	0.0 (0)	0.0 (0)
Locals	Human (non-researcher)	2.2 (0.9)	11.8 (10.6)	2.4 (1.3)	92.4 (17.3)	170.1 (57.9)	71.8 (29.5)
Avahi laniger	Eastern Wooly lemur	0.62	0.67	0.39	0.40	0.43	0.72
Eulemur albifrons	White-fronted brown lemur	0.47	0.21	0.17	0.21	0.13	0.33
Microcebus rufus	Eastern Mouse lemur	0.71	0.69	0.49	0.29	0.53	1.61

Table 4. Top model results for single-season, single-species occupancy for each target species, including model name, Akaike Information Criterion (AIC), AIC model weight, number of parameters (k), -2 log likelihood value, as well as occupancy (Ψ) and probability of detection (p) with standard error.

Species	Model	AIC	AIC wgt	k	-2LogLikelihood	Ψ (SE) *	p (SE) *
Cryptoprocta ferox	psi(.)[1], p(Under)[2]	762.35	0.25	3	756.35	0.63 (0.06)	0.18 (0.02)
	psi(Locals)[3], p(Under)	762.74	0.21	4	754.74	0.63 (0.08)	0.18 (0.02)
	psi(.), p(Village)[4]	763.05	0.18	3	757.05	0.67 (0.07)	0.16 (0.02)
Galidia elegans ǂ	psi(Under), p(Dog)[5]	459.11	0.64	4	451.11	0.58 (0.10)	0.10 (0.02)
	psi(Under), p(.)	462.19	0.14	3	456.19	0.56 (0.11)	0.11 (0.02)
Canis familiaris	psi(Under), p(Time)[6]	1063.81	0.14	15	1033.81	0.64 (0.06)	0.37 (0.06)
	psi(Locals), p(Time)	1078.61	<0.01	15	1048.61	0.64 (0.06)	0.37 (0.06)
Felis silvestris catus	psi(Under), p(Time)	312.46	0.97	15	282.46	0.30 (0.08)	0.12 (0.05)

Locals	psi(Dog), p(Under,Time)	1139.11	0.99	16	1107.11	0.82 (0.06)	0.41 (0.05)
Avahi laniger	psi(Locals), p(Fosa)[7]	292.28	0.17	4	284.28	0.90 (0.09)	0.20 (0.03)
	psi(.), p(Fosa)	292.34	0.16	3	286.34	0.90 (0.10)	0.20 (0.04)
	psi(Fosa), p(Fosa)	292.91	0.12	4	284.91	0.91 (0.10)	0.20 (0.04)
Microcebus rufus	psi(Can ht.)[8], p(.)	188.79	0.10	3	182.79	0.53 (0.14)	0.32 (0.06)
	psi(Can ht.), p(Edge)[9]	189.01	0.09	4	181.01	0.53 (0.14)	0.33 (0.08)
	psi(.), p(.)	189.25	0.08	2	185.25	0.52 (0.10)	0.32 (0.06)

1 (.) – constant rate of occupancy and/or detection; 2 Under – understory cover; 3 Locals – Human (non-researcher) trap success; 4 Village – distance to nearest village; 5 Dog – *Canis familaris* trap success; 6 Time – survey specific rate of occupancy and/or detection; 7 Fosa – *Cryptoprocta ferox* trap success; 8 Can ht. – Canopy height; 9 Edge – distance to forest edge.

* Average occupancy and detection reported based on mean covariate value for models without constant detection.

ǂ No *a priori* model fit observed data based on GOF test, thus the highest ranking, model was chosen after removal of models that did not fit the data.

Table 5. Best model results for single season, two-species interaction occupancy models for each predator-lemur species comparison in either contiguous forest (Contig), or fragmented forest (Frag). Model results include model name, probability of occupancy (SE) of species A (psiA) and B (psiB), the species interaction factor (SIF), as well as detection probability (SE) for both species A (pA) and B (pB).

