RESPONSE OF MADAGASCAR'S ENDEMIC CARNIVORES TO FRAGMENTATION, HUNTING, AND EXOTIC CARNIVORES ACROSS THE MASOSALA-MAKIRA LANDSCAPE.

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Dissertation submitted to the faculty of the Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree of

Doctor of Philosophy
In
Fish & Wildlife

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ABSTRACT

The carnivores of Madagascar are likely the least studied of the world's carnivores, thus little is known about threats to their persistence. I provide the first long-term assessment of Madagascar's rainforest carnivore community, including: 1) how multiple forms of habitat degradation (i.e., fragmentation, exotic carnivores, human encroachment, and hunting) affect native and exotic carnivore occupancy; 2) how native and exotic carnivore temporal activity overlap and how body size and niche explain these patterns; 3) how native and exotic carnivores spatially co-occur across the landscape and which variables explain these relationships; and 4) how native and exotic carnivores and humans co-occur with lemurs across Madagascar's largest protected landscape: the Masoala-Makira landscape. From 2008 to 2013 I photographically sampled carnivores and conducted line-transect surveys of lemurs at seven study sites with varying degrees of degradation and human encroachment, including repeat surveys of two sites. As degradation increased, exotic carnivores showed increases in activity and occupancy while endemic carnivore, small mammal, and lemur occupancy and/or activity decreased. Wild/feral cats (*Felis sp.*) and dogs (*Canis familiaris*) had higher occupancy (0.37 ± SE 0.08 and 0.61 ± SE 0.07, respectively) than half of the endemic carnivore species across the landscape. Additionally, exotic carnivores had both direct and indirect negative effects on native carnivore occupancy. For example, spotted fanaloka (*Fossa fossana*) occupancy (0.70 ± SE 0.07) was negatively impacted by both wild/feral cat (beta = -2.65) and Indian civets (beta = -1.20). My results revealed intense pressure from hunting (ex. n = 31 fosa *Cryptoprocta ferox* consumed per year from 2005-2011 across four villages), including evidence that hunters target intact forest where native carnivore and lemur occupancy and/or activity are highest. I found evidence of high temporal overlap between native and exotic carnivores (ex. temporal overlap between brown-tail vontsira *Salanoia concolor* and dogs is 0.88), including fosa (*Cryptoprocta ferox*) avoiding dogs and humans across all seasons. However, I found no evidence of body size or correlates of ecological niche explaining temporal overlap among carnivores. Estimates of spatial co-occurrence among native and exotic carnivores in rainforest habitat revealed strong evidence that native and exotic carnivores occur together less often than expected and that exotic carnivores may be replacing native carnivores in forests close to human settlements. For example, falanouc show a strong increase in occupancy when dogs are absent (0.69 ± SE 0.11) compared to when they are present (0.23 ± SE 0.05). Finally, the two-species interaction occupancy models for carnivores and lemurs, revealed a higher number of interactions among species across contiguous forest where carnivore and lemur occupancy were highest. These various anthropogenic pressures and their effects on carnivore and lemur populations, particularly increases in exotic carnivores and hunting, have wide-ranging, global implications and demand effective management plans to target the influx of exotic carnivores and unsustainable hunting affecting carnivore and primate populations across Madagascar and worldwide.

Dedicated to

Alisha, aka “*Skinny love*”
Oliver, “*Tiny prancer*”
& &
Fletcher “*Stinky Pete*”

Nothing will ever compare to the great joy of being a part of your lives.
Your humor, excitement, and outright craziness made this experience a blast!
Thanks for being part of this crazy ride.

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First and foremost, I am truly grateful to my wife Alisha and two boys, Oliver and Fletcher. Your amazing support and ridiculous humor helped me stay sane. I would follow you three anywhere!

I am thankful to my advisers Sarah Karpanty and Marcella Kelly for this amazing opportunity. From your last minute edits, to your miraculous and mysterious sources of funding, to your encouraging and kind emails after a tough day, you both went above and beyond your role as an adviser. I consider you both as great mentors, colleagues, and friends.

I am thankful to my additional committee members, Dean Stauffer and Steig Johnson. Dean, you indeed live by the motto that has accompanied your emails all these years, “Integrity is when what you think, say, and do are all in alignment.” Steig, you played a big role in shaping my career early on as a researcher in Madagascar. I am grateful that you were able to serve as one of my committee members.

I am thankful to all the members of the Whapa lab (L. Rich, A. Hillborne, M. Kane. K. Thapa, D. Montague, D. Morin, E. Poor, C. Wultsch, C. Tredick, M. St. Germain, Sunarto, C. Rowe, C. Satter, B. Augustine, B. Mesa, and C. Proctor), the Karpanty lab (K. Davis, T. and K. Geider, A. Murphy, M. Wura, B. Gerber, M. Kotschwar, K. Ray, and M. Hillman), and Fraser lab (S. Ritter, A. DeRose-Wilson, D. Catlin, J. Cohen, J. Felio, D. Fraser, K. Hunt, M. Friedrich, and J. Fraser) for their friendship,

encouragement, humor, and support these many years. I am also thankful to all the remaining staff, faculty, and students of Virginia Tech FiW for their role they have played over the last five years to help me get to this point. I am grateful to Tom (“Tboy”) who played a massive role in making this experience really enjoyable for me and my family (not so much my kids though as you have scarred them for life).

The truly immense data set collected from 2008 to 2013 in Madagascar would not have been possible without the assistance of countless organizations and their supporting staff. I am indebted to Chris Holmes and his family for providing this opportunity, for offering his unending support, and for looking out for my family while in Madagascar. The numerous researchers and staff of the Wildlife Conservation Society Madagascar Program are the reason all these data and subsequent results are coming to light. Felix Ratelolahy is a fearless researcher and true friend. Vonjy Andrianjakarivelo, I am thankful for your extensive insight and impressive knowledge of the Masoala-Makira landscape and its diverse wildlife. To the remaining staff and researchers of WCS Madagascar your fingerprints are all over these vitally important results on the worlds least known and most threatened carnivores. Your tireless work to conserve Madagascar’s biodiversity is truly inspiring and does not go unnoticed.

I am truly thankful to Donah, Marka’Helin, and Wilson for their amazing work ethic and their fabulous sense of humor all those days and nights as we trekked through impenetrable rainforest and suffered through some of the hardest conditions imaginable. I am also thankful to the numerous Malagasy assistants that played a significant role in this project (C.B. Beandraina, B.A. Salofo, R.C. Christian, Didice, B. Papin, Rabeson, Tobey, Cressent, J. Fernando, and Sassid). I am grateful to each student who sacrificed their lives, their budgets, and their sanity to travel to Madagascar to assist on this project (Andi Evans, Toby Nowlan, Kat Miles, Hunter Doughty, Kate Galbreath, Chelsea Miller, Joe Larson, and Hanna Davis) Further, without the countless Virginia Tech undergraduate volunteers who helped enter the plethora of photos and ID carnivores I would have been here another 10 years. I am thankful for the opportunity to collaborate with Chris Golden and his well-qualified team, as well as with Brian Gerber.

I would like to acknowledge my numerous funders including: Cleveland Metroparks Zoo, European Association for Zoos and Aquariums, Idea Wild, National Geographic Society-Waitts grant (#W96-10), Peoples Trust for Endangered Species, Virginia Tech Chapter of Sigma Xi, Virginia Tech McGinnis fellowship and Mosby fellowship, as well as logistical and financial support from the Wildlife Conservation Society Madagascar Program. In addition, I acknowledge the funders would supported the bushmeat surveys by Chris Golden and his team, including: Margot Marsh Biodiversity Fund (grant #023815), Mohammed bin Zayed Species Conservation Fund (grant #1025935), National Geographic Society Conservation Trust (grant #C135-08), National Science Foundation Doctoral Dissertation Improvement grant (#1011714) and Coupled Human Natural Systems grant (NSF-GEO 1115057).

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Attribution

A brief description of the contributions made by colleagues that assisted with the preparation of my thesis chapters is outlined below. Contributions rose to the level of co-author for manuscript publication for four of my chapters.

Chapter 2. Effects of hunting, exotic carnivores, habitat, and landscape features on carnivore occupancy across the Masoala-Makira landscape, Madagascar.

Christopher Golden (Harvard University & Wildlife Conservation Society HEAL Program) provided bushmeat survey data and assistance with analyses of these data. Sarah Karpanty and Marcella Kelly (Department of Fish & Wildlife Conservation, Virginia Tech) provided study design, financial, logistic, and statistical assistance and provided edits of the manuscript. Asia Murphy (Department of Fish & Wildlife Conservation, Virginia Tech) provided assistance on field work, contributed data, and provided edits of the manuscript. Dean Stauffer (Department of Fish & Wildlife Conservation, Virginia Tech) provided assistance with study design and edits to manuscript. Vonjy Andrianjakarivelo, Felix Ratelolahy, and Christopher Holmes (Wildlife Conservation Society Madagascar Program) provided assistance with data collection, study design, and edits to manuscript.

Chapter 3. When carnivores roam: Temporal patterns and partitioning among Madagascar's native and exotic carnivores.

Brian Gerber (Colorado Cooperative Fish and Wildlife Research Unit, Department of Fish, Wildlife, and Conservation Biology, Colorado State University) completed statistical analyses and modeling and provided edits to the manuscript. Marcella Kelly and Sarah Karpanty (Department of Fish & Wildlife Conservation, Virginia Tech) provided study design, financial, logistic, and statistical assistance and provided edits of the manuscript. Asia Murphy (Department of Fish & Wildlife Conservation, Virginia Tech) provided assistance on field work, contributed data, and provided edits of the manuscript. Vonjy Andrianjakarivelo (Wildlife Conservation Society Madagascar Program) provided assistance with data collection, study design, and edits to manuscript.

Chapter 4. Patterns of spatial co-occurrence among endemic and exotic carnivores, NE Madagascar.

Sarah Karpanty and Marcella Kelly (Department of Fish & Wildlife Conservation, Virginia Tech) provided study design, financial, logistic, and statistical assistance and provided edits of the manuscript. Vonjy Andrianjakarivelo, Felix Ratelolahy, and Christopher Holmes (Wildlife Conservation Society Madagascar Program) provided assistance with data collection, study design, and edits to manuscript.

Chapter 5. Predator-primate distribution, activity, and co-occurrence in relation to habitat and human activity across fragmented and contiguous forests in NE Madagascar.

Sarah Karpanty and Marcella Kelly (Department of Fish & Wildlife Conservation, Virginia Tech) provided study design, financial, logistic, and statistical assistance and provided edits of the manuscript. Felix Ratelolahy (Wildlife Conservation Society Madagascar Program) provided assistance with data collection, study design, and edits to manuscript.

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Chapter 1

RESPONSE OF MADAGASCAR'S ENDEMIC CARNIVORES TO FRAGMENTATION, HUNTING, AND EXOTIC CARNIVORES ACROSS THE MASOSALA-MAKIRA LANDSCAPE.

Introduction

Madagascar is consistently ranked as one of the top ten global biodiversity hotspots and a top conservation priority (Mittermeier et al. 2004). Of the unique wildlife in Madagascar, top carnivores are critically important as they may exert significant influence on ecosystem structure and serve as "umbrella species" due to their large home ranges (Gittleman et al. 2001, Noss 1990). Unfortunately, our current knowledge of Malagasy carnivores is poor, severely limiting efforts to conserve them or the diverse species that fall under their 'umbrella.' Due to anthropogenic disturbances, forest fragmentation is increasingly widespread and biodiversity loss continues to mount. Currently, only 10-20% of Madagascar remains forested and that which remains is increasingly threatened by logging and other threats related to ongoing political instability (Green and Sussman 1990, Harper et al. 2007), although recent internationally recognized elections in 2013 create hope that political stability may be returning. Studies investigating the effects of fragmentation on carnivores and their primary prey (lemurs) are lacking. Forest fragmentation reduces habitat quality (Harper et al. 2007), impedes gene flow (Craul et al. 2009), and even exacerbates predation events on lemurs (Irwin et al. 2009), thus studies investigating habitat fragmentation from a broad ecological standpoint are needed.

Madagascar's carnivores arguably are both the least studied and most threatened Family of Carnivora in the world (Brooke et al. 2014). Ten endemic (Eupleridae) and three exotic carnivore species have been identified across Madagascar (Goodman 2012). To date, a handful of studies have been conducted on the food habits (Dollar 2006, Goodman et al. 1997, Hawkins and Racey 2008, Rasoloarison et al. 1995, Wright et al. 1997), activity patterns (Dollar 1999, Hawkins 1998, Wright et al. 1997), and population density (Gerber et al. 2012b, Hawkins 1998) of the largest endemic carnivore, the fosa (*Cryptoprocta ferox*). Most of these studies come from western deciduous forest. There has been little data collected concerning fosa population density, sex ratio, activity patterns, and home range within eastern rainforest habitat where the most dramatic rates of deforestation are occurring. Fosa, currently classified by IUCN as Vulnerable (Schipper[1] et al. 2008), live in low population densities throughout Madagascar, with an estimated 0.26 individuals per km^2 in deciduous forest (Hawkins 2003, Hawkins 1998) and 0.17 per km^2 in eastern rainforest (Gerber et al. 2012b). Studies in the eastern rainforests of Ranomafana National Park indicate not only low densities of this top predator within the protected area, but also a complete absence of fosa from fragmented forest areas < 25 km from the park (Gerber et al. 2012b). However, a recent camera-trapping study in rainforest fragments < 2.5 km from contiguous forest did find one individual fosa indicating some use of fragments is possible but that distance to contiguous forest may be important (Gerber et al. 2012b). Further, fosa has recently been confirmed at the Kinjavato area in south-eastern Madagascar which is located > 25 km from contiguous forests (Steig Johnson, personal communication). Similarly, interviews of villagers living 0-20 km from the border of Ranomafana National Park demonstrated that fosa are observed outside of protected areas, but never > 6.1 km from the park boundary (Kotschwar et al. 2014). As a result of these low population densities and preliminary work indicating a negative relationship between fosa presence and both fragmentation and distance to protected areas, fosa may be the most vulnerable of all carnivores to the current ecological changes in Madagascar (Hawkins 2003).

As the largest extant carnivore in Madagascar, the fosa plays a wide-ranging role in this ecosystem as a significant lemur predator. Currently, there is strong evidence that fosa impacts both lemur behavior and population dynamics in forests across Madagascar, particularly in rainforest habitat (Irwin et al. 2009, Karpanty and Wright 2007, Wright et al. 1997). As fosa and lemurs are increasingly forced into isolated fragments of forest, natural or exacerbated predation rates by fosa may negatively impact lemur populations which are simultaneously being limited by declining habitat quality and human encroachment. For example, Irwin et al. (2009) showed how fosa killed an entire group of diademed sifakas (*Propithecus diadema*) at the Tsinjoarivo forest, extirpating this species from a forest fragment. In addition to elucidating the ecology of the carnivore community, my study investigated how the dynamics of fosa -lemur interactions may change across fragmented and non-fragmented forests.

Madagascar’s co-occurring native carnivores are even less studied than fosa and many questions surrounding their natural history, range, and behavior remain unanswered. Gerber et al. (2012) provided the first assessment of Madagascar’s carnivore community to date, including how forest logging and fragmentation influence native carnivore occupancy and/or density. In addition, Gerber et al. (2010) provided the first estimate of exotic carnivore population parameters and highlighted an increase in exotic species as fragmentation increases. Their work also brought attention to the negative relationships among multiple native-exotic carnivore pairings. Little is known about the influence of exotic carnivores on Madagascar’s native wildlife, particularly the native carnivore community. Additional work is needed to understand how exotic carnivore populations respond to anthropogenic disturbance and how their presence influences native carnivore, lemur, bird, and small mammal populations.

The Masoala-Makira landscape represents one of the last remaining large tracts of primary rainforest (732,750ha) that is critical for the long-term conservation of Madagascar’s severely threatened flora and fauna (Golden 2009, Kremen 2003). This area is a top conservation priority as it contains the highest levels of biodiversity in all of Madagascar, including 6 of 10 endemic carnivores (Farris et al. 2012, Goodman 2012). Further, these forests also protect regional watersheds providing water to more than 100,000 people (Holmes 2007). Recent studies within this region have highlighted strong human-wildlife conflicts, including human encroachment of forest habitat, predation of chickens and ducks, and extensive use of carnivores, lemurs, and small-mammals as bushmeat (Golden 2009). Despite this widespread, unsustainable hunting of carnivores and lemurs across the landscape we have no knowledge of how these carnivore and lemur populations are responding to this increasing human pressure. Additionally, due to the recent political turmoil in Madagascar, an increase in illegal and now government-sanctioned logging has been reported for regions of Masoala (Butler 2010). The effects of these ongoing and new disturbances on carnivores, lemurs, and other wildlife are not known and need investigation.

Goals and Objectives:

My ultimate goal was to address gaps in our understanding of carnivore ecology, as identified above, and to quantify the impacts of forest fragmentation, human encroachment, exotic species, and hunting on carnivores, thereby aiding in conservation of this complex, diverse ecosystem. The following four chapters of my dissertation include detailed objectives, each designed to address this goal:

I. Effects of hunting, exotic carnivores, habitat, and landscape features on carnivore occupancy across the Masoala-Makira landscape, Madagascar.

Submitted for publication to PlosOne November 2014.
Authors: Farris Z.J., Golden C., Karpanty S., Murphy, A., Stauffer D., Andrianjakarivelo V., Ratelolahy F., Holmes C , and Kelly M.J

Objectives:

1. Photographically sample wildlife across seven sites with varying levels of degradation, and thus varying levels of fragmentation, exotic species, human presence, and hunting.
2. Estimate occupancy and detection for six endemic and three exotic carnivore species at the individual sites, and across the landscape.
3. Identify the covariates (station-level habitat and landscape features, co-occurring endemic and exotic carnivore species, prey species, and human presence) that have the greatest influence on endemic and exotic carnivore occupancy.
4. Investigate the effects of hunting pressures (total consumption, trapping, purchasing, and hunting with dogs) on carnivore occupancy and detection at four study sites in the landscape.