Species: A B	Forest Type	Model	psiA (SE)	psiB (SE)	pA (SE)	pB (SE)	SIF (SE) [1]
C.familiaris - *E.albifrons*	Contig	NI & E[2], p(fixed) [3]	0.55 (0.06)	0.55 (0.06)	0.15	0.15	0.98 (0.17)
	Frag	NI & NE[4], I & NE[5]	0.76 (0.10)	0.71 (0.13)	0.78 (0.06)	0.08 (0.07)	1.09 (0.17)
C.familiaris - *M.rufus*	Contig	NI & NE, p(fixed)	0.81 (0.13)	0.60 (0.12)	0.21	0.21	0.16 (0.13)
	Frag	NI & E, p(fixed)	0.75 (0.08)	0.75 (0.08)	0.52	0.36	1.11 (0.09)
C.familiaris - *A. laniger*	Contig	NI & E, NI & NE	0.60 (0.07)	0.60 (0.07)	0.22 (0.03)	0.09 (0.04)	0.61 (0.14)
	Frag	NI & E, p(.)[6]	0.68 (0.09)	0.68 (0.09)	0.28 (0.02)	0.28 (0.02)	1.24 (0.14)
Locals - *E. albifrons*	Contig	NI & E, p(fixed)	0.59 (0.06)	0.59 (0.06)	0.24	0.24	1.17 (0.13)
	Frag	NI & NE, p(fixed)	0.85 (0.09)	0.61 (0.13)	0.29	0.29	1.11 (0.20)
Locals - *M. rufus*	Contig	NI & E, p(fixed)	0.55 (0.07)	0.55 (0.07)	0.46	0.21	1.24 (0.15)
	Frag	NI & NE, p(fixed)	0.83 (0.09)	0.67 (0.12)	0.54	0.36	1.14 (0.16)

Locals - *A. laniger*	Contig	NI & NE, p(fixed)	0.55 (0.07)	0.87 (0.07)	0.24	0.24	0.99 (0.08)
	Frag	NI & NE, p(.)	0.81 (0.09)	0.61 (0.12)	0.27 (0.02)	0.27 (0.02)	1.13 (0.19)
F.s.catus- M. rufus	Contig	NI & E, p(fixed)	0.45 (0.05)	0.45 (0.05)	0.19	0.12	0.53 (0.23)
	Frag	-	-	-	-	-	-
F.s.catus - A.laniger	Contig	NI & E, p(fixed)	0.87 (0.11)	0.87 (0.11)	0.19	0.16	1.06 (0.07)
	Frag	-	-	-	-	-	-
C.ferox - E. albifrons	Contig	NI & NE, p(.)	0.84 (0.10)	0.64 (0.09)	0.13 (0.02)	0.13 (0.02)	1.03 (0.10)
	Frag	NI & E, p(fixed)	0.54 (0.07)	0.54 (0.07)	0.04	0.04	0.46 (0.23)
C.ferox - A. laniger	Contig	NI & E, p(.)	0.88 (0.07)	0.88 (0.07)	0.14 (0.01)	0.14 (0.01)	1.01 (0.06)
	Frag	NI & E, p(.)	0.71 (0.10)	0.71 (0.10)	0.14 (0.02)	0.14 (0.02)	0.96 (0.16)
C.ferox - M.rufus	Contig	NI & NE, p(.)	0.80 (0.09)	0.45 (0.09)	0.15	0.15	0.83 (0.14)
	Frag	NI & E, p(fixed)	0.80 (0.12)	0.80 (0.12)	0.12	0.36	0.97 (0.11)
G.elegans vs. M.rufus	Contig	NI & E, p(fixed)	0.36(0.05)	0.36 (0.05)	0.09	0.21	0.16 (0.16)
	Frag	NI & E, p(fixed)	0.71 (0.14)	0.71 (0.14)	0.05	0.36	1.13 (0.20)
G.elegans vs. A.laniger	Contig	-	-	-	-	-	-
	Frag	NI & E, p(fixed)	0.76 (0.14)	0.76 (0.14)	0.05	0.28	1.14 (0.18)

[1]SIF = Species Interaction Factor; [2] NI & E = Non-independent occurrence and equal detection; [3] p (fixed) = Fixed probability of detection based on detection estimated from single-season, single-species occupancy modeling; [4] NI & NE = Non-independent occurrence and non-equal detection;[5] I & NE = Independent occurrence and equal detection; [6] p (.) = Constant probability of detection

Literature Cited:

Arroyo-Rodríguez, V., & Dias, P. A. D. (2010). Effects of habitat fragmentation and disturbance on howler monkeys: a review. *American Journal of Primatology, 72*(1), 1-16.

Bailey, L. L., Reid, J. A., Forsman, E. D., & Nichols, J. D. (2009). Modeling co-occurrence of northern spotted and barred owls: accounting for detection probability differences. *Biological Conservation, 142*(12), 2983-2989.

Bailey, L. L., Simons, T. R., & Pollock, K. H. (2004). Estimating site occupancy and species detection probability parameters for terrestrial salamanders. *Ecological Applications, 14*(3), 692-702.

Boyle, S. A., & Smith, A. T. (2010). Behavioral modifications in northern bearded saki monkeys (Chiropotes satanas chiropotes) in forest fragments of central Amazonia. *Primates, 51*(1), 43-51.

Braczkowski, A., Watson, L., Coulson, D., & Randall, R. (2012). Diet of leopards in the southern Cape, South Africa. *African Journal of Ecology, 50*(3), 377-380.

Burnham, D., Bearder, S., Cheyne, S., Dunbar, R., & Macdonald, D. (2013). Predation by Mammalian Carnivores on Nocturnal Primates: Is the Lack of Evidence Support for the Effectiveness of Nocturnality as an Antipredator Strategy? *Folia Primatologica, 83*(3-6), 236-251.

Colquhoun, I. C. (2006). Predation and Cathemerality. *Folia Primatologica, 77*(1-2), 143-165.

Creel, S. (2011). Toward a predictive theory of risk effects: hypotheses for prey attributes and compensatory mortality. *Ecology, 92*(12), 2190-2195.

Dillon, A., & Kelly, M. J. (2007). Ocelot Leopardus pardalis in Belize: the impact of trap spacing and distance moved on density estimates. *ORYX-LONDON-, 41*(4), 469.

Estrada, A., Raboy, B. E., & Oliveira, L. C. (2012). Agroecosystems and Primate Conservation in The Tropics: A Review. *American Journal of Primatology, 74*(8), 696-711.

Farris, Z. (2012). Brown-tailed Vontsira Salanoia concolor (Eupleridae) documented in Makira Natural Park, Madagascar: new insights on distribution and camera-trap success. *Small Carnivore Conservation, 47*, 82-86.

Ganzhorn, J. U. (1988). Food partitioning among Malagasy primates. *Oecologia, 75*(3), 436-450.

Ganzhorn, J. U. (1995). Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology*, 2084-2096.

Ganzhorn, J. U., Goodman, S., & Dehgan, A. (2003). Effects of forest fragmentation on small mammals and lemurs. *The natural history of Madagascar*, 1228-1234.

Garbutt, N. (2007). *Mammals of Madagascar: a complete guide*: Yale University Press.

Gerber, B., Williams, P., & Bailey, L. (In Review). Primates and Cameras: Non-invasive sampling to make population-level inferences while accounting for imperfect detection. *International journal of primatology*.

Gerber, B. D. (2010). *Comparing density analyses and carnivore ecology in Madagascar's southeastern rainforest.* Unpublished Masters Thesis.

Gerber, B. D., Karpanty, S. M., & Randrianantenaina, J. (2012). The impact of forest logging and fragmentation on carnivore species composition, density and occupancy in Madagascar's rainforests. *Oryx, 46*(03), 414-422.

Gilbert, K. (2003). Primates and Fragmentation of the Amazon Forest. In L. Marsh (Ed.), *Primates in Fragments* (pp. 145-157): Springer US.

Golden, C. D. (2009). Bushmeat hunting and use in the Makira Forest, north-eastern Madagascar: a conservation and livelihoods issue. *Oryx, 43*(3), 386.

Golden, C. D., Fernald, L. C., Brashares, J. S., Rasolofoniaina, B. R., & Kremen, C. (2011). Benefits of wildlife consumption to child nutrition in a biodiversity hotspot. *Proceedings of the National Academy of Sciences, 108*(49), 19653-19656.

Goodman, S. (2003). Predation on lemurs. In S. a. B. Goodman, J.P. (Ed.), *The Natural History of Madagascar* (pp. 1159-1186). The University of Chicago Press.

Harcourt, A. H., & Doherty, D. A. (2005). Species–area relationships of primates in tropical forest fragments: a global analysis. *Journal of Applied Ecology, 42*(4), 630-637.