II. When carnivores roam: Temporal patterns and partitioning among Madagascar's native and exotic carnivores.

Submitted for publication to Journal of Zoology September 2014.
Authors: Farris Z.J., Gerber B., Kelly M.J., Karpanty S., Murphy, F., and Andrianjakarivelo V.

Objectives:

1. Quantify the temporal activity patterns (day, dawn, dusk, and night) for Madagascar's six native and three exotic carnivores across the landscape.
2. Investigate the impact of season and site on native and exotic carnivore activity patterns within the complete diel cycle.
3. Investigate overlap of temporal activity within the diel cycle among all carnivore pairings to assess the effect of body size and ecological niche.

III. Patterns of spatial co-occurrence among endemic and exotic carnivores, NE Madagascar.

To be submitted to Biological Conservation December 2014.
Authors: Farris Z.J., Kelly M., Karpanty S., Ratelolahy F., and Holmes C.

Objectives:

1. Photographically sample carnivores across a diverse rainforest landscape and estimate the co-occurrence and/or co-detection among all native (fosa *Cryptoprocta ferox*, falanouc *Eupleres goudotii*, spotted fanaloka *Fossa fossana*, ring-tail vontsira *Galidia elegans*, broad-stripe vontsira *Galidictis fasciata*, and brown-tail vontsira *Salanoia concolor*) and exotic (domestic dog *Canis familiaris*, feral cat *Felis species*, and Indian civet *Viverricula indica*) carnivore pairings having sufficient captures for model convergence.

2. Investigate the influence of station-level habitat and landscape variables, prey species, and human presence on the co-occurrence and co-detection among native-exotic carnivore pairings by incorporating these variables as covariates in my two-species occupancy models.

IV. Predator-primate distribution, activity, and co-occurrence in relation to habitat and human activity across fragmented and contiguous forests in NE Madagascar.

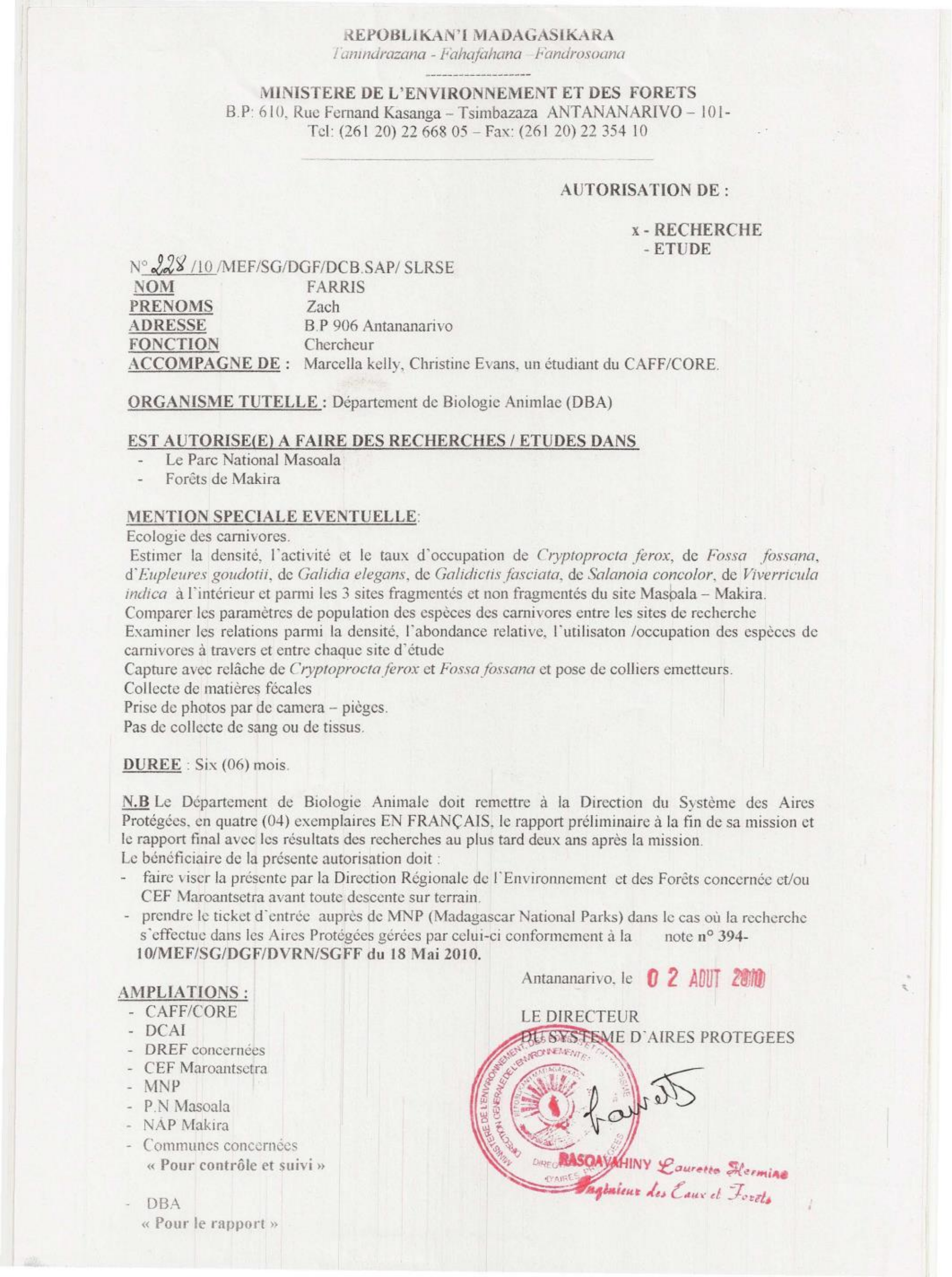
Published in International Journal of Primatology (Farris et al. 2014).
Authors: Farris Z.J., Karpanty S., Ratelolahy F., and Kelly M.J.

Objectives:

1. Compare the relative activity of Madagascar’s native and exotic carnivores and lemurs across contiguous and fragmented forests.
2. Estimate the probability of occupancy and detection for native and exotic carnivores and lemurs across the landscape.
3. Estimate predator-primate and human-primate co-occurrence across the landscape.
4. Assess which landscape and station-level habitat variables influence occupancy, detection, and co-occurrence for predators, humans, and lemurs across both contiguous and fragmented forest.

Appendices

Appendix A. Research permit issued by the Government of Madagascar granting permission to conduct photographic and line-transect sampling across the Masoala-Makira landscape for first field season (2010-2011).



REPOBLIKAN'I MADAGASIKARA
Tanindrazana - Fahafahana - Fandrosoana

MINISTERE DE L'ENVIRONNEMENT ET DES FORETS
B.P: 610, Rue Fernand Kasanga – Tsimbazaza ANTANANARIVO – 101-
Tel: (261 20) 22 668 05 – Fax: (261 20) 22 354 10

AUTORISATION DE :

x - RECHERCHE
- ETUDE

N° 228 /10 /MEF/SG/DGF/DCB.SAP/ SLRSE
NOM FARRIS
PRENOMS Zach
ADRESSE B.P 906 Antananarivo
FONCTION Chercheur
ACCOMPAGNE DE : Marcella kelly, Christine Evans, un étudiant du CAFF/CORE.

ORGANISME TUTELLE : Département de Biologie Animlae (DBA)

EST AUTORISE(E) A FAIRE DES RECHERCHES / ETUDES DANS

- Le Parc National Masoala
- Forêts de Makira

MENTION SPECIALE EVENTUELLE:

Ecologie des carnivores.
Estimer la densité, l'activité et le taux d'occupation de *Cryptoprocta ferox*, de *Fossa fossana*, d'*Eupleures goudotii*, de *Galidia elegans*, de *Galidictis fasciata*, de *Salanoia concolor*, de *Viverricula indica* à l'intérieur et parmi les 3 sites fragmentés et non fragmentés du site Masoala – Makira.
Comparer les paramètres de population des espèces des carnivores entre les sites de recherche
Examiner les relations parmi la densité, l'abondance relative, l'utilisaton /occupation des espèces de carnivores à travers et entre chaque site d'étude
Capture avec relâche de *Cryptoprocta ferox* et *Fossa fossana* et pose de colliers emetteurs.
Collecte de matières fécales
Prise de photos par de camera – pièges.
Pas de collecte de sang ou de tissus.

DUREE : Six (06) mois.

N.B Le Département de Biologie Animale doit remettre à la Direction du Système des Aires Protégées, en quatre (04) exemplaires EN FRANÇAIS, le rapport préliminaire à la fin de sa mission et le rapport final avec les résultats des recherches au plus tard deux ans après la mission.

Le bénéficiaire de la présente autorisation doit :

- faire viser la présente par la Direction Régionale de l'Environnement et des Forêts concernée et/ou CEF Maroantsetra avant toute descente sur terrain.
- prendre le ticket d'entrée auprès de MNP (Madagascar National Parks) dans le cas où la recherche s'effectue dans les Aires Protégées gérées par celui-ci conformement à la note **n° 394-10/MEF/SG/DGF/DVRN/SGFF du 18 Mai 2010.**

Antananarivo, le 02 AOUT 2010

LE DIRECTEUR
DU SYSTEME D'AIRES PROTEGEES

RASOAVAHINY Laurette Hermine
Ingénieur des Eaux et Forêts

AMPLIATIONS :

- CAFF/CORE
- DCAI
- DREF concernées
- CEF Maroantsetra
- MNP
- P.N Masoala
- NAP Makira
- Communes concernées
  « Pour contrôle et suivi »

- DBA
  « Pour le rapport »

Appendix B. Research permit issued by the Government of Madagascar granting permission to conduct photographic and line-transect sampling across the Masoala-Makira landscape for second field season (2011-2012).

REPOBLIKAN'I MADAGASIKARA
Fitiavana-Tanindrazana–Fandrosoana

SECRETARIAT GENERAL

DIRECTION GENERALE DES FORETS

DIRECTION DE LA CONSERVATION
DE LA BIODIVERSITE ET DU SYSTEME
DES AIRES PROTEGEES

AUTORISATION DE :
x- RECHERCHE
- ETUDE

N° 128 /12/MEF/SG/DGF/DCB.SAP/ SCB
(Renouvellement de l'Aut N° 128/11 du 20/05/2011)

NOM	FARRIS
PRENOMS	Zach
ADRESSE	B.P 906 Antananarivo
FONCTION	Chercheur
ACCOMPAGNE DE :	Marcella Kelly, Christopher Holmes, Charles Beandraina, un représentant du CAFF/CORE

ORGANISME TUTELLE : Département de Biologie Animale (DBA)
EST AUTORISE(E) A FAIRE DES RECHERCHES / ETUDES DANS
P.N Masoala et les Forêts de Makira.
MENTION SPECIALE EVENTUELLE:
Ecologie des carnivores.
Estimer la densité, l'activité et le taux d'occupation de *Cryptoprocta ferox*, de *Fossa fossana*, d'*Eupleures goudotii*, de *Galidia elegans*, de *Galidictis fasciata*, de *Salanoia concolor*, de *Viverricula indica* à l'intérieur et parmi les 3 sites fragmentés et non fragmentés du site Masoala.
Comparer les paramètres de population des espèces des carnivores entre les sites de recherche
Examiner les relations parmi la densité, l'abondance relative, l'utilisation /occupation des espèces de carnivores à travers et entre chaque site d'étude
Capture avec relâche d'au maximum 5 individus par espèce de *Cryptoprocta ferox*, *Fossa fossana et d'autres carnivores* après prélèvement d'échantillons de sang de 1,5ml par individu, de tissu et pose de colliers émetteurs.
Collecte de matières fécales
Prise de photos par de camera – pièges.

DUREE : Six (06) mois.

N.B Le Département de Biologie Animale doit remettre à la Direction du Système des Aires Protégées, en quatre (04) exemplaires EN FRANÇAIS, le rapport préliminaire à la fin de sa mission et le rapport final avec les résultats des recherches au plus tard deux ans après la mission.
Le bénéficiaire de la présente autorisation doit :

- faire viser la présente par la Direction Régionale de l'Environnement et des Forêts Analanjirofo
- et/ou CEF Maroantsetra
  avant toute descente sur terrain, conformement à la note
  n° 394- 10/MEF/SG/DGF/DVRN/SGFF du 18 Mai 2010.
- prendre le ticket d'entrée auprès de MNP (Madagascar National Parks) dans le cas où la recherche s'effectue dans les Aires Protégées gérées par celui-ci.

AMPLIATIONS :
-CAFF/CORE
-DCAI
-DREF Analanjirofo
-CEF Maroantsetra
-MNP
-P.N Masoala
-Communes concernées
« Pour contrôle et suivi »
- DBA
« Pour le rapport »

Antananarivo, le 08 MAI 2012

LE DIRECTEUR DE LA CONSERVATION DE
LA BIODIVERSITE ET DU SYSTEME DES
AIRES PROTEGEES

RASOVAHINY *Laurette Hortense*
Ingénieur des Eaux et Forêts

Appendix C. Research permit issued by the Government of Madagascar granting permission to conduct photographic and line-transect sampling across the Masoala-Makira landscape for third field season (2012-2013).

REPOBLIKAN'I MADAGASIKARA
Fitiavana-Tanindrazana–Fandrosoana

SECRETARIAT GENERAL

DIRECTION GENERALE DES FORETS

DIRECTION DE LA CONSERVATION DE LA BIODIVERSITE ET DU SYSTEME DES AIRES PROTEGEES

AUTORISATION DE :
x- RECHERCHE
- ETUDE

N° 123/12/MEF/SG/DGF/DCB.SAP/ SCB
(Renouvellement de l'Aut N° 128/12 du 08/05/2012)

NOM	MURPHY
PRENOMS	Asia
ADRESSE	B.P 906 Antananarivo
FONCTION	Chercheur

ACCOMPAGNE DE : Zach Farris, Marcella Kelly, Christopher Holmes, Safia Salimo, 05 étudiants volontaires américains, un représentant du CAFF/CORE.

ORGANISME TUTELLE : Département de Biologie Animale (DBA)

EST AUTORISE(E) A FAIRE DES RECHERCHES / ETUDES DANS :
P.N Masoala et les Forêts de Makira.

MENTION SPECIALE EVENTUELLE:
Ecologie des carnivores.
Estimer la densité, l'activité et le taux d'occupation de *Cryptoprocta ferox*, de *Fossa fossana*, d'*Eupleures goudotii*, de *Galidia elegans*, de *Galidictis fasciata*, de *Salanoia concolor*, de *Viverricula indica* à l'intérieur et parmi les 3 sites fragmentés et non fragmentés du site Masoala.
Comparer les paramètres de population des espèces des carnivores entre les sites de recherche
Examiner les relations parmi la densité, l'abondance relative, l'utilisation /occupation des espèces de carnivores à travers et entre chaque site d'étude. Estimer la densite et l'habitat des especes non carnivore aux sept sites.
Collecte de matières fécales
Prise de photos par de camera – pièges.
Etudes sur les lémuriens dans chaque site de caméra.

DUREE : Six (06) mois.

N.B Le Département de Biologie Animale doit remettre à la Direction du Système des Aires Protégées, en quatre (04) exemplaires EN FRANÇAIS, le rapport préliminaire à la fin de sa mission et le rapport final avec les résultats des recherches au plus tard deux ans après la mission.
Le bénéficiaire de la présente autorisation doit :

- faire viser la présente par la Direction Régionale de l'Environnement et des Forêts Analanjirofo
- et/ou CEF Maroantsetra
  avant toute descente sur terrain, conformement à la note
  n° 394- 10/MEF/SG/DGF/DVRN/SGFF du 18 Mai 2010.
- prendre le ticket d'entrée auprès de MNP (Madagascar National Parks) dans le cas où la recherche s'effectue dans les Aires Protégées gérées par celui-ci.

Antananarivo, le 28 MAI 2013

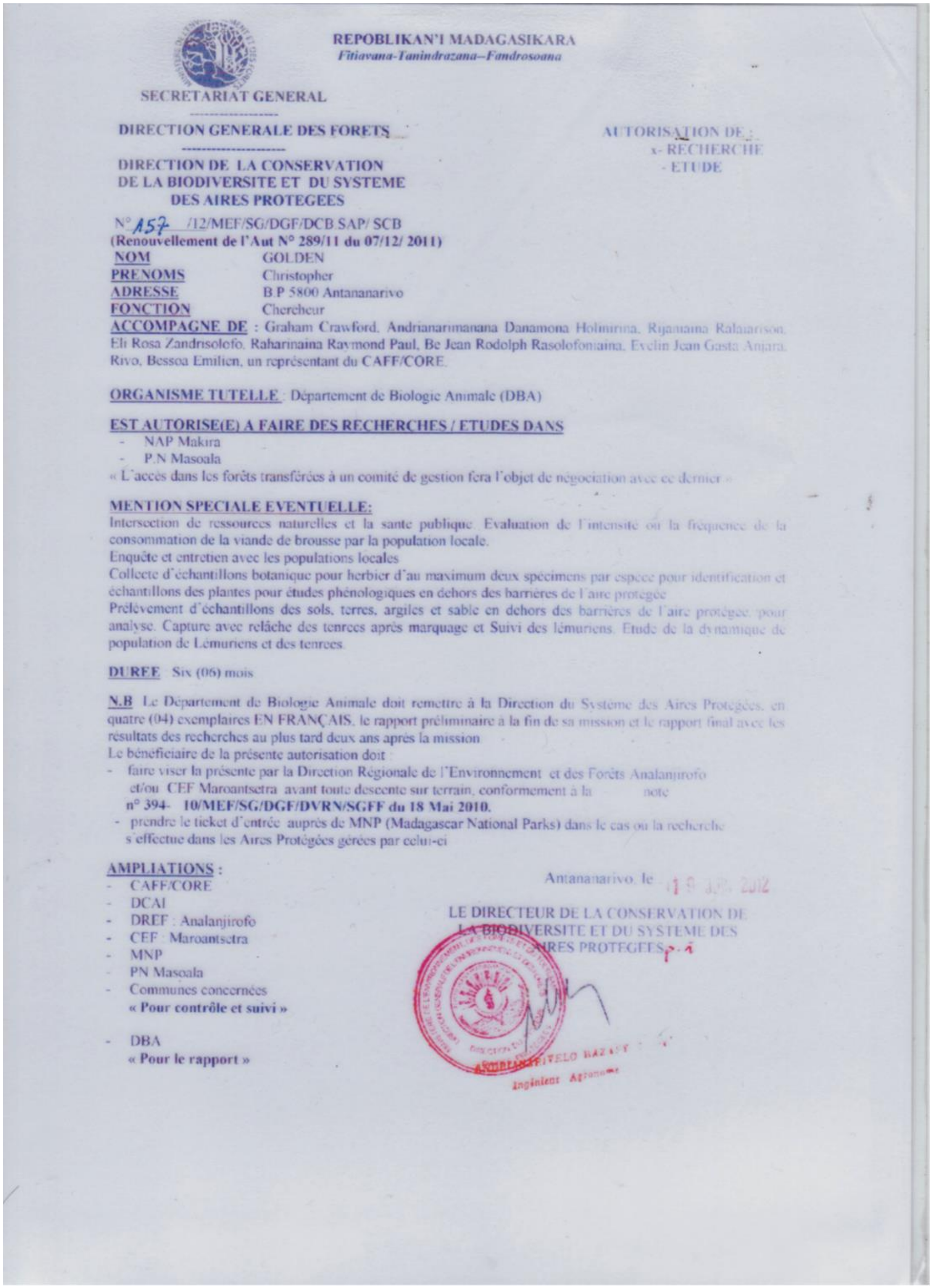
AMPLIATIONS :
-CAFF/CORE
-DCAI
-DREF Analanjirofo
-CEF Maroantsetra
-MNP
-P.N Masoala
-Communes concernées
« Pour contrôle et suivi »

- DBA
« Pour le rapport »

LE DIRECTEUR DE LA CONSERVATION DE LA BIODIVERSITE ET DU SYSTEME DES AIRES PROTEGEES

RASOAVAHINY Laurette Hermine
Ingénieur des Eaux et Forêts

Appendix D. Research permit issued by the Government of Madagascar granting Chris Golden permission to conduct bushmeat surveys across the Masoala-Makira landscape for first field season (2010-2011).



REPOBLIKAN'I MADAGASIKARA
Fitiavana-Tanindrazana–Fandrosoana

SECRETARIAT GENERAL

DIRECTION GENERALE DES FORETS

DIRECTION DE LA CONSERVATION
DE LA BIODIVERSITE ET DU SYSTEME
DES AIRES PROTEGEES

AUTORISATION DE :
x- RECHERCHE
- ETUDE

N° 157 /12/MEF/SG/DGF/DCB.SAP/ SCB
(Renouvellement de l'Aut N° 289/11 du 07/12/ 2011)

NOM	GOLDEN
PRENOMS	Christopher
ADRESSE	B.P 5800 Antananarivo
FONCTION	Chercheur

ACCOMPAGNE DE : Graham Crawford, Andrianarimanana Danamona Holinirina, Rijaniaina Ralaiarison, Eli Rosa Zandrisolofo, Raharinaina Raymond Paul, Be Jean Rodolph Rasolofoniaina, Evelin Jean Gasta Anjara, Rivo, Bessoa Emilien, un représentant du CAFF/CORE.

ORGANISME TUTELLE : Département de Biologie Animale (DBA)

EST AUTORISE(E) A FAIRE DES RECHERCHES / ETUDES DANS

- NAP Makira
- P.N Masoala

« L'accès dans les forêts transférées à un comité de gestion fera l'objet de négociation avec ce dernier »

MENTION SPECIALE EVENTUELLE:

Intersection de ressources naturelles et la sante publique. Evaluation de l'intensité ou la fréquence de la consommation de la viande de brousse par la population locale.

Enquête et entretien avec les populations locales

Collecte d'échantillons botanique pour herbier d'au maximum deux spécimens par espèce pour identification et échantillons des plantes pour études phénologiques en dehors des barrières de l'aire protégée

Prélèvement d'échantillons des sols, terres, argiles et sable en dehors des barrières de l'aire protégée, pour analyse. Capture avec relâche des tenrecs après marquage et Suivi des lémuriens. Etude de la dynamique de population de Lémuriens et des tenrecs.

DUREE Six (06) mois

N.B Le Département de Biologie Animale doit remettre à la Direction du Système des Aires Protégées, en quatre (04) exemplaires EN FRANÇAIS, le rapport préliminaire à la fin de sa mission et le rapport final avec les résultats des recherches au plus tard deux ans après la mission

Le bénéficiaire de la présente autorisation doit :

- faire viser la présente par la Direction Régionale de l'Environnement et des Forêts Analanjirofo et/ou CEF Maroantsetra avant toute descente sur terrain, conformement à la note **n° 394- 10/MEF/SG/DGF/DVRN/SGFF du 18 Mai 2010.**
- prendre le ticket d'entrée auprès de MNP (Madagascar National Parks) dans le cas où la recherche s'effectue dans les Aires Protégées gérées par celui-ci

AMPLIATIONS :

- CAFF/CORE
- DCAI
- DREF : Analanjirofo
- CEF : Maroantsetra
- MNP
- PN Masoala
- Communes concernées

« Pour contrôle et suivi »

- DBA

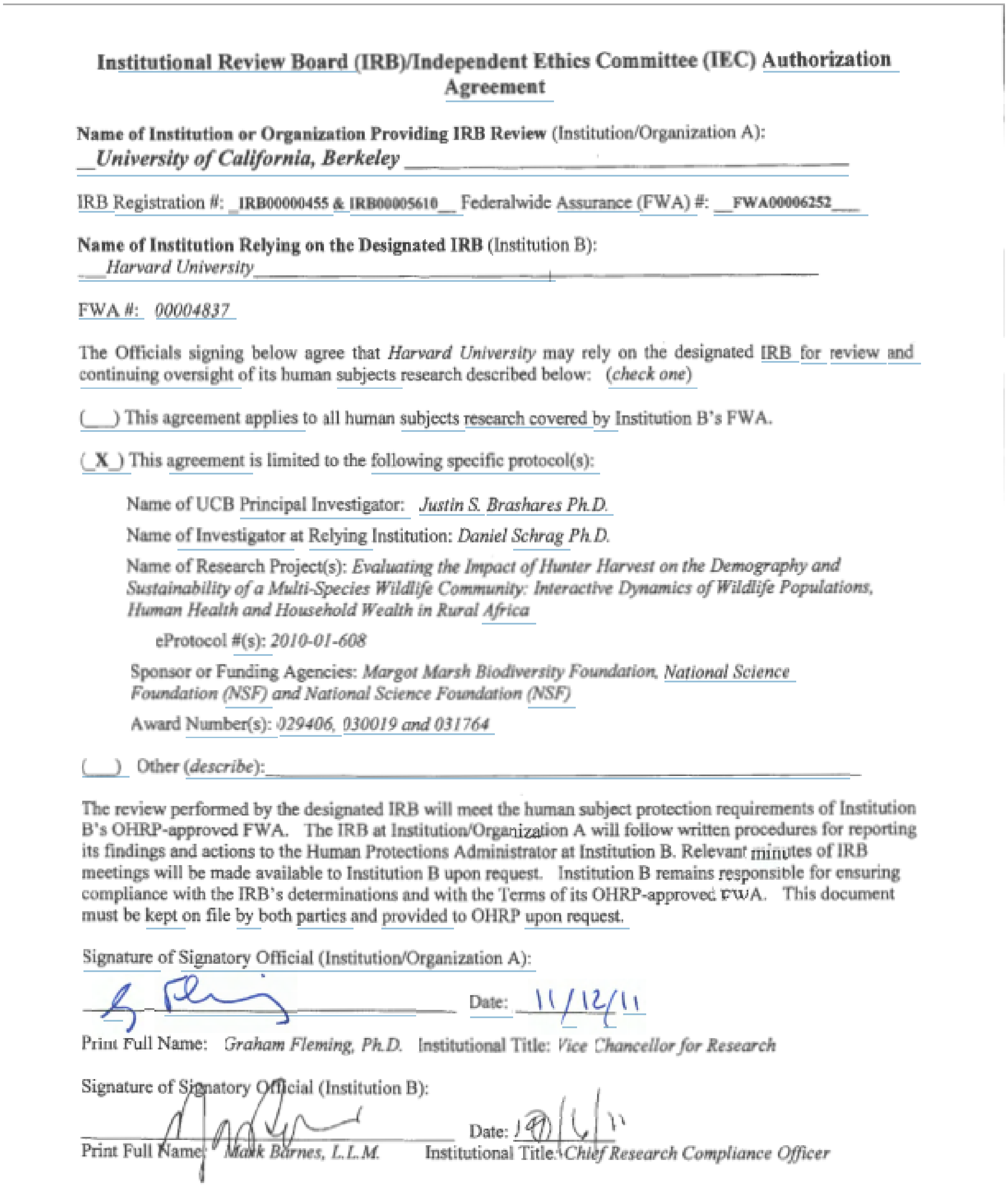
« Pour le rapport »

Antananarivo, le 19 JAN 2012

LE DIRECTEUR DE LA CONSERVATION DE LA BIODIVERSITE ET DU SYSTEME DES AIRES PROTEGEES p.i

[illegible]IVELO RAZAFY
Ingénieur Agronome

Appendix E. Copy of Institutional Review Board (IRB) approval granted by UC Berkeley for bushmeat surveys to be conducted across the Masoala-Makira landscape by Justin S. Brashares (adviser to Chris Golden, Harvard University) and his research team.



Institutional Review Board (IRB)/Independent Ethics Committee (IEC) Authorization Agreement

Name of Institution or Organization Providing IRB Review (Institution/Organization A):
__*University of California, Berkeley*________________________

IRB Registration #: _IRB00000455 & IRB00005610__ Federalwide Assurance (FWA) #: __FWA00006252___

Name of Institution Relying on the Designated IRB (Institution B):
___*Harvard University*________________________

FWA #: *00004837*

The Officials signing below agree that *Harvard University* may rely on the designated IRB for review and continuing oversight of its human subjects research described below: (*check one*)

(___) This agreement applies to all human subjects research covered by Institution B's FWA.

(_X_) This agreement is limited to the following specific protocol(s):

Name of UCB Principal Investigator: *Justin S. Brashares Ph.D.*

Name of Investigator at Relying Institution: *Daniel Schrag Ph.D.*

Name of Research Project(s): *Evaluating the Impact of Hunter Harvest on the Demography and Sustainability of a Multi-Species Wildlife Community: Interactive Dynamics of Wildlife Populations, Human Health and Household Wealth in Rural Africa*

eProtocol #(s): *2010-01-608*

Sponsor or Funding Agencies: *Margot Marsh Biodiversity Foundation, National Science Foundation (NSF) and National Science Foundation (NSF)*

Award Number(s): *029406, 030019 and 031764*

(___) Other (*describe*):________________________

The review performed by the designated IRB will meet the human subject protection requirements of Institution B's OHRP-approved FWA. The IRB at Institution/Organization A will follow written procedures for reporting its findings and actions to the Human Protections Administrator at Institution B. Relevant minutes of IRB meetings will be made available to Institution B upon request. Institution B remains responsible for ensuring compliance with the IRB's determinations and with the Terms of its OHRP-approved FWA. This document must be kept on file by both parties and provided to OHRP upon request.

Signature of Signatory Official (Institution/Organization A):

________________________ Date: 11/12/11

Print Full Name: *Graham Fleming, Ph.D.* Institutional Title: *Vice Chancellor for Research*

Signature of Signatory Official (Institution B):

________________________ Date: 12/6/11

Print Full Name: *Mark Barnes, L.L.M.* Institutional Title: *Chief Research Compliance Officer*

Appendix F. Copy of Virginia Tech Institutional Animal Care and Use Committee approval issued to Sarah Karpanty, co-adviser to Zach Farris and Asia Murphy who conducted field work for this research project.

Institutional Animal Care and Use Committee
North End Center, Suite 4120 (MC 0497) Blacksburg, Virginia 24061 540/231-2166 Fax 540/231-0959 e-mail iacuc@vt.edu Website: www.acc.vt.edu

MEMORANDUM

DATE: August 6, 2013

TO: Sarah Karpanty

FROM: Virginia Tech Institutional Animal Care and Use Committee

IACUC NUMBER: **13-100-FWC**

SUBJECT: Review of Research Protocol Involving Animals Entitled **“Carnivore and lemur ecology in Makira Natural Park, northeastern Madagascar”**

The purpose of this memo is to verify that, on **August 5, 2013**, the Virginia Tech Institutional Animal Care and Use Committee (IACUC) reviewed and granted approval of the above described Protocol submission.

Period of Protocol Approval

This Research Protocol is approved for the following period, from **August 5, 2013** to **August 4, 2016**. All protocols must undergo continuing review on an annual basis for as long as the protocol is active, even if the protocol is only active for a portion of the first year after approval. The principal investigator must submit an annual continuing review form when notified by the IACUC Office.

If the research proposed under this protocol will continue to be conducted after the end of the three-year approval period, a new protocol must be submitted and approved prior to the three-year anniversary of the original approval date if uninterrupted work is desired to continue. The principal investigator is responsible for submitting all paperwork required to maintain IACUC approval.

Changes to Approved Protocols

Any changes in study personnel, animal numbers, species, procedures/treatments, or any other minor or significant change to your protocol must be submitted to the IACUC for review and approval before those changes are implemented. Failure to seek IACUC approval for amending approved protocol procedures may result in withdrawal of permission to conduct the research.

PI Responsibility for Adequate Staff Training

Federal laws and regulations require that research staff have the requisite training for humane care and use of animals, and are aware of risks inherent in handling of animals and their tissues. As the principal investigator, you are responsible for ensuring that your staff have sufficient training and expertise with the technical procedures that they are listed as performing in the protocol. You are required to ensure that they are proficient in the procedures, and will, as necessary, provide additional training to ensure their competency when performing the procedures. You are also responsible for identifying needed PPE (Personal protective Equipment) and ensuring its proper use by your staff, and, as appropriate, directing staff to EHS for additional training and monitoring.

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Chapter 2

EFFECTS OF HUNTING, EXOTIC CARNIVORES, HABITAT, AND LANDSCAPE FEATURES ON CARNIVORE OCCUPANCY ACROSS THE MASOALA-MAKIRA LANDSCAPE, MADAGASCAR

Abstract

The carnivores of Madagascar are likely the least studied of the world's carnivores, thus little is known about threats to their persistence. I provided the first investigation, via photographic sampling, of how multiple forms of habitat degradation (fragmentation, exotic carnivores, human encroachment, and hunting) affect carnivore occupancy across Madagascar's largest protected area: the Masoala-Makira landscape. I found that as degradation increased, exotic carnivores showed increases in activity and occupancy while endemic carnivore, small mammal, and lemur occupancy and/or activity decreased. Wild/feral cats (*Felis species*) and dogs (*Canis familiaris*) had higher occupancy than half of the endemic carnivore species across the landscape. Bird and small mammal activity were negatively associated with exotic carnivore occupancy, but positively associated with the occupancy of four endemic carnivore species. Spotted fanaloka (*Fossa fossana*) occupancy was constrained by the presence of wild/feral cats and Indian civet (*Viverricula indica*), both introduced carnivores. Hunting was intense across the four study sites surveyed with the highest rates for Indian civet ($\bar{x} = 90$ individuals consumed/year), ring-tailed vontsira (*Galidia elegans*) ($\bar{x} = 58$ consumed/year), and fosa (*Cryptoprocta ferox*) ($\bar{x} = 31$ consumed/year). My modeling results suggest that hunters target intact forest where carnivore occupancy, as well as lemur activity, abundance, and species richness, are highest. These various anthropogenic pressures and their effects on

carnivore and lemur populations, particularly increases in exotic carnivores and hunting, have wide-ranging, global implications and demand effective management plans to target the influx of exotic carnivores and unsustainable hunting affecting carnivore and primate populations across Madagascar and worldwide.

Introduction

Madagascar has received much conservation attention over the last decade as a result of its high levels of biodiversity and endemism, as well as the increasing anthropogenic pressures threatening it (Brooks et al. 2006, Goodman and Benstead 2005, Harper et al. 2007, Kremen et al. 2008, Rakotomanana et al. 2013). On-going trends in forest loss, degradation, and fragmentation pose serious threats to the endemic wildlife of Madagascar (Allnutt et al. 2008, Ganzhorn et al. 2001, Harper et al. 2007, Irwin et al. 2010). In addition, recent research in Madagascar has highlighted the growing threats to wildlife resulting from an influx of exotic species (Brockman et al. 2008, Farris et al. 2012, Farris et al. 2014, Farris and Kelly 2011, Gerber 2011, Gerber et al. 2012a, b, Goodman 2012, Kolby 2014) and from unsustainable hunting rates (Barrett and Ratsimbazafy 2009, Golden 2009, Gardner and Davies 2014, Golden et al. 2014, Kotschwar et al. 2014). These various anthropogenic pressures have been shown to negatively affect a number of species of carnivores (Farris et al. 2012, Farris and Kelly 2011, Gerber 2011, Gerber et al. 2012b, Golden 2009, Golden et al. 2014) and lemurs (Brockman et al. 2008, Dehgan 2003, Farris et al. 2014, Ganzhorn et al. 1997, Godfrey and Irwin 2007, Golden 2009, Golden et al. 2014, Irwin et al. 2010, Schwitzer 2011). Our knowledge, however, of how Madagascar's endemic wildlife is responding to increases in specific types of anthropogenic pressures remains limited, particularly for Madagascar's rainforest carnivores about which we know very little.