Hart, D. (2007). Predation on primates: a biogeographical analysis. In *Primate anti-predator strategies* (pp. 27-59): Springer.

Henschel, P., Hunter, L., Coad, L., Abernethy, K., & Mühlenberg, M. (2011). Leopard prey choice in the Congo Basin rainforest suggests exploitative competition with human bushmeat hunters. *Journal of Zoology, 285*(1), 11-20.

Hill, R., & Lee, P. (1998). Predation risk as an influence on group size in cercopithecoid primates: implications for social structure. *Journal of Zoology, 245*(4), 447-456.

Hines, J. E. (2006). Program PRESENCE. *See http://www. mbrpwrc. usgs. gov/software/doc/presence/presence. html*.

Holmes, C. (2007). *Linking livelihoods, land stewardship, and resource conservation in the Antongil Bay Landscape, Madagascar.* (Working Paper).

Irwin, M., Raharison, J. L., & Wright, P. (2009). Spatial and temporal variability in predation on rainforest primates: do forest fragmentation and predation act synergistically? *Animal Conservation, 12*(3), 220-230.

Isbell, L. A. (1994). Predation on primates: ecological patterns and evolutionary consequences. *Evolutionary Anthropology: Issues, News, and Reviews, 3*(2), 61-71.

Johns, A., & Skorupa, J. (1987). Responses of rain-forest primates to habitat disturbance: A review. *International journal of primatology, 8*(2), 157-191.

Jooste, E., Pitman, R., Van Hoven, W., & Swanepoel, L. (2013). Unusually High Predation on Chacma Baboons (Papio ursinus) by Female Leopards (Panthera pardus) in the Waterberg Mountains, South Africa. *Folia Primatologica, 83*(3-6), 353-360.

Kankam, B. O., & Sicotte, P. (2013). The Effect of Forest Fragment Characteristics on Abundance of Colobus vellerosus in the Forest-Savanna Transition Zone of Ghana. *Folia Primatologica, 84*(2), 74-86.

Karpanty, S. M. (2006). Direct and indirect impacts of raptor predation on lemurs in southeastern Madagascar. *International journal of primatology, 27*(1), 239-261.

Karpanty, S. M., & Wright, P. C. (2007). Predation on lemurs in the rainforest of Madagascar by multiple predator species: observations and experiments. In *Primate anti-predator strategies* (pp. 77-99): Springer.

Kremen, C. (2003). The Masoala Peninsula. *The natural history of Madagascar (SM Goodman and JP Benstead, eds.). University of Chicago Press, Chicago, Illinois*, 1459-1466.

Lande, R. (1998). Anthropogenic, ecological and genetic factors in extinction and conservation. *Researches on Population Ecology, 40*(3), 259-269.

Lima, S. L. (1998). Nonlethal effects in the ecology of predator-prey interactions. *Bioscience, 48*(1), 25-34.

MacKenzie, D. I. (2006). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*: Access Online via Elsevier.

MacKenzie, D. I., Bailey, L. L., & Nichols, J. (2004). Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology, 73*(3), 546-555.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Andrew Royle, J., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology, 83*(8), 2248-2255.

Maffei, L., Cuéllar, E., & Noss, A. (2004). One thousand jaguars (Panthera onca) in Bolivia's Chaco? Camera trapping in the Kaa-Iya National Park. *Journal of Zoology, 262*(3), 295-304.

Miller, L. E. (2002). *Eat or be eaten: predator sensitive foraging among primates*: Cambridge University Press.

Miller, L. E., & Treves, A. (2007). Predation on primates: past studies, current challenges, and directions for the future. *Primates in perspective*, 525-543.

Morino, L. (2011). Clouded leopard predation on a wild juvenile siamang. *Folia Primatologica, 81*(6), 362-368.

Onderdonk, D., & Chapman, C. (2000). Coping with Forest Fragmentation: The Primates of Kibale National Park, Uganda. *International journal of primatology, 21*(4), 587-611.

Pollard, J. (1971). On distance estimators of density in randomly distributed forests. *Biometrics*, 991-1002.

Rahlfs, M., & Fichtel, C. (2010). Anti-Predator Behaviour in a Nocturnal Primate, the Grey Mouse Lemur (Microcebus murinus). *Ethology, 116*(5), 429-439.