Carnivores may be under greater threat from habitat loss, fragmentation, exotic species, and hunting compared to co-occurring taxa because of their more extinction-prone characteristics such as large body size, wide ranging behavior, low density, low recruitment, and specialized diet (Brooks et al. 2006, Carbone et al. 2011, Cardillo et al. 2008, Cardillo et al. 2005, Forero-Medina et al. 2009, Gittleman et al. 2001). Carnivore populations worldwide have been shown to be negatively affected by forest loss and fragmentation (Crooks 2002, Crooks et al. 2011, Gerber et al. 2012b, Michalski and Peres 2005, Mudappa et al. 2007, Ryall and Fahrig 2006), the presence of exotic species (Gerber et al. 2012a, Roemer et al. 2002, Vanak and Gompper 2009, Young et al. 2011), and hunting (Becker et al. 2013, Fa and Brown 2009, Fa et al. 2002, Golden 2009, Golden et al. 2014, Goodrich et al. 2008). While these studies provide important insight into the effects of anthropogenic pressures, we need a better understanding of how these pressures act collectively on carnivore populations over a gradient of disturbance across a large spatial area.

My goal was to provide the first investigation of how multiple forms of anthropogenic pressure, which cumulatively result in habitat degradation, affect carnivore population parameters across Madagascar's largest protected area complex: the Masoala-Makira landscape. I focused on both endemic carnivores (fosa *Cryptoprocta ferox*, spotted fanaloka *Fossa fossana*, falanouc *Eupleres goudotii*, ring-tailed vontsira *Galidia elegans*, broad-striped vontsira *Galidictis fasciata*, and brown-tailed vontsira *Salanoia concolor*) and exotic carnivores (domestic dog *Canis familiaris*, wild/feral cat *Felis species*, and Indian civet *Viverricula indica*). My specific objectives were to: 1) photographically sample wildlife across seven sites with varying levels of degradation; 2) estimate occupancy and detection for six endemic and three exotic carnivore species at the individual sites, and across the landscape; 3) identify the covariates (station-level habitat and landscape features, co-occurring endemic and exotic carnivore species, prey species, and human presence) that have the greatest influence on endemic and exotic carnivore occupancy; and 4) investigate the effects of hunting pressures (total consumption, trapping, purchasing, and hunting with dogs) on carnivore occupancy and detection at four study sites in the landscape.

Methods

Study sites

The Makira Natural Park, recently established in 2013, (hereafter Makira) is Madagascar's largest protected area with 372,470 ha of protected area and 351,037 ha of community management zone (Holmes 2007). Madagascar's second largest protected area, Masoala National Park (hereafter Masoala), contains 240,000 ha in protected forest and borders Makira NP to the south-west (Kremen et al. 2008). This Masoala-Makira protected landscape (Figure 1), is the largest contiguous forest and is estimated to have the highest levels of biodiversity in Madagascar, including at least 22 species of lemurs and six species of endemic carnivores (Farris et al. 2012, Garbutt 2007, Holmes 2007). Despite its expansive size and high level of biodiversity, the Masoala-Makira landscape faces numerous anthropogenic pressures common to Madagascar's forests, such as hunting (Golden 2009, Golden et al. 2014), habitat degradation and fragmentation (Holmes 2007, Kremen 2003, Kremen et al. 1999), and an influx of exotic species (Farris et al. 2012, Farris et al. 2014). Across the Masoala-Makira landscape I selected seven study sites with varying levels of degradation (Figure 1; Table 1). I sampled sites within the Makira protected area (n = 4), within a fragmented reserve near Masoala (n = 1), outside the protected area near Makira (n = 1) and near the Masoala-Makira corridor (n = 1; Figure 1).

Photographic Sampling

From 2008 to 2012 I established camera grids, consisting of 18-25 camera stations per grid, at each of the seven study sites across the Masoala-Makira landscape (Figure 1). I surveyed each of the seven study sites an average of 67 days (Table 2). Within each of the seven grids, I spaced camera stations consisting of two digital (Reconyx PC85 & HC500, Wisconsin, USA; Moultrie D50 & D55, Alabama, USA; Cuddeback IR, Wisconsin, USA) and/or film-loaded (DeerCam DC300) remote sensing cameras, approximately 500 m apart. I placed cameras on opposing sides of human (0.5-2.0 m wide) and game (< 0.5 m wide) trails (establishing newly cut trails was avoided whenever possible) to capture both flanks of passing wildlife. Cameras were offset to prevent mutual flash interference and were paired with an opposing brand or model of camera to compensate for inefficiency in detection speed, flash, or photo quality of various camera models. I checked cameras every 5-10 days to change batteries, memory cards and/or film, and to ensure proper functioning. I placed cameras 20-30 cm off the ground, allowed them to run for 24 h each day, and used no bait or lure.

Sampling Metrics of Degradation and/or Anthropogenic Pressure

Station-Level Habitat and Landscape Sampling

To measure station-level habitat features (Table 1) for use in occupancy models, I sampled vegetation at each camera station by walking a 50 m transect in three directions (0, 120, and 240 degrees) starting at each individual camera station. I estimated canopy height at 5-10 m intervals and percent cover at 10 m intervals along each transect. At 25 m and 50 m on each transect I used the point-quarter method (Pollard 1971) to estimate tree density and basal area, recording DBH and distance to the nearest tree ≥ 5 cm DBH in each quarter. At 20 m and 40 m I established a 20 m transect running perpendicular to the established 50 m station-level habitat transect and I measured understory cover at three levels (0-0.5 m, 0.5-1.0 m, and 1.0-2.0 m) by holding a 2 m pole perpendicular to the ground at one meter intervals and recording presence (1 = vegetation touching pole) or absence (0 = no vegetation touching pole) of understory cover (Davis et al. 2011). I used this sampling array, including the sampling distances, to provide station-level habitat sampling covariates for Madagascar’s small-bodied endemic carnivores for use in my landscape and site-specific occupancy models.

To understand how landscape features varied by site and how they influence carnivore population parameters, I used Landsat satellite imagery (2004, 2006, and 2009) and classified the following cover types using Erdas Imagine (Intergraph Corporation): rainforest (intact forest with little to no logging present), degraded forest (forest exhibiting disturbance from forest loss, logging, and fragmentation), and matrix (non-forest area exhibiting early succession, cultivation, or open fields for cattle). I placed a 500 m (landscape level) buffer around individual camera stations, I dissolved these individual buffers, and clipped the classified imagery for each of the resulting seven camera grid buffers (each providing an approximately 10 – 15 km^2 area) for analysis in program FragStats [University of Massachusetts, USA] (McGarigal et al. 2012). For fosa I placed a 2000 m buffer around individual camera stations, rather than the initial 500 m buffer, to extract more meaningful, species-specific landscape covariates given the estimated home range of this larger carnivore (Hawkins and Racey 2005).

Using program FragStats and the clipped imagery from each camera grid buffer (~10-15 km^2, except for fosa which was ~13-18 km^2), I created the following landscape level covariates (Table 1) for use in my occupancy models: 1) number of patches: total number of rainforest, degraded forest, and matrix patches (based on habitat classifications from satellite imagery) within the buffer; 2) largest patch index with an edge buffer of 50 m: the percentage of total buffered area composed by the largest rainforest patch; 3) LSI: landscape shape index or the standardized measure of total edge adjusted for the size of the buffered area (McGarigal et al. 2012); 4) percent rainforest within the buffered area; 5) percent matrix or non-forest, cultivated area within the buffered area; 6) total rainforest core area: the sum of the core areas (accounting for 500m edge depth) of each rainforest patch within the buffer; and 7) edge index (in meters per hectare); (McGarigal et al. 2012). Further, I estimated an average distance of each camera station to the nearest forest edge (Avg. Dist. to Edge) and to the nearest village (Avg. Dist to Village; Table 1) using the measuring tool in ArcGIS, as well as Google Earth to validate my estimates.

I quantified levels of degradation (excluding hunting rates) and, using a principle components analysis (PCA) maximum likelihood estimation method, I ranked the seven study sites from least to most degraded based on the Eigen vectors and resulting bi-plot generated from the list of habitat and landscape features measured for this study (Appendix A). To reduce multicollinearity for my occupancy modeling, I examined correlations among individual variables within my metrics of degradation and eliminated variables that were highly correlated ($|r| > 0.7$). To protect the identities of local villages due to the sensitivity of my hunting data and as required by our human subjects protocols, I labelled sites based on their level of degradation (01 = least degraded; 07 = most degraded), rather than using the village or forest names.

Co-Occurring Species Activity

I defined a ‘capture event’ as all photographs of a given species within a 30 min time period (Di Bitetti et al. 2006). To provide a measure of activity for endemic and exotic carnivores, zebu, bush pigs, small mammals, birds, and humans for comparison across study sites (camera grids) and for use in my occupancy models, I calculated the trap success (TS) for each species by dividing the number of capture events by the number of trap nights at each camera station, minus malfunctions, and multiplied by 100. I defined a trap night as a 24 h period in which at least one of the two cameras at a camera station is functioning properly and is meant to represent animal activity at the station.

To investigate the relationship of lemur prey to carnivore occupancy and to compare lemur species richness and abundance across sites I established three, two kilometer long transects within the camera grid and surveyed each transect five to six times diurnally during the hours of 07:00 to 11:00 and five to six times nocturnally during the hours of 18:00 to 23:00. For each lemur observed I recorded the species, compass direction, distance to observed lemur, height from the ground, number of individuals within the group, and behavior of the individual or group. I calculated an index of lemur abundance (# / km) for each camera grid by dividing the number of lemur observations, where lemur groups were counted as a single observation, by the total number of kilometers surveyed both diurnally and nocturnally.

Hunting rates

From 2005 to 2011, Christopher Golden (Harvard University, Wildlife Conservation Society HEAL) and his team surveyed 417 households in 26 villages across

Makira and 224 households in 13 villages across Masoala to estimate annual household consumption rates of bushmeat (Golden 2009, Golden et al. 2014, Golden et al. 2011). Survey teams made repeat visits to villages and re-surveyed households over the six year period (mean = 1 visit/year for 3 years). For my analyses, I used hunting data for carnivores, where available, from villages bordering my study sites. This provided us with hunting data for seven carnivore species (fosa, spotted fanaloka, falanouc, ring-tail vontsira, broad-striped vontsira, wild/feral cat, and Indian civet) from four of my seven study sites (S01, S02, S03, S06). I used the bushmeat data set to estimate the total number of individual animals consumed per village per year for each of the seven carnivore species. I totaled the number consumed for each carnivore species then divided by the number of years the household was surveyed to get the average number consumed each year for each village. In addition, I included the following sub-categories that contributed to the total consumption: 1) the number of individuals trapped per year; 2) the number of individuals purchased per year; and 3) the number of individuals hunted with domestic dogs. It is very likely that all purchased animals, a very small proportion of total consumption, are sold in the community in which they are harvested (Golden et al. 2014). Therefore, it is appropriate to include purchased species as a variable that could affect the local stock of a given species and variation in the number of purchased species indicates a village-level preference for a particular species (a potential proxy for intensity of pressure or targeting). Further, while total consumption may be consistent for a given carnivore species across multiple sites, the way in which the carnivore was obtained (i.e. trapping and hunting with dogs) may vary across these sites and thus provide a different relationship with carnivore occupancy and/or detection across sites. As a result, I used total consumption, as well as the other three sub-categories of total consumption for my analyses. To reduce multicollinearity, I examined correlations among all forms of hunting (total consumption, number trapped, number purchased, and number hunted with dogs) for each carnivore species and I removed correlated variables ($|r| > 0.7$) from my occupancy analyses (denoted by footnote in results) to reduce redundancy. For any variables found to be correlated, I retained variables that were shown to be important from previous modeling (Farris and Kelly 2011) or from modeling by Gerber et al. (2011). To provide an estimate of each hunting rate for the four villages I averaged the household hunting rates and multiplied the average hunting rate by the number of households for the entire village. Where surveys existed for two villages bordering my study sites I averaged the hunting rates for the two villages to provide a single hunting rate for the study site.

Carnivore Occupancy Estimation

Occupancy: Landscape and Site Specific

To investigate the effects of each metric of degradation on carnivore populations, I conducted three separate occupancy analyses: landscape occupancy, site specific occupancy, and hunting occupancy. To estimate carnivore occupancy and assess the effect of degradation (i.e., fragmentation, exotic carnivores, and human presence) across the landscape (landscape occupancy) and within each of the seven camera grids (site specific occupancy) I created capture histories for each of the six endemic and three exotic carnivore species using daily capture events to determine the presence (1) or absence (0) of each species at each camera station. As a result of the reduced data set for hunting occupancy, I analyzed those sites separately (see below). I analyzed capture histories in program PRESENCE [Patuxent Wildlife Research Centre, USGS, Maryland, USA] (Hines 2006) to provide an estimate of species occurrence and detection while accounting for spatial variation and variation in detection probability (Bailey et al. 2004). I used station-level habitat and landscape features, co-occurring species activity (i.e. trap success), prey species activity, and human activity as covariates in my landscape and site-specific occupancy models to determine factors that influence endemic and exotic carnivore occupancy at both landscape and site specific levels. To normalize all covariate values and improve maximum likelihood convergence for my occupancy models, I used the Z-score method in which each value was subtracted by the mean and divided by the standard deviation (Ragazzini and Zadeh 1952).

I developed a priori models for each carnivore species for both landscape and site specific occupancy analyses. I used Akaike Information Criterion, corrected for small sample sizes (AICc), and model selection to rank models (Akaike 1973). Further, after assessing my top-ranking models I developed 1-3 post hoc models on the highest ranking covariates for both occupancy and detection. Finally, for each carnivore species I reported all competing a priori and post hoc models (model likelihood ≥ 0.125), used model averaging (averaged the fits using model weights for all top ranking models) to provide an estimate of occupancy and detection, and evaluated the importance and/or effect of covariates on carnivore occupancy using beta estimates from my highest-ranking model. I assessed goodness of fit for the most heavily parameterized model for each species' model set (for both landscape and site specific occupancy) using Pearson's goodness-of-fit test ($P = 0.05$) and evaluated over-dispersion using the c-hat value. For any c-hat value > 3.0 or goodness of fit value > 0.05 (indicating the data did not fit the model) I used the naïve estimate (i.e. number of sites capturing the target species out of the total sampling area without accounting for imperfect detection) rather than the estimated value from the model.

Occupancy: Hunting

Hunting data were available for only four of my seven study sites and the use of these variables in my landscape occupancy models would exclude detection/non-detection data from the remaining three sites, thus biasing the final estimation of occupancy across the Masoala-Makira landscape. As a result, I conducted additional occupancy analyses using only hunting rates (hereafter referred to as hunting occupancy) as covariates for these four sites to evaluate how hunting rates (total individuals consumed, trapped, purchased, or hunted with dogs per year) influence the occupancy and detection of carnivores across these four study sites. For each carnivore species estimated with my hunting occupancy models I reported all competing models (model likelihood ≥ 0.125) and evaluated the importance and/or effect of hunting covariates on carnivore occupancy using beta estimates from my highest-ranking model.

Results

Trends in station-level habitat and landscape features

I ranked my seven study sites based on their level of degradation using the Eigen vectors and resulting bi-plot from my principle components analysis (Table 1; Appendix A). My photographic surveys accumulated a total of 8,854 trap nights (mean = 1,264 per grid) across my seven study sites and captured all six endemic and three exotic species of carnivore known to occupy the Masoala-Makira landscape (Farris et al. 2012, Garbutt 2007) (Table 2). I found no trends, based on overlapping confidence intervals, between endemic carnivore trap success and degradation; however, exotic carnivores showed higher trap success in degraded sites (S05 and S07) compared to less degraded sites (S01 and S02; Table 2). In addition, I found no trend, based on overlapping confidence intervals, between bird trap success and degradation; however, small mammal trap success was considerably higher in non-degraded forest (avg. = 41.18) compared to degraded sites (avg. = 19.23; Table 2). Lemur species richness and relative abundance was highest in the non-degraded S01 site (n = 9 and 1.52 ± SE 0.11, respectively) and diminished as degradation increased (Table 2).

Carnivore consumption/hunting

The highest total human consumption of carnivores occurred at less degraded sites (S02 and S03) whereas the lowest rates occurred at the highly degraded site (S06; Table 3). Across my four study sites my data indicate that all hunting rates, particularly trapping, purchasing, and hunting with dogs, are higher for less degraded sites (S01 and S02) compared to more degraded sites (S03 and S06). The exotic Indian civet was the most heavily consumed carnivore across the landscape (mean = 90 individuals/year) followed by endemic ring-tail vontsira (mean = 58 individuals/year) and fosa (mean = 31 individuals/year). Spotted fanaloka was the least consumed carnivore across the four surveyed sites (mean = 5 individuals/year); however, insufficient data on broad-stripe vontsira at two sites prevented comparison with co-occurring carnivores. Finally, Indian civet and ring-tail vontsira were also consistently the highest trapped species per year (23 and 12, respectively), the highest number purchased per year (3 and 1, respectively), and highest number hunted with dogs per year (9 and 7, respectively).

Occupancy: Landscape

Spotted fanaloka had the highest occupancy (0.70 ± SE 0.07) of any endemic carnivore across the landscape, followed closely by fosa (0.68 ± SE 0.08), while the domestic dog had the highest occupancy (0.61 ± SE 0.07) for any exotic carnivore (Table 4). Brown-tailed vontsira, an apparent low-elevation forest specialist, had the lowest occupancy (0.25 ± SE 0.09) of any endemic carnivore across the landscape while Indian civet had the lowest (0.11 ± SE 0.03) for any exotic carnivore (Table 4). Domestic dog had a higher estimate of occupancy than four of the six endemic carnivore species while wild/feral cat had a higher occupancy (0.37 ± SE 0.08) than three of the six endemic species across the landscape (Table 4).

I found bird trap success to be the most important variable for predicting carnivore occupancy across species, based on my top-ranking occupancy models (Table 4; Appendix B) with a positive relationship for three endemics and a negative relationship for wild/feral cat (Figure 2a). Further, I found a similar relationship between small mammals and endemic broad-striped vontsira (positive) and domestic dogs (negative) (Figure 2b; Appendix B). Additionally, exotic carnivores (wild/feral cat and Indian civet) negatively affected the occupancy of spotted fanaloka (Figure 3). Human trap success was the most common variable for predicting carnivore detection, negatively influencing detection of two endemic species (broad-striped vontsira and brown-tailed vontsira) and positively influencing domestic dog detection. Percent matrix (percentage of the landscape consisting of non-forest and/or cultivated area) negatively affected fosa detection while positively affecting falanouc detection. Total amount of edge negatively affected the detection of both endemics (spotted fanaloka and ring-tail vontsira) and exotics (wild/feral cat) while distance to village (average distance of each camera to the nearest village) negatively affected falanouc and positively affected Indian civet (Table 4; Appendix C).

Occupancy: Site Specific

When exploring within species trends in occupancy across the continuum of degradation, I found no clear patterns in occupancy rates for endemic carnivores moving from non-degraded to degraded forest (Figure 4a). However, all three exotic carnivore species show an increase in site specific occupancy with increases in degradation (Figure 4b).

Occupancy: Hunting

I found a positive relationship between metrics of carnivore consumption and hunting and carnivore occupancy at all four sites (for example see fosa in Figure 4A; Table 5). Thus, high carnivore occupancy is associated with high rates of carnivore consumption and all three metrics of hunting (Table 5). In addition, I found a positive relationship between carnivore detection and hunting rates for all species except ring-tail vontsira and wild/feral cat (Table 5).

Discussion

My results highlight trends associated with exotic carnivores and hunting across the landscape; however, I found mixed results regarding endemic carnivores and increasing degradation. In particular, my results show that measures of anthropogenic disturbance (ex. human trap success, distance to village, and distance to forest edge) are associated with increasing exotic carnivore occupancy and activity, as well as increasing fragmentation (more edge, more patches, less core rainforest), which has been shown in other studies to reduce gene flow, impede movement across the landscape, reduce population size, and increase the likelihood of disease and pathogen transfer for wide-ranging carnivores (Crooks 2002, Crooks et al. 2011, Saunders et al. 1991, Woodroffe and Ginsberg 1998). In addition, I found negative relationships among exotic carnivores and endemic prey species, as well as negative trends in lemur species richness and relative abundance as degradation increases. The negative association between these anthropogenic pressures (exotic carnivores, degradation, and fragmentation) and multiple prey species presents a serious threat to endemic carnivores given the positive relationships in endemic carnivore occupancy and these prey species.

My study consisted of single-season surveys over a gradient of degraded sites in which I found no trends in endemic carnivore occupancy as degradation increases. Moderate habitat disturbance has been shown to positively affect some small carnivore populations (Mudappa et al. 2007, Oehler and Litvaitis 1996, Ray and Sunquist 2001) and my data may represent a similar trend with site specific occupancy revealing a higher occupancy in moderately degraded sites. However, endemic carnivores still face intense pressure across these degraded sites as evidenced by: 1) the absence of multiple carnivore species and lower occupancy rates at one or more heavily degraded forest sites; 2) a strong influx of exotic species with increasing degradation; and 3) intense hunting pressure, particularly where carnivore occupancy is highest.

I suggest these findings for endemic carnivores are evidence of extinction debt (i.e. impending extinction due to on-going and/or past events) occurring across the landscape(Tilman et al. 1995). This hypothesis is further supported by my on-going, multi-season surveys of carnivores across multiple sites which have revealed strong decreases in endemic carnivore occupancy and strong increases in exotic carnivore occupancy over a six year period (Farris, unpublished data). Additional longitudinal studies across sites and years are needed to further test these predictions. While pristine, contiguous forest does exist for the Masoala-Makira landscape (one of the last regions of Madagascar where pristine sites remain) they were not surveyed for this study. Surveys of these contiguous, non-degraded forest sites are needed to increase our understanding of how carnivore populations are impacted by widespread forest loss and degradation across Madagascar.

The low estimates of endemic carnivore activity and occupancy at the least degraded site (S01) may be attributed to the placement of cameras along newly cut trails, given the absence of existing trails at this contiguous forest site. The importance of sampling along existing trails is demonstrated both in the fosa models which highlight a decrease in occupancy (negative regression coefficient) as trails decrease in width (Table 4, Appendix B), as well as in existing literature (Dillon and Kelly 2007, Gerber 2011). Spotted fanaloka and fosa had the highest estimates of occupancy across the landscape; however, spotted fanaloka exhibits one of the most restricted ranges, being absent at two sites and exhibiting very low occupancy at another, while fosa was found at all study sites, exhibiting higher occupancy where trails are widest and well maintained. Brown-tailed vontsira had the most restrictive range and lowest occupancy of any endemic carnivore; these findings shed further light on the overall rarity of this endemic carnivore and I suggest it may face the greatest threat from on-going forest loss and fragmentation, as lower elevation forest is being lost at a faster rate (Green and Sussman 1990, Harper et al. 2007).

I found exotic carnivore activity and occupancy increased with increases in degradation, according to my site-specific occupancy models. Further, I found a higher estimate of occupancy for wild/feral cat and domestic dog across the landscape than half of the endemic carnivores. My results highlight the negative relationship between endemic birds and wild/feral cat, and a negative relationship between small mammals and domestic dog. These relationships are particularly alarming given the importance of these prey species for the occupancy of falanouc, ring-tail vontsira, broad-striped vontsira, and brown-tailed vontsira. Further, my results highlight a decrease in lemur relative abundance where exotic carnivore occupancy is high. These findings, in addition to recent findings by Farris et al. (2014) that show decreases in lemur occupancy in degraded forests, as well as negative interactions between multiple lemur and exotic carnivore pairings, provide valuable insight into the potential direct impact of exotic carnivores on lemur populations and the indirect impact on Madagascar's confirmed endemic lemur predators fosa and ring-tail vontsira (Goodman 2003b, Goodman 2012). In addition, my results highlight the direct negative relationship in spotted fanaloka occupancy and wild/feral cat and Indian civet activity. my findings for exotic carnivores in degraded forest are congruent with those by Gerber et al. (2012a; 2012b), which highlighted increases in exotic carnivores in fragmented and degraded forest sites, as well as negative relationships in occupancy and temporal interactions between endemic and exotic carnivores.

My results provide further insight into the widespread, unsustainable hunting trends threatening the carnivore community across the Masoala-Makira landscape (Golden 2009, Golden et al. 2014), including exceedingly high rates of consumption (≥

10 individuals per village per year) for half of Madagascar's endemic carnivores. My surveys revealed the exotic Indian civet and the endemic ring-tail vontsira were the two most consumed, trapped, hunted, and purchased carnivores; a result likely reflecting their increased activity and/or density in matrix and edge habitat near anthropogenic areas (Gerber et al. 2010, Goodman 2003a, Goodman 2012) where hunting pressure is more intense (Golden, unpublished data). This hypothesis is further supported by my findings that reveal higher hunting rates for wide-ranging species that use matrix habitat (fosa and wild/feral cat) compared to the more restrictive species (spotted fanaloka and falanouc), which have been shown in previous studies to show reliance on contiguous, non-degraded forest (Gerber et al. 2012b, Goodman 2012, Kerridge et al. 2003).

Given that high hunting and consumption rates of wildlife across this region are likely leading to population declines for multiple carnivore, lemur, and small mammal species (Golden 2009, Golden et al. 2014), I expected to find lower endemic carnivore occupancy and detection at sites where hunting rates were highest; however, the opposite was observed at the four study sites I surveyed. I suggest my findings reveal a disturbing trend reflecting the "hunting out" of other more degraded sites with local hunters targeting non-degraded, contiguous forest sites, where wildlife populations occur at higher densities, in their effort to increase the number of successful hunts. My occupancy analyses using hunting data provide additional support for this hypothesis as I observed a positive relationship between occupancy (Ψ) and hunting rates for all four endemic species modelled and a positive relationship between detection (p) and hunting rates for three of the four species modelled. Therefore, I believe that in this case, where hunting is nearly entirely passive (i.e. traps and snares), animals are harvested in a density-dependent fashion in accordance with their prevalence in the forest.

Conclusion

My results clearly demonstrate the threat facing Madagascar's carnivore community from increases in numerous anthropogenic pressures. The trends in increased exotic carnivore occupancy and their negative relationship with endemic carnivores, small mammals, and birds demonstrated by this study and by Gerber et al. (2012a; 2012b) merit immediate, targeted conservation and management plans to reduce the influx of exotic carnivore species in Madagascar's eastern rainforests. I recommend an effective capture-removal program for wild/feral cats and dogs to diminish the threat posed to Madagascar's endemic wildlife. Hunting presents an intense, augmenting pressure for carnivores across this region and the positive relationship with carnivore occupancy must be addressed. If unchecked these anthropogenic pressures are likely to result in the local extinction of numerous endemic carnivore, lemur, bird, and small mammal species across the Masoala-Makira landscape. These various anthropogenic pressures are known to negatively affect carnivore populations worldwide, thus these findings, including how these variables act synergistically across the landscape, have wide-ranging implications for managers working to conserve carnivore populations worldwide.

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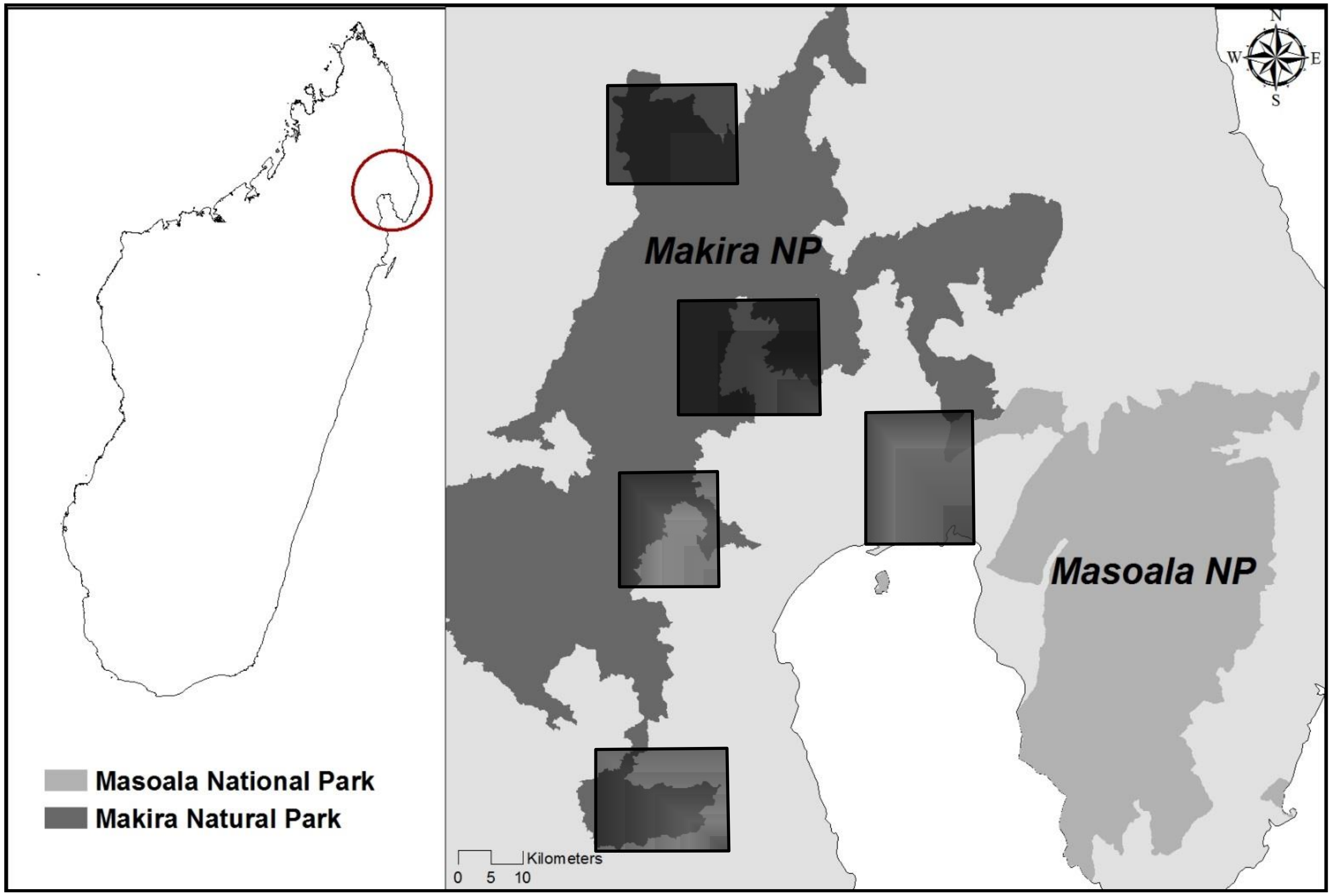


Figure 1. Map of the Masoala-Makira landscape including the outline of the regions in which the surveys were conducted at seven study sites. Bushmeat surveys across the region occurred from 2005-2011 while photographic surveys occurred from 2008-2012. Names of the study sites and/or villages are withheld as required due to our bushmeat survey data.

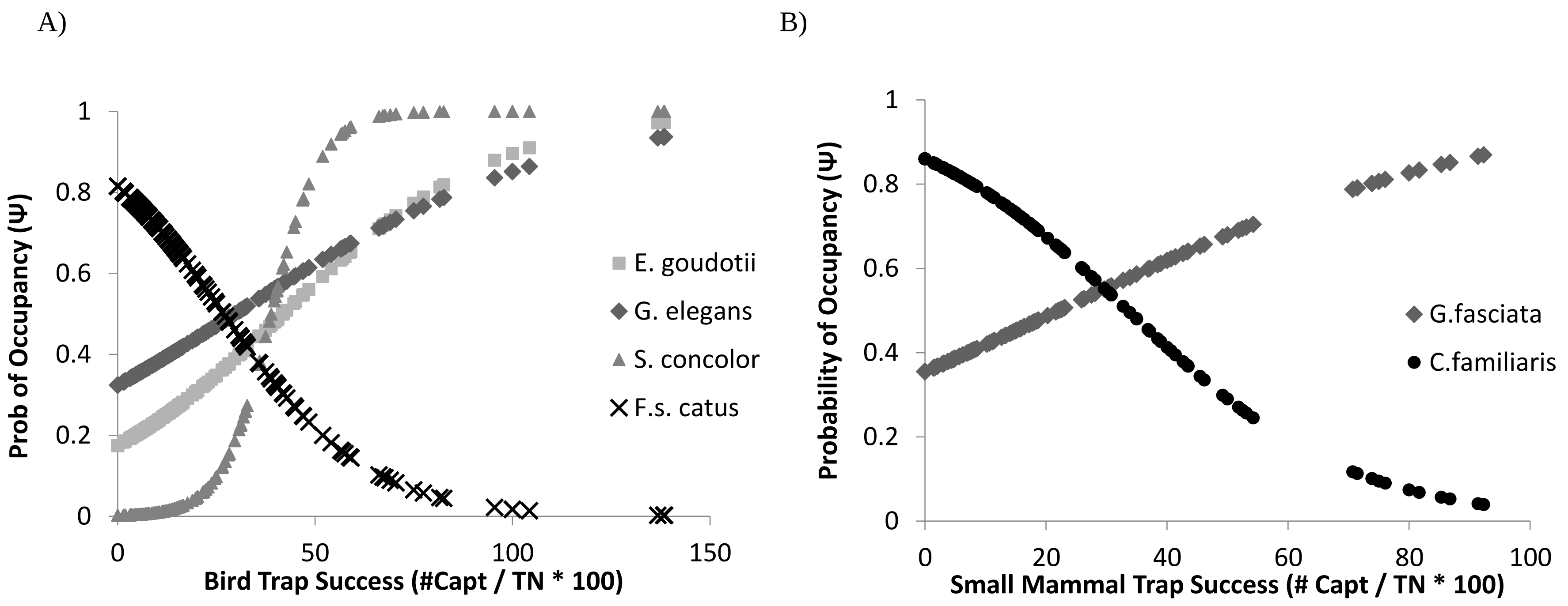


Figure 2. Probability of occupancy for multiple endemic (grey symbols) and exotic (black symbols) carnivores as a function of A) bird trap success (number of captures/trap night * 100) and B) small mammal trap success based on regression coefficients (β) resulting from landscape level occupancy models across all seven sites combined.