Schel, A. M., & Zuberbühler, K. (2012). Predator and non-predator long-distance calls in Guereza colobus monkeys. *Behavioural processes, 91*(1), 41-49.

Schwitzer, C., Glatt, L., Nekaris, K., & Ganzhorn, J. U. (2011). Responses of animals to habitat alteration: an overview focussing on primates. *Endang Species Res, 14*, 31-38.

Shultz, S., Noë, R., McGraw, W. S., & Dunbar, R. (2004). A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 271*(1540), 725-732.

Terborgh, J., & Janson, C. (1986). The socioecology of primate groups. *Annual review of ecology and systematics, 17*, 111-136.

Thompson, W. (2004). *Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters*: Island Press.

Waddle, J. H., Dorazio, R. M., Walls, S. C., Rice, K. G., Beauchamp, J., Schuman, M. J., et al. (2010). A new parameterization for estimating co-occurrence of interacting species. *Ecological Applications, 20*(5), 1467-1475.

Willems, E. P., & Hill, R. A. (2009). Predator-specific landscapes of fear and resource distribution: effects on spatial range use. *Ecology, 90*(2), 546-555.

Wright, P., Heckscher, S., & Dunham, A. (1997). Predation on Milne-Edward's sifaka (Propithecus diadema edwardsi) by the fossa (Cryptoprocta ferox) in the rain forest of southeastern Madagascar. *Folia Primatologica, 68*(1), 34-43.

Yanuar, A., & Chivers, D. J. (2010). Impact of forest fragmentation on ranging and home range of siamang (Symphalangus syndactylus) and agile gibbons (Hylobates agilis). In *Indonesian Primates* (pp. 97-119): Springer.

Zuberbühler, K., & Jenny, D. (2002). Leopard predation and primate evolution. *Journal of Human Evolution, 43*(6), 873-886.

Figure 1
Click here to download Figure: Figure 1 - Farris et al. Patterns in predator-primate co-occupancy.docx

Figure 1. Map of study sites across the Makira Natural Park highlighting the location of Masoala National Park, Makira Natural Park, as well as the two contiguous study sites: Anjanaharibe (AJB) and Mangabe (MGB) and the two fragmented study sites: Lohan'sahanjinja (SLJ) and Farakarina (FRK).