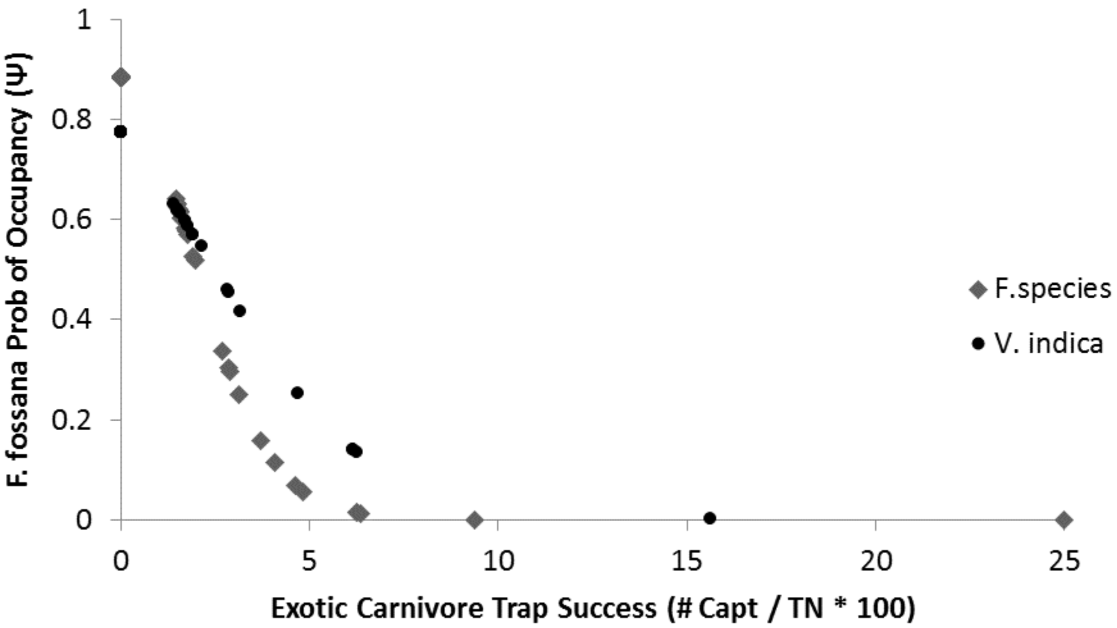
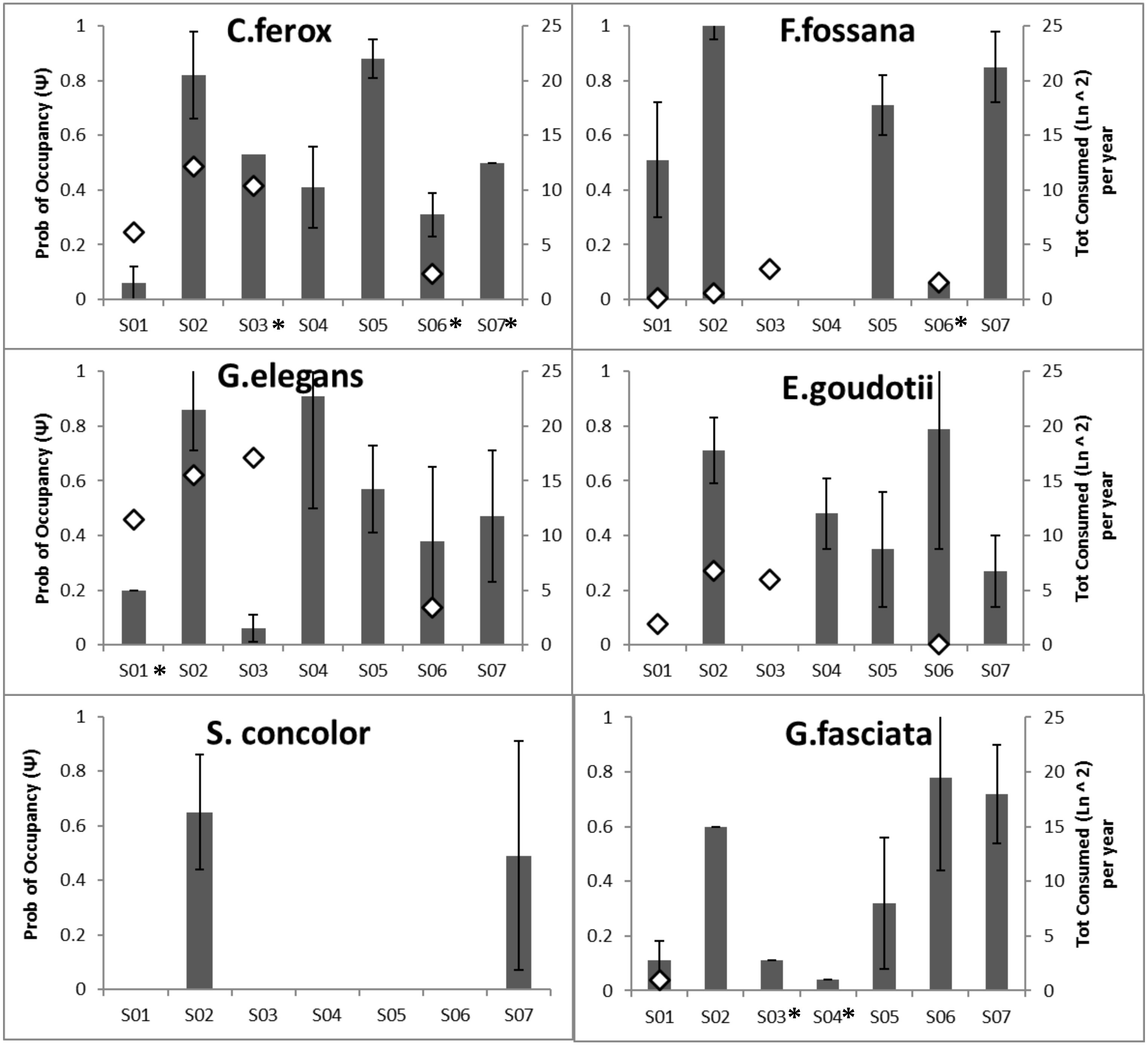


Figure 3. Probability of spotted fanaloka *Fossa fossana* occupancy as a function of wild/feral cat *Felis species* ◆) and Indian civet *Viverricula indica* (●) trap success based on regression coefficients (β) resulting from landscape level occupancy models across all seven sites.

A.)


C.ferox
F.fossana
G.elegans
E.goudotii
S. concolor
G.fasciata
Prob of Occupancy (Ψ)
Tot Consumed (Ln^2) per year
0
0.2
0.4
0.6
0.8
1
0
5
10
15
20
25
S01
S02
S03
S04
S05
S06
S07
*

B)

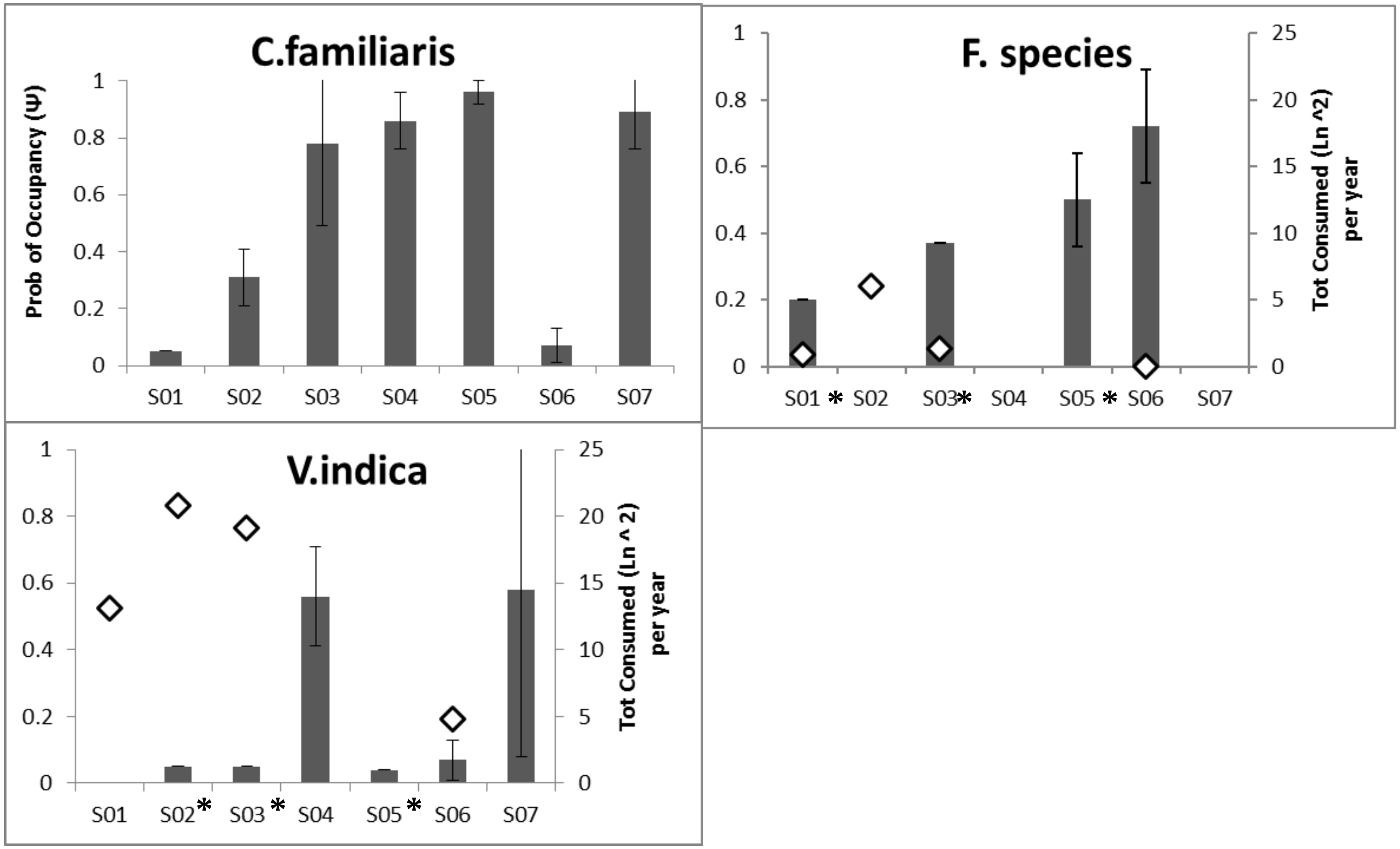


Figure 4. Site-specific occupancy estimates (± SE) for each endemic A) and exotic B) carnivore species across the seven study sites, ranked from least degraded (S01) to most degraded (S07), with the estimated total number of animals consumed per year (natural log squared) by site on secondary axis. The * indicates the naïve occupancy estimate was used.

Table 1. Station-level habitat (camera station) and landscape (500 m grid buffer) features (SE) for the seven study sites, ranked from least degraded (S01) to most degraded (S07), across the Masoala-Makira landscape. Sampling of habitat occurred at 152 camera stations across the seven study sites from 2008-2013. Study sites were ranked by conducting a principle components analysis using all habitat and landscape variables sampled. Trap success (TS) is calculated by the number of photo captures divided by the total trap nights multiplied by 100.

			← Least		Level of Degradation		Most →	
Level	Study site	Site S01	Site S02	Site S03	Site S04	Site S05	Site S06	Site S07
Station-level habitat	TreeDen (stems ≥5cm / ha) [a]	1,200 (300)	3,500 (900)	4,100 (1,600)	4,600 (1,700)	4,400 (1,100)	-	3,000 (700)
	BA (stems ≥5cm, m^2/ha) [b]	82.00 (10.22)	57.4 (6.11)	22.85 (4.59)	73.54 (13.03)	76.54 (8.48)	-	49.85 (6.35)
	Can Ht (m) [c]	16.97 (1.95)	12.50 (0.96)	7.48 (0.67)	10.55 (1.23)	12.89 (1.08)	-	9.75 (1.27)
	% Can Cover [d]	64.15 (5.58)	57.05 (4.89)	62.75 (3.17)	43.52 (6.82)	60.84 (4.09)	-	42.45 (5.14)
	% Understory Cover (0-2 m)	0.50 (0.05)	0.44 (0.04)	0.53 (0.03)	0.46 (0.04)	0.44 (0.05)	-	0.52 (0.04)
Landscape	# Patches [e]	3	10	22	21	31	116	190
	Largest Patch Index [f]	60.38	52.33	44.88	51.30	39.90	43.72	50.36
	LSI [g]	1.04	1.34	2.12	1.95	2.02	3.11	6.76
	%Rainforest	99.94	98.89	94.48	95.19	96.87	96.06	81.07
	%Matrix [h]	0.05	0.66	4.38	0.59	0.76	0.19	4.07
	Tot Core Rainforest (ha) [i]	0.88	0.99	0.85	0.87	1.14	0.72	0.59
	Tot Edge (m per ha)	0.03	0.59	1.85	1.53	2.13	3.51	7.89
	Avg. Dist. to Village (km)	10.96	2.80	3.33	2.08	4.82	2.71	1.45
	Avg. Dist. to Edge (km)	1.14	0.68	0.29	0.36	0.34	0.60	0.18

[a] TreeDen = tree density averaged across all camera stations (*n* = 18-25) for each study site;

[b] BA = average basal area;

[c] Can Ht = average canopy height;

[d] % Can Cover = average percent canopy cover;

[e] #Patches: total number of rainforest, degraded forest, and matrix patches within the camera grid buffer;

[f] Largest patch index: the percentage of total landscape area comprised by the largest rainforest patch;

[g] LSI: landscape shape index or the standardized measure of total edge adjusted for the size of the landscape;

[h] %Matrix: percent matrix defined as non-forest land cover consisting of cultivation, open field, or early succession;

[i] Tot Core Area: total core area defined as the sum of the core areas within the camera grid buffer (accounting for 500m edge depth) of each rainforest patch

Table 2. Survey details for the seven study sites (camera trapping grids), ranked from least degraded (S01) to most degraded (S07), across the Masoala-Makira landscape, including the trap success and standard error (TS, SE) for each of the six endemic and three exotic carnivore species.

		Least		Level of Degradation		Most	
Study site	Site S01	Site S02	Site S03	Site S04	Site S05	Site S06	Site S07
Survey Dates	Mar 2009 – May 2009	Sept 2008 – Nov 2008	Aug 2009 – Oct 2009	Jun 2011 – Aug 2011	Mar 2011 – May 2011	Nov 2009 – Jan 2010	Dec 2010 – Feb 2011
# of Camera Stations	20	25	19	23	23	18	24
Trap Nights	1050	1257	1067	1462	1509	881	1570
Elevation (m)	1000-1400	350-690	380-550	21-385	324-786	580-820	93-507
Fosa TS*	0.41 (0.41)	3.01 (0.98)	1.19 (0.30)	1.03 (0.35)	7.15 (1.05)	0.57 (0.20)	1.96 (0.73)
Spotted fanaloka TS	1.03 (0.49)	13.91 (2.64)	0 (0)	0 (0)	5.08 (1.35)	0.18 (0.16)	2.04 (0.36)
Falanouc TS	0 (0)	3.08 (0.89)	0 (0)	2.64 (0.82)	0.33 (0.21)	0.79 (0.27)	0.48 (0.20)
Ring-tail vontsira TS	0.39 (0.18)	1.33 (0.45)	0.09 (0.09)	1.11 (0.29)	3.75 (1.63)	0.51 (0.37)	0.45 (0.20)
Broad-striped vontsira TS	0.18 (0.13)	2.57 (0.86)	0.19 (0.13)	0.13 (0.13)	0.20 (0.11)	1.31 (0.40)	1.08 (0.37)
Brown-tailed vontsira TS	0 (0)	0.98 (0.30)	0 (0)	0 (0)	0 (0)	0 (0)	0.30 (0.17)
Domestic dog TS	0.14 (0.19)	1.97 (1.15)	4.78 (1.77)	14.91 (7.41)	26.06 (4.46)	0.09 (0.08)	19.56 (7.33)
Wild/feral cat TS	0.39 (0.19)	0 (0)	0.74 (0.26)	0 (0)	1.32 (0.48)	3.13 (1.18)	0 (0)

Table 2. Continued from previous page

Indian civet TS	0 (0)	0.14 (0.14)	0.10 (0.10)	1.96 (0.74)	0.13 (0.13)	0.12 (0.10)	0.40 (0.16)
Total Bird TS	13.64 (2.76)	62.85 (9.26)	9.22 (1.78)	24.07 (3.93)	23.35 (5.04)	22.61 (3.58)	31.18 (5.48)
Total Small Mammal TS	40.05 (5.30)	42.31 (6.84)	15.15 (3.52)	4.34 (1.20)	4.34 (1.24)	31.59 (4.31)	6.86 (1.50)
Lemur species richness	9	7	3	3	6	NA	4
Total Lemur Abundance**	1.52 (0.11)	0.89 (0.10)	0.45 (0.04)	0.98 (0.17)	0.93 (0.05)	NA	0.45 (0.03)

* TS: trap success is the number of independent photos of a target species divided by the trap nights multiplied by 100
** Relative abundance = number of lemur species (diurnal and nocturnal) observed per km

Table 3. Total hunting results, including the total number of animals consumed, trapped, purchased, and hunted with dogs per village per year, for five endemic and two exotic carnivores. A subset of households across four villages (S01, S02, S03, and S06) was surveyed an average of three times between 2005 and 2011 and the total number of carnivores consumed, trapped, purchased, and hunted each year surveyed was provided for each village. Number of households per village ranged from 12 to 177.