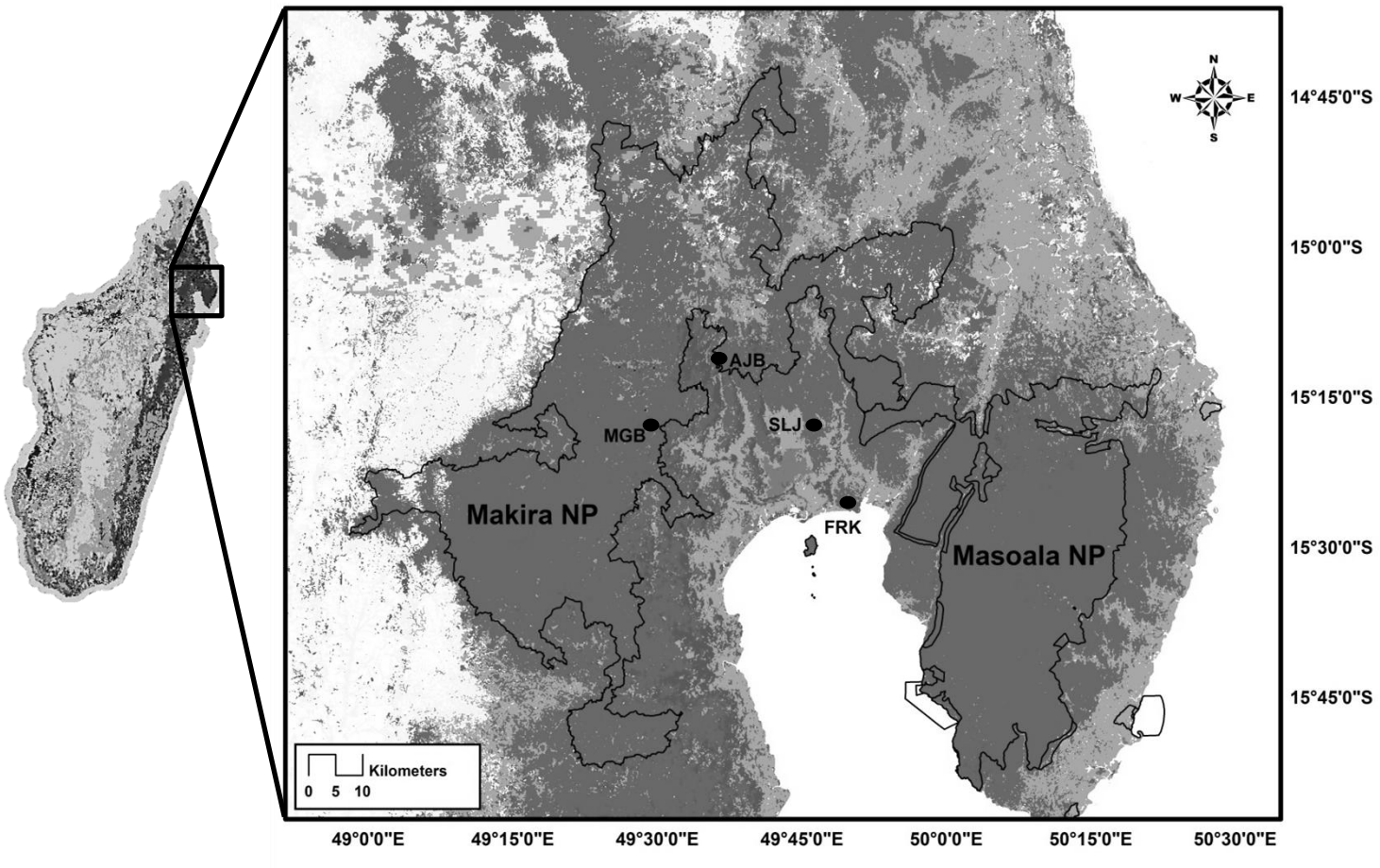


Figure 2
Click here to download Figure: Figure 2 - Farris et al. Patterns in predator-primate co-occupancy.docx

Figure 2. Capture locations of *Canis familiaris* (White circles) and *Avahi laniger* (Black diamonds) which displays the A.) species "avoidance" [SIF = 1.24 (0.14)] at the Anjanaharibe study site (AJB) in contiguous forest and the B.) species "attraction" [SIF = 1.24 (0.14] at the Lohan' sahanjinja study site (SLJ) in fragmented forest.