Hunting averages per village per year	Site	Fossa (C. ferox)	Malagasy civet (F. fossana)	Falanouc (E. goudotii)	Ring-tail vontsira (G. elegans)	Broad-stripe vontsira (G. fasciata)	Wild/feral cat (Felis sp.)	Indian civet (V. indica)	Total
# Consumed [a]	S01	3	< 1	1	8	1	1	10	24
	S02	16	2	5	25	-	5	47	100
	S03	7	2	3	18	-	1	23	54
	S06	5	1	1	7	1	1	10	26
# Trapped [b]	S01	< 1	0	1	4	1	< 1	2	8
	S02	4	< 1	2	4	-	0	14	24
	S03	0	0	0	3	-	0	3	6
	S06	3	0	1	1	0	0	4	9
# Purchased [c]	S01	0	0	0	< 1	0	0	1	1
	S02	< 1	1	1	0	-	0	2	4
	S03	0	0	0	0	-	0	0	0
	S06	0	0	0	0	0	0	0	0
# Hunted with Dogs [d]	S01	0	0	0	2	0	0	1	3
	S02	0	1	0	4	-	1	5	11
	S03	0	0	0	< 1	-	0	< 1	0
	S06	0	0	0	1	< 1	0	3	4

a – Total number of individuals consumed per year where individuals were acquired via trapping, purchasing, hunting, or other additional measures.
b – Total number of individuals actively trapped per year; contributed to number consumed, but not correlated.
c – Total number of individuals purchased per year from local market or from an individual within their village; contributed to number consumed, but not correlated.
d – Total number of individuals actively hunted with personal domestic dog per year; contributed to number consumed, but not correlated.

Table 4. Top ranking (model likelihood ≥ 0.125) landscape occupancy models and the estimate of occupancy (Ψ) and detection (p) for six endemic and three exotic Malagasy carnivore species across the Masoala-Makira landscape. Photographic surveys were conducted from 2008-2012 and were combined across all seven sites. Covariates in bold signify a positive relationship and non-bold a negative relationship with occupancy (Ψ) and/or detection (p). Relationships (direction and magnitude) denoted by the betas for occupancy and detection are provided in Appendix B and C (respectively).

Common Name	Model *	AIC	Delta AIC	AIC wt.	Model Likelihood	# Par.	Psi (Ψ) SE	p (SE)
Fosa	psi(TrType+**PhysDes**), p(%Matrix+**Cover**)	856.26	0	0.74	1.00	6	0.68 (0.08)	0.15 (0.02)
Spotted fanaloka	psi(VI+Cat), p(TotEdge+**#Patches**)	748.69	0	0.46	1.00	6	0.70 (0.07)	0.17 (0.02)
	psi(CanHt+Cat), p(TotEdge+**#Patches**)	748.83	0.14	0.43	0.93	6		
Falanouc	psi(**Bird**+**VI**), p(**%Matrix**+Village)	466.64	0	0.64	1.00	6	0.31 (0.07)	0.20 (0.05)
	psi(**Bird**+**Village**), p(**%Matrix**+Village)	468.95	2.31	0.20	0.32	6		
	psi(**Bird**+Lemur), p(**%Matrix**+Village)	470.48	3.84	0.09	0.15	6		
Ring-tail vontsira	psi(**Bird**+**Under**), p(TotEdge+Cat)	468.44	0	0.71	1.00	6	0.48 (0.08)	0.10 (0.03)
	psi(**Under**), p(TotEdge+Cat)	471.80	3.36	0.13	0.19	5		
Broad-striped vonts.	psi(SmMamm+Village), p(Human+Camera)	415.25	0	0.61	1.00	6	0.28 †	0.06 (0.01)

Table 4. Continued from previous page.

Brown-tailed vonts.	psi(**Bird**), p(Human)	125.25	0	0.99	1.00	4	0.25 (0.09)	0.05 (0.02)
Domestic dog	psi(**Human**+SmMamm), p(**Human**+TrType)	851.02	0	0.98	1.00	6	0.61 (0.07)	0.27 (0.02)
Wild/feral cat	psi(Bird+Cover), p(TotEdge)	337.27	0	0.53	1.00	5	0.37 (0.08)	0.08 (0.02)
	psi(Village+Cover), p(TotEdge)	337.54	0.27	0.46	0.87	5		
Indian civet	psi(**Village**), p(%Rain)	237.91	0	0.35	1.00	4	0.11 (0.03)	0.05 (0.02)
	psi(**Village**), p(%Rain+**Village**)	239.62	1.71	0.15	0.43	5		

* = variable descriptions for each model provided below; † = naïve estimate of occupancy due to the model not fitting the data (GOF > 0.05; c-hat > 3.0); TrType = trail type (ordered widest to smallest); PhysDes = physical description (ordered ridge, valley, slope); %Matrix = percent of landscape consisting of non-forest, cultivated area; Cover = percent canopy cover; VI = Indian civet *(Viverricula indica)* trap success; Cat = wild/feral cat trap success; TotEdge = total edge (in meters per hectare); #Patches = total number of rainforest, degraded forest, and matrix patches within the camera grid buffer; CanHt = average canopy height; Bird = bird trap success (all species); Village = average distance of each camera station to the nearest village; Lemur = lemur relative abundance (all species); Under = total understory cover from 0 to 2.0 m; SmMamm = small mammal trap success (all species); Human = human trap success; Camera =

camera model combination (Reconyx, Moultrie, Cuddieback, DeerCam brands); %Rain = percent of landscape consisting of rainforest cover.

Table 5. Top ranking (model likelihood > 0.125) occupancy models and estimates of occupancy (Ψ) and detection (p) across the four sites with hunting data (excluding any additional variables) for four endemic and one exotic Malagasy carnivore species, across the Masoala-Makira landscape. Photographic surveys were conducted from 2008-2012 and bushmeat surveys from 2005-2011. Covariates in bold signify a positive relationship and non-bold a negative relationship with occupancy and/or detection. Betas (SE) for occupancy and detection (p) also included.

Common Name	Model	AIC	Delta AIC	AIC wt.	# Par.	Beta (Ψ)	Beta (p)	Psi (Ψ)	p (SE)
Fosa	psi(.), p(**#Purchased**)	317.11	0	0.59	3	.	0.74 (0.16)	0.74 (0.12)	0.10 (0.02)
	psi(**#Consumed**), p(**#Purchased**)	318.05	0.94	0.37	4	0.52 (0.42)	0.64 (0.18)		
Spotted fanaloka	psi(**#Trapped**), p(**#Trapped**) [a]	309.59	0	0.97	4	12.65 (23.36)	1.11 (0.23)	0.40 (0.06)	0.26 (0.05)
Falanouc	psi(.), p(**#Purchased**) [b]	228.95	0	0.45	3	.	1.06 (0.20)	0.69 (0.13)	0.09 (0.02)
	psi(**#Purchased**), p(**#Purchased**)	229.04	0.09	0.43	4	0.91 (0.46)	0.60 (0.33)		
	psi(**#Purchased**), p(.)	231.55	2.6	0.12	3	1.35 (0.39)	.		
Ring-tail vontsira	psi(**AllDogHunts**) [c], p(#Purchased)	186.08	0	0.95	4	4.02 (1.45)	-0.81 (0.27)	0.48 (0.08)	0.12 (0.04)
Wild/feral cat	psi(.), p(#Consumed)	216.07	0	0.96	3	.	-2.31 (0.62)	0.78 (0.15)	0.07 (0.02)

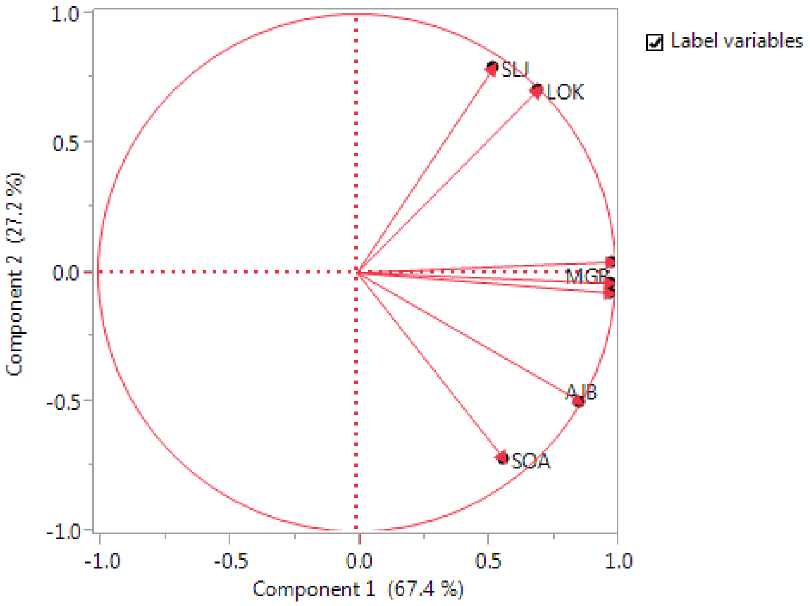
a - #Trapped was correlated with #Purchased for this model set, thus #Purchased was not used.

b - #Purchased was correlated with #DogHunts for this model set, thus #DogHunts was not used.

c - AllDogHunts = total number of wildlife species hunted with domestic dogs per year

Appendices

Appendix B.1. Results of the Principle Components Analysis (PCA) using habitat and landscape level covariates to rank my seven study sites based on their level of degradation. Sites are plotted based on their relationship according to the top two principle components. Sampling of habitat and landscape variables took place across the Masoala-Makira landscape from 2010 to 2013.



Appendix B.2. Logistic regression coefficients, β (SE) for top occupancy models for each endemic and exotic carnivore species across the Masoala-Makira landscape, Madagascar. Sampling occurred from Aug 2008 – October 2012. Bold font signifies support for relationship between the variable and species occupancy (i.e. CI does not overlap zero).

Parameter	Fosa (*C. ferox*)	Spotted fanaloka (*F. fossana*)	Falanouc (*E. goudotii*)	Ring-tail vontsira (*G. elegans*)	Broad-stripe vontsira (*G. fasciata*)	Brown-tail vontsira (*S. concolor*)	Domestic dog (*C. familiaris*)	Wild/feral cat (*Felis sp.*)	Indian civet (*V. indica*)
Intercept	**2.79 (0.75)**	**1.04 (0.48)**	**-0.66 (0.28)**	**-0.80 (0.34)**	**-0.83 (0.39)**	**-1.93 (0.91)**	0.34 (0.56)	**-2.01 (0.70)**	**-1.75 (0.63)**
Cat	-	**-2.65 (1.0)**	-	-	-	-		-	-
Indian civet		**-1.20 (0.52)**	0.72 (0.37)	-	-	-	-	-	-
TrType	**-2.29 (0.60)**	-	-	-	-	-	-	-	-
Bird	-		**1.00 (0.41)**	0.78 (0.43)	-	4.54 (3.26)	-	**-4.05 (0.99)**	-
DistVillage	-	-	-	-	**-0.93 (0.38)**	-	-	-	**-1.59 (0.87)**
Human	-	-	-	-	-	-	3.55 (2.09)	-	-
SmMamm	-	-	-	-	0.81 (0.46)	-	**-0.92 (0.34)**	-	-
CanCover	-	-	-	-	-	-	-	<0.01	-
PhysDes	0.09 (0.32)	-	-	-	-	-	-	-	-
Understory	-	-	-	<0.01	-	-	-	-	-

Appendix B.3. Logistic regression coefficients, β (SE) for detection probabilities resulting from top landscape occupancy models for each endemic and exotic carnivore species across the Masoala-Makira landscape, Madagascar. Sampling occurred from Aug 2008 – October 2012. Bold font signifies support for relationship between the variable and species detection (i.e. CIs do not overlap zero).

Parameter	Fosa (*C. ferox*)	Spotted fanaloka (*F. fossana*)	Falanouc (*E. goudotii*)	Ring-tail vontsira (*G. elegans*)	Broad-stripe vontsira (*G. fasciata*)	Brown-tail vontsira (*S. concolor*)	Domestic dog (*C. familiaris*)	Wild/feral cat (*Felis sp.*)	Indian civet (*V. indica*)
Intercept	**-0.92 (0.16)**	**-3.10 (0.48)**	**-2.44 (0.33)**	**-0.90 (0.32)**	**-3.84 (0.66)**	-10.92 (6.68)	**1.48 (0.67)**	**-1.58 (0.22)**	-0.28 (0.71)
CanCover	<0.01	-	-	-	-	-	-	-	-
%Matrix	-0.10 (0.18)	-	**0.08 (0.02)**	-	-	-	-	-	-
%Rain	-	-	-	-	-	-	-	-	**-0.03 (0.01)**
TotEdge	-	**-6.30 (0.81)**	-	**-5.42 (1.21)**	-	-	-	**-4.10 (1.26)**	-
Human	-	-	-	-	**-0.75 (0.37)**	-19.08 (15.06)	**1.16 (0.12)**	-	-
TrailType	-	-	-	-	-	-	**-2.19 (0.65)**	-	-
CameraType	-	-	-	-	**7.14 (2.71)**	-	-	-	-
Cat	-	-	-	**-0.98 (0.46)**	-	-	-	-	-
DistVillage	-	-	-0.47 (0.39)	-	-	-	-	-	-
#Patches	-	**4.49 (0.57)**	-	-	-	-	-	-	-

Chapter 3

WHEN CARNIVORES ROAM: TEMPORAL PATTERNS AND PARTITIONING AMONG MADAGASCAR’S NATIVE AND EXOTIC CARNIVORES

Abstract

Madagascar’s Eupleridae carnivores are perhaps the least studied and most threatened Family of Carnivora. Investigating the potential for direct and indirect competition among these species, particularly among native and exotic carnivores, is a necessary first step to better direct conservation actions. From 2008 to 2013, I photographically surveyed carnivores across a diverse rainforest landscape and compared how six native and three exotic carnivores distributed their activity throughout the diel cycle. I used hierarchical Bayesian poisson analysis to describe the activity patterns of Madagascar’s carnivore community, assessed the effect of season and site on carnivore temporal activity patterns, and estimated the coefficient of overlap between all carnivore pairings to assess the effect of body size and ecological niche on temporal overlap among native and exotic carnivores. Activity patterns were congruent with a previous study by Gerber et al. (2012a); however, I observed changes in temporal activity across seasons, particularly during the austral summer (hot-dry season), for four native and two exotic carnivores, including evidence of fosa *Cryptoprocta ferox* altering their temporal activity, more diurnal activity, during their mating season (hot-dry season). I found evidence of high overlap between native and exotic carnivores indicting the potential for increased interactions and competition. The greatest overlap in temporal activity among native and exotic carnivores occurred between both ring-tail *Galidia elegans* and brown-tail vontsira *Salanoia concolor* and dogs *Canis familiaris* (0.88 and 0.87, respectively). Fosa, falanouc

Eupleres goudotii, and spotted fanaloka *Fossa fossana* also overlapped in activity with the nocturnal, exotic Indian civet *Viverricula indica*. Fosa avoided humans and dogs across all seasons. Finally, I found that carnivore body size and ecological niche were not important predictors of temporal overlap. Previous research has shown these native and exotic carnivores overlap spatially and these new findings of temporal overlap among native and carnivores adds urgency to the need to manage exotic carnivores across Madagascar.

Introduction

Understanding the mechanisms driving community structure is important for sound conservation and management of wildlife species. Community structure may be shaped by chance events (Hubbell 2001) or by a multitude of spatio-temporal, intra- and inter-species interactions including competition, predation, mutualism, parasitism, commensalism, or ammenalism. For sympatric species that fill similar ecological roles, partitioning of the temporal niche dimension may be an important mechanism enabling coexistence, as this may reduce the potential for direct competitive interactions for food or space (Kronfeld-Schor and Dayan 2003, Santos and Presley 2010). Therefore, investigating temporal activity patterns can aid in understanding co-existence (Pianka 1973) especially for carnivores of similar body size and diet, because temporal avoidance may be a primary driver in reducing competition, leading to increased co-existence and thus enhanced biodiversity (Kronfeld-Schor and Dayan 2003).

Madagascar's carnivores arguably are both the least studied and most threatened Family of Carnivora in the world (Brooke et al. 2014). To date, ten endemic (Eupleridae) and three exotic carnivore species (Appendix A) have been identified across Madagascar (Goodman 2012). Recent work has confirmed the presence of six endemic (hereafter 'native') and three exotic carnivore species across north-eastern Madagascar (Farris et al. 2012). The overall ecological niche (e.g., temporal activity, habitat use, and diet) as currently understood for these six native carnivores is quite variable and is summarized in Table 1. However, there are similarities in habitat, body size, and resource use between falanouc and spotted fanaloka and among the three vontsira carnivores (Goodman 2012). Little is currently known about brown-tail vontsira behavior, range, and habitat selection making comparisons with other carnivores difficult. Our understanding of temporal activity patterns among Madagascar carnivores comes from anecdotal accounts and a single quantitative study from south-eastern Madagascar (Gerber et al. 2012a). Gerber et al. (2012a) highlighted the negative relationship between domestic and/or feral dogs *Canis familiaris* (hereafter ‘dogs’) and exotic Indian civets *Viverricula indica* on native carnivore activity patterns. Negative activity pattern relationships between native and exotic carnivores could result from exploitation competition, interference competition (including intraguild predation), niche separation, or transmission of pathogens (Clout and Russell 2008, Funk et al. 2001, Salo et al. 2007, Vanak and Gompper 2010). Of particular concern is our limited understanding of activity patterns of exotic and feral carnivores given their negative impacts on wildlife in Madagascar (Farris, Chapter 2; Farris 2014; Gerber 2012a, b) and in other habitats worldwide (Gompper 2013). The similar body size between the native fosa and the exotic feral cat *Felis species* and dogs, as well as between the medium-sized native carnivores (falanouc and spotted fanaloka) and the exotic Indian civet are of great concern because exotic and feral species may competitively exclude native species as these exotic carnivores continue to increase in distribution and perhaps abundance across the landscape. Determining the temporal activity patterns of exotic and native carnivores across habitat types and seasons is important to predict whether it may be necessary to remove exotic animals from protected areas to protect native species.

The effect of season on Malagasy carnivore activity patterns, including the overlap in activity among exotic and native species across seasons, has not been investigated. Variation in seasonal activity patterns may occur if seasonal variation in temperature, precipitation, and photoperiod drive behavioral shifts. Moreover, seasonal changes in activity may result from changes in mating, reproductive status, prey availability, and/or competition (Clutton-Brock and Harvey 1978, Kavanau and Ramos 1975). For example, the breeding season of fosa occurs from October through December; when females advertise via vocalizations and scent marking from a fixed location and then mate with many males multiple times over a several day period (Goodman 2012). It is likely that fosa exhibit variation in activity patterns during this time period as a result of this behavior, which could increase the possibility of interacting with co-occurring carnivores, including exotic carnivores. I currently lack information on how fosa and co-occurring carnivores in Madagascar might alter their temporal activity across seasonal periods in Madagascar.