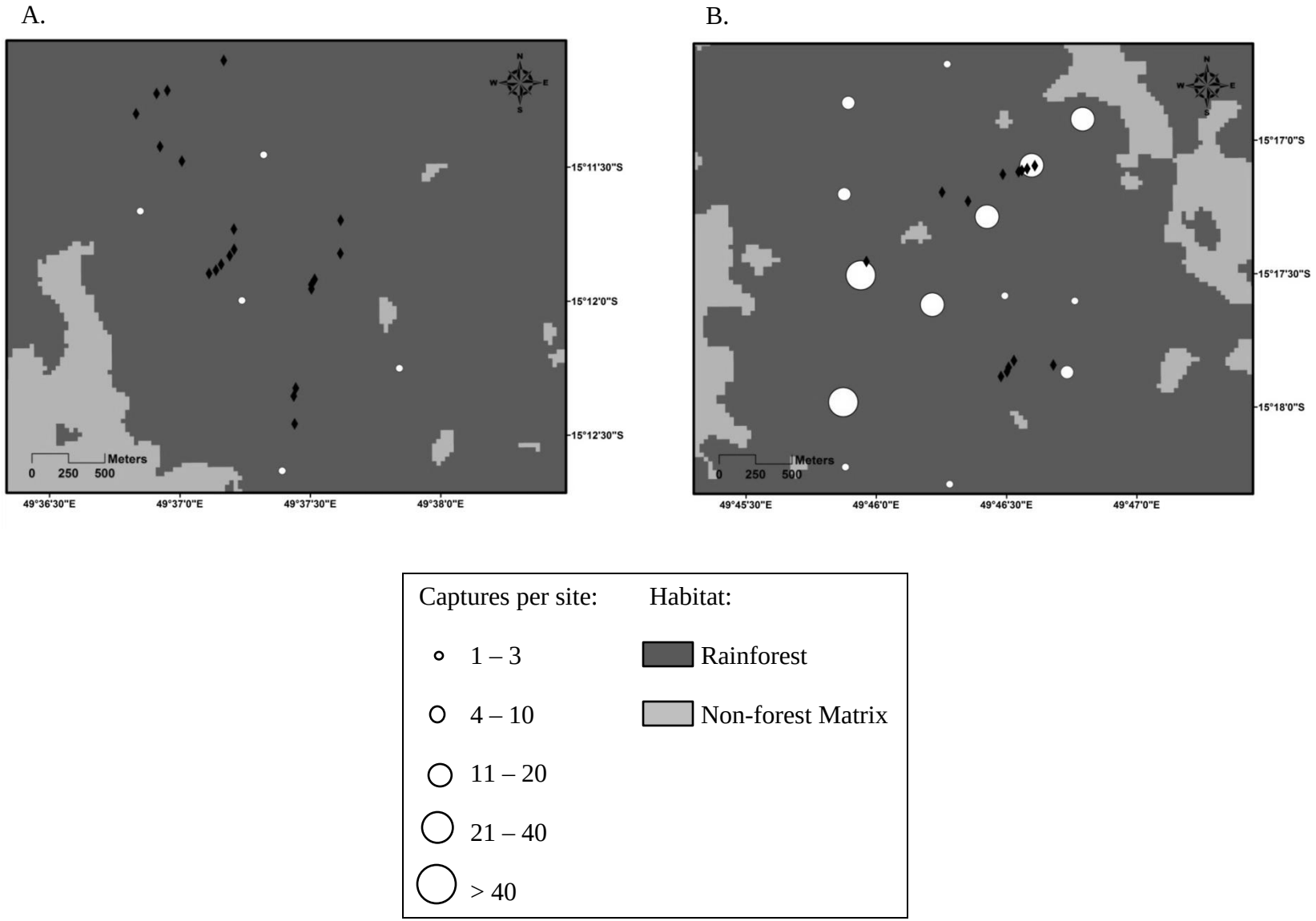
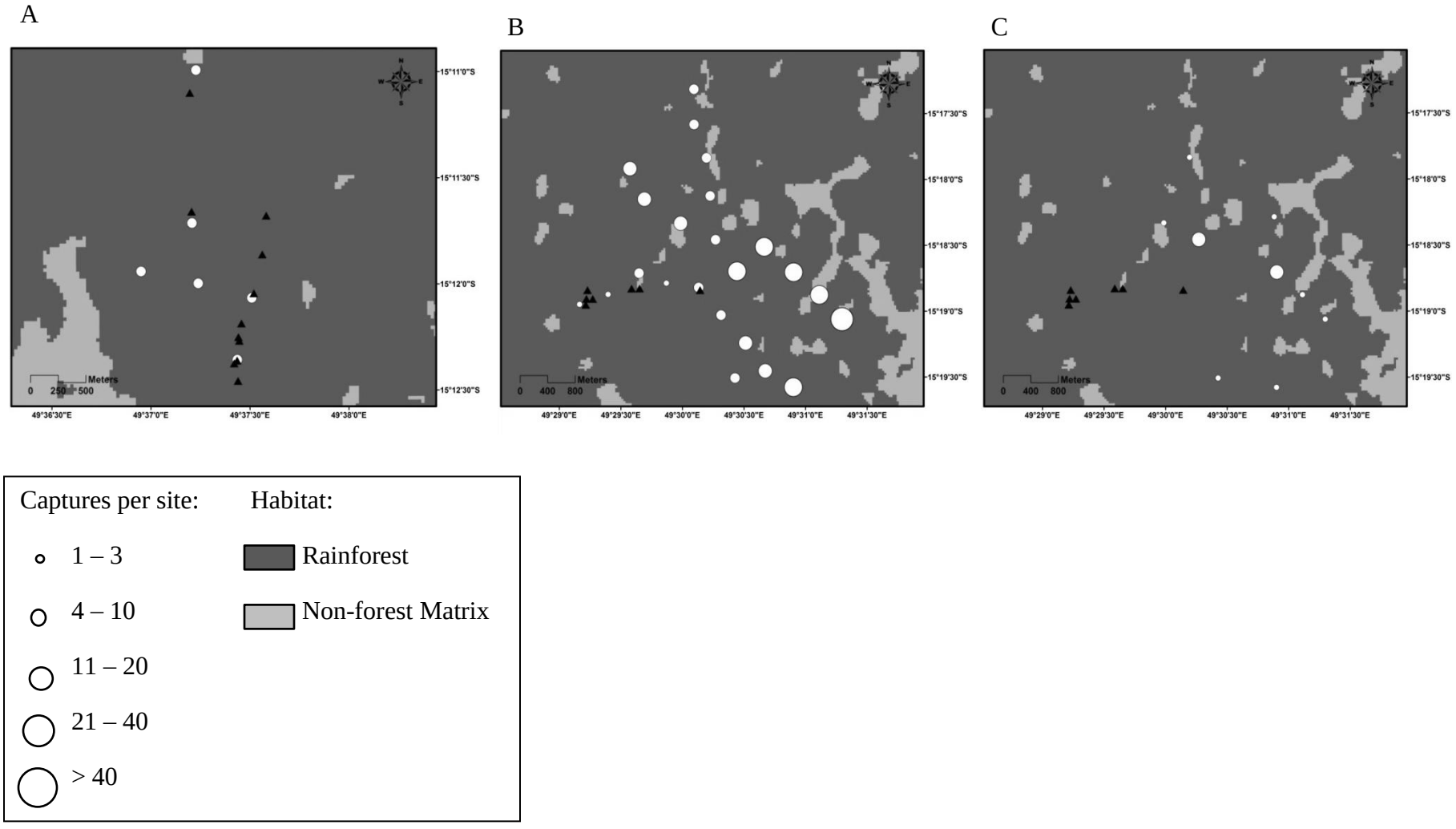


Figure 3
Click here to download Figure: Figure 3 - Farris et al. Patterns in predator-primate co-occupancy.docx

Figure 3. Capture locations for A) Locals (White circles) and *Microcebus rufus* (Black triangles) highlighting the species "attraction" [SIF = 1.24 (0.15)] at the Anjanaharibe study site (AJB) in contiguous forest; B) *Canis familiaris* (White circles) and *Microcebus rufus* highlighting the species "avoidance" [SIF = 0.16 (0.13)] at the Mangabe study site (MGB) in contiguous forest; and C) *Galidia elegans* (White circles) and *Microcebus rufus* highlighting the species "avoidance" [SIF = 0.16 (0.16)] at the MGB study site in contiguous forest.



Appendix I

Appendix I. The total number of observations (line-transect sampling) and/or captures (photographic surveys) of endemic carnivores, exotic carnivores, and lemurs during our surveys of Anjanaharibe, Mangabe, Farankarina, and Lohan'sahanjinja forest sites across the Masoala-Makira landscape. Species included in analyses for this manuscript are in bold.

Scientific Name	Common Name	Total Observations/Captures
Endemic Carnivores		
Cryptoprocta ferox	**Fosa**	244
Fossa fossana	Malagasy civet	486
Eupleres goudotii	Falanouc	141
Galidia elegans	**Ring-tail vontsira**	112
Galidictis fasciata	Broad-striped vontsira	53
Salanoia concolor	Brown-tail vontsira	44
Exotic Carnivores		
Viverricula indica	Indian civet	44
Canis familiaris	**Domestic dog**	1195
Felis silvestris familiaris	**Feral cat**	62
Lemurs		
Eulemur albifrons	**White-fronted brown lemur**	57
Eulemur rubriventer	Red-bellied lemur	1
Hapalemur griseus	Eastern lesser bamboo lemur	P *
Varecia rubra	Red-ruffed lemur	3
Varecia variegata	White-ruffed lemur	2

Propithecus candidus	Silky sifaka	1
Indri indri	Indri	25
Microcebus rufus	**Eastern mouse lemur**	67
Avahi laniger	**Eastern wooly lemur**	101
Cheirogaleus major	Greater dwarf lemur	13
Phaner furcifer	Forked-marked lemur	P *
Daubentonia madagascariensis	Aye-aye	P *

* - Species was present and observed but not detected during line-transect sampling.