My goal was to explore the activity patterns of Madagascar's native and exotic carnivore community to determine how activity patterns vary among native carnivores of similar body size and niche (defined by habitat use and diet), by season, and in relation to exotic carnivores. To achieve this goal I 1) quantified activity patterns (day, dawn, dusk, and night) for Madagascar's six native and three exotic carnivores across the landscape; 2) investigated the impact of season and site on native and exotic carnivore activity patterns within the complete diel cycle; and 3) investigated overlap of temporal activity within the diel cycle among all carnivore pairings to assess the effect of body size and ecological niche (diet and habitat preference). I hypothesized that: 1) both native and exotic carnivores would show similar temporal activity patterns as were observed in SE Madagascar (Gerber et al. (2012a); 2) native and exotic carnivores would demonstrate variation in activity patterns across seasons due to variability in temperature, resource availability, and mating behavior; 3) native carnivores would avoid sites where exotic carnivore activity is high; and 4) native and exotic carnivores of similar body size and ecological niche would demonstrate divergence in activity patterns, in particular I expected to see temporal segregation among the three small-bodied vontsira carnivores; the three medium sized carnivores (falanouc, spotted fanaloka, and exotic Indian civet); and the three large-bodied carnivores (fosa, dogs, and feral cats).

Methods

Study site

I photographically surveyed carnivores from 2008-2013 across Madagascar's largest protected area complex, the Masoala-Makira landscape (Fig. 1). The Masoala-Makira landscape consists of Masoala National Park (240,000 ha; hereafter Masoala) and Makira Natural Park (372,470 ha of protected area and 351,037 ha of community management zone; hereafter Makira) (Kremen 2003). The Masoala-Makira landscape has the highest estimated levels of biodiversity in Madagascar, but faces numerous anthropogenic pressures threatening the endemic wildlife therein (Farris, Chapter 2; Golden 2009). I surveyed a total of seven study sites across the Masoala-Makira landscape, two of which were surveyed repeatedly for a total of 12 surveys. Study sites were selected to capture a wide variation of habitat degradation and fragmentation as part of an on-going research project (Farris 2012; Farris chapter 2; Farris 2014). I labelled sites based on their level of degradation (01 = least degraded; 07 = most degraded; Appendix B), rather than using the village or forest names (Farris Chapter 2).

Seasons

I defined climatic seasons using daily measurements of temperature and rainfall. I recorded rainfall and temperature measurements at 06:00, 12:00, and 18:00 each day during the course of the photographic surveys from locations within the camera grid/study site.

Of the 12 total surveys, I conducted two surveys (n = 2 sites) during the hot-wet season (February – May; mean temperature = 23.0ºC ± SD 1.5; mean rainfall = 4.3 cm ± SD 7.3), seven surveys (n = 5 sites) during the cool-wet season (June – September; mean temperature = 16.1ºC ± SD 2.3; mean rainfall = 3.7 cm ± SD 5.2), and three surveys (n = 2 sites) during the hot-dry season (October – January; mean temperature = 21.3ºC ± SD 3.7; mean rainfall = 4.5 cm ± SD 8.2). Given the high variability of rainfall data collected during my study, resulting from numerous cyclone events, I also used existing historical climate data (www.data.worldbank.org) and additional studies measuring climate patterns within this region to validate the categorization of seasonal periods. My two sites with repeated surveys (sites S02 and S05) were sampled over more than one season.

Carnivore sampling

I sampled carnivores using remote sensing cameras; I established 18 to 25 individual camera stations (with two cameras per station) for each study site (i.e., camera grid) using both digital (Reconyx PC85 & HC500, Moultrie D50 & D55, Cuddeback IR) and film-loaded cameras (DeerCam DC300). I placed cameras on either side of human (0.5 – 2.0 m wide) and wildlife (< 0.5 m wide) trails. I placed camera stations approximately 500 m apart in a grid pattern (Gerber et al. 2012b). Cameras operated 24 hours a day for an average of 67 days (SD = 8.10) per study site and I checked each camera station every 5-10 days between the hours of 06:00 and 17:00 to change memory cards or film, batteries, and to ensure cameras were functioning properly. I positioned cameras between 20-30 cm off the ground and I used no bait or lure.

Analysis of temporal activity data

I defined an independent capture event as all photos of a given carnivore species within a 30 min period (Di Bitetti et al. 2006). I defined the ‘dawn’ and ‘dusk’ time periods as one hour prior to and one-hour post sunrise and sunset, respectively. Species that primarily are active during dawn and dusk are referred to as crepuscular. I defined ‘day’ time period (denoted as diurnal) as between dawn and dusk, while ‘night’ time period (denoted as nocturnal) was between dusk and dawn. This provided us with approximately 10 hours of available time for both day and night time periods and two hours of available activity each for dusk and dawn time periods.

Hierarchical Bayesian Poisson analysis

To achieve my first objective, I investigated how carnivore species selectively used different periods of the diel cycle by modeling captures (capture events/available hours; hereafter photographic rate) for each time category. I modeled the daily count y_{ijk} (e.g. capture event), on each sampling day i, at study site k, for each time category j using a hierarchical Bayesian poisson model (see Appendix C). Because the time categories are not all equal in length I corrected for the number of hours available in each category using an offset equal to the number of hours available. To make inference about each study site and the general activity of the species across all sites, I treated each time category as a random effect, allowing us to simultaneously make inference about activity at each study site and summarize species-level activity across all study sites. I applied this model to each of the nine carnivore species of interest.

Kernel density analysis

To evaluate alternative hypotheses of how season, study site, and season by study site influence carnivore temporal activity within the complete diel cycle I assumed the photographic times (converted to radians) followed the circular von Mises distribution with parameters κ (concentration) and a mean direction of linear predictors following μ + 2*atan ($\boldsymbol{\beta}$*$\mathbf{X}$), where μ and $\boldsymbol{\beta}$ are unknown coefficients to be estimated via maximum likelihood and $\mathbf{X}$ is a matrix of predictor variables (Fisher and Lee 1992). I used the R package ‘circular’ to fit these models (Agostinelli and Lund 2013). I conducted model selection using Akaike’s Information Criterion (AIC), where the minimum AIC of a model set is the most parsimonious (tradeoff of model fit and complexity) model for the data (Akaike 1973). I made inference from the most simple model (no variation by camera survey) and from the most parsimonious model by estimating the probability density of temporal activity distribution for each species using a nonparametric kernel density analyses (Ridout and Linkie 2009).

For each species I determined its dominant activity pattern as diurnal, nocturnal, or crepuscular by examining its continuous activity throughout the diel cycle (i.e., kernel density analysis) and noting any preference for a given time period (i.e., Poisson analysis). Preference was described as a higher expected number of photographs per hour, based on the time available for each time period.

To achieve my third objective, to assess the effect of ecological niche and body size on temporal overlap, I estimated the coefficient of overlap between all paired carnivore species' probability densities. I did this using an estimator supported for small sample size [Δ_1] (Ridout and Linkie 2009). I compared the overlap coefficient, Δ_1, between all species pairings to determine if their Δ_1 was lower, indicating temporal avoidance, than between more dissimilar species.

Results

My surveys resulted in a total of 15,253 trap nights (mean = 1,270 ± SD = 229 per study site) and provided a total of 2,991 photographic captures of carnivores (1,639 captures of six native carnivores and 1,352 captures of three exotic carnivores; Appendix B). Of the nine carnivores in this study, dogs had the highest number of captures (n = 1,135) while exotic Indian civet had the fewest captures (n = 44; Table 2). Based on my kernel analysis and resulting mean photographic rates (i.e. expected capture events per available hours) I found most carnivores did not show strict diurnal or nocturnal activity. Rather, I found variation or flexibility in how a carnivore used the 24 hour period. However, overall I found that fosa, falanouc, spotted fanaloka, broad-stripe vontsira, and Indian civet selected the night time period while ring-tail vontsira, brown-tail vontsira, and dogs selected the day time period (Table 3; Fig. 2a-b; Appendix D). I found fosa, falanouc, and Indian civet also used additional time periods to a lesser extent (photographic rate ≤ 0.06), thus I suggest these carnivores may exhibit crepuscular activity with a preference for night across the landscape (Fig. 2a). Ring-tail and brown-tail vontsira demonstrated differences in peak activity with brown-tail vontsira more active just after dawn and ring-tail vontsira more active prior to dusk (Fig. 2a). Finally, I found exotic feral cats had wide-ranging activity patterns across the landscape with a slight preference for the day time period (Table 3; Appendix D); based on these variable patterns I suggest this carnivore demonstrates crepuscular activity (Fig. 2b).

My model selection from the kernel density estimates revealed the null model, combining all captures across the landscape and across seasons, was best for explaining activity patterns for half of the carnivores (fosa, falanouc and dogs; Appendix E). However, for three species I also found site (i.e. ring-tail vontsira), season (i.e. feral cats), and site by season (i.e. spotted fanaloka) were also important for explaining activity patterns (Appendix E). Brown-tail and broad-tail vontsira and Indian civet had insufficient captures (< 15) at multiple study sites which prevented us from including them in the model selection process. Ring-tail vontsira was exclusively diurnal at study site S04 during the cool-wet season; but at study sites S02 (hot-dry, cool-wet) and S05 (cool-wet) I observed moderate levels of crepuscular activity and even limited nocturnal activity (Fig. 3a). Feral cats decreased nocturnal activity during hot-wet and hot-dry seasons compared to the cool-wet season where activity peaked at midnight, dusk, and dawn (Fig. 3b). Despite the consistent nocturnal activity throughout all surveys for spotted fanaloka, this nocturnal carnivore appears to shift its peak activity from early evening (18:00 – 0:00) during the cool-wet season to early morning (0:00 – 06:00) during the two hot seasons (Fig. 3c). This is supported further by my repeated surveys at study site 02 where spotted fanaloka greatly altered its nocturnal activity from hot-dry to cool-wet season (Fig. 3c).

Despite the null model being highest ranking for half the carnivore species, I still found striking trends for these carnivore in activity patterns across season and/or study site, with moderate model weight suggesting some support for these models (Appendix

E). For example, during the hot-dry season I found dogs greatly diminished activity during midday and increased crepuscular activity (Fig. 3d) while fosa exhibited a decrease in nocturnal activity and a slight increase in activity during dusk hours (Fig. 3e). This altering of activity during the hot-dry season for fosa occurred during their breeding season (October to December). During the hot-dry season falanouc showed more variable activity across all four time periods, rather than the strong peaks in crepuscular activity during the cool-wet (Fig. 3f).

I found evidence of native carnivores shifting their temporal activity patterns in the presence of exotic carnivores. The shift in spotted fanaloka activity during the hot seasons occurred at study sites S02 and S05 where human and dog activity was very high (Fig. 3c; Appendix B). In addition, fosa exhibited nocturnal activity where humans and similar sized dogs were highly active (study site S07) and diurnal activity where they were rare (study site S02). I found no brown-tail vontsira at study sites having very high captures rates of dogs, which exhibits strong temporal overlap with this rare native carnivore ($\widehat{\Delta}_1$ = 0.88; Table 4). Additionally, feral cats showed exclusively crepuscular and almost no nocturnal activity at study site S06 where co-occurring carnivore occupancy and activity was very low and small mammal activity was high (Appendix B).

I found that carnivore body size and ecological niche were not strong predictors of temporal overlap among carnivore pairings (Table 4). The average degree of overlap among all carnivore pairings was $\widehat{\Delta}_1 = 0.57 \pm \text{SD } 0.23$ (median = 0.61). I observed a high degree of overlap in activity patterns between numerous carnivore pairings. In particular, the small-bodied diurnal ring-tail and brown-tail vontsira demonstrated the greatest overlap among native carnivores ($\widehat{\Delta}_1$ = 0.91; Table 4, Fig. 4a), but limited overlap with the similar sized nocturnal broad-stripe vontsira ($\widehat{\Delta}_1$ = 0.21 and $\widehat{\Delta}_1$ = 0.19, respectively; Fig. 4b-c). The ecological niche requirements and diet of broad-stripe and brown-tail vontsira appear to be very similar, but show strong divergence with ring-tail vontsira (Table 1). Further, fosa and falanouc who show night-day and night-dawn activity (respectively) show considerable overlap in activity ($\widehat{\Delta}_1$ = 0.86; Table 4); however, these two native carnivores demonstrate strong differences in body size, diet, and habitat preference (Table 1). The similar sized falanouc and spotted fanaloka, which also show great overlap in body size and habitat preference (Table 1) show only moderate overlap in activity ($\widehat{\Delta}_1$ = 0.67; Table 4).

Among native-exotic pairings, the diurnal native carnivore's ring-tail and brown-tail vontsira show strong overlap with larger bodied dogs ($\widehat{\Delta}_1$ = 0.87 and $\widehat{\Delta}_1$ = 0.88, respectively; Table 4; Fig. 5a, b) and moderate overlap with feral cats ($\widehat{\Delta}_1$ = 0.56 and $\widehat{\Delta}_1$ = 0.61, respectively; Table 4). There is strong overlap in niche requirements between ring-tail vontsira and these two exotic carnivores (Table 1). Moreover, the similar sized, nocturnal falanouc and Indian civet, as well as spotted fanaloka and Indian civet also demonstrate strong overlap in activity ($\widehat{\Delta}_1$ = 0.74 and $\widehat{\Delta}_1$ = 0.80, respectively; Table 4; Fig. 5c); however, there is strong divergence in niche requirements between these two native carnivores and the exotic Indian civet (Table 1). Fosa was most similar in body size to the three exotic carnivores and showed strong overlap with Indian civet ($\widehat{\Delta}_1$ = 0.83; Fig. 5d), moderate overlap with feral cats ($\widehat{\Delta}_1$ = 0.66), and little overlap with dogs ($\widehat{\Delta}_1$ = 0.44; Table 4). However, the niche requirements and diet of fosa are quite different compared to the three exotic carnivores (Table 1). Finally, among the exotic carnivores the medium-sized, nocturnal Indian civet showed the greatest number of overlapping relationships with native carnivores (Table 4).

Discussion

Quantifying Activity Patterns

My findings regarding native carnivore activity patterns across the Masoala-Makira landscape are congruent with Gerber et al. (2012a) from south-east (SE) Madagascar for most of the carnivore species. However, important differences exist, including the primarily crepuscular activity of falanouc in this study compared to the strictly nocturnal activity from SE Madagascar (Gerber et al. 2012a). In addition, dogs appear to be strictly diurnal across my seven study sites compared to the highly variable activity found in SE Madagascar. The wide-spread negative impacts of dogs have been documented worldwide (Gompper 2013) and their activity may vary based on a host of variables, particularly the activity of humans. This variation in activity makes it difficult to generalize findings about how dogs may interact with local wildlife. Additionally, this highly variable activity has been observed for feral cats as I found strong peaks in crepuscular activity across my seven study sites compared to their uniform activity in SE Madagascar. Variation in activity across seasons, which was not investigated by Gerber et al. (2012a), may provide explanation for this discrepancy in activity patterns for these carnivore species. Finally, I suggest the highly variable activity of fosa, the largest native species, including its activity across all four time periods (dawn, day, dusk, and night) provides evidence of their generalist behavior. This finding, along with their differences in diet compared to co-occurring carnivores, and their ability to climb and use the forest canopy, provides evidence of limited niche overlap among fosa and the other carnivore species.

Influence of Season and Site on Activity Patterns

I found mixed results relative to my prediction that native and exotic carnivores will show variation in temporal activity across seasons. In particular, I found that fosa may increase dusk activity during their mating season (hot-dry season). Their noisy, conspicuous, and localized mating behavior is likely to influence activity patterns during this period, particularly among males who travel long distances and sometimes fight over females (Goodman 2012). However, the activity of fosa also appears to be influenced by human and dog activity and my ability to distinguish between these two influences is limited. Fosa demonstrated more nocturnal activity at study sites having exceptionally high activity of humans and dogs (study sites S04, S05, and S07) and more diurnal activity at study sites where human activity was low (study site S02; Appendix B), regardless of the season during which they occurred. I was unable to determine any difference in fosa response towards humans versus dogs because captures of humans and dogs were highly correlated (Farris, unpublished data); however, the negative impacts of dogs on native wildlife are likely to diminish if local people stop bringing dogs with them into the forest.

I also found seasonal influences on activity for falanouc and spotted fanaloka, which both exhibited increased nocturnal activity during the hot-dry season compared to the cool-wet season. I observed this change in activity across seasons for both carnivores at study site S02, one of my repeated survey sites, which signifies that this slight shift in activity likely results from seasonal change alone. However, I have observed a strong increase in feral cat occupancy from 2008 to 2013 at this study site (Farris, unpublished data) and this may be influencing native carnivore activity at this study site. For spotted fanaloka this change in activity, particularly at study site S07, may also be influenced by an increase in human and dog activity. In addition, I observed similar seasonal changes in activity patterns for exotic carnivores. For example, both dogs and feral cats showed slight changes in activity during the hot-dry and hot-wet seasons, respectively. In the case of dogs I suggest the strong decrease in activity during midday hours during the hot-dry season results from the strong correlation with human activity/captures given most of the dogs appeared to be domestic pets rather than feral (Farris, personal observation; Felix Ratelolahy, personal communication). Most humans were not active during the hottest part of the day during this season and the dogs traveling with them were also not captured during those hours. The shift in activity for feral cats during the hot-wet season is believed to result from seasonal change, rather than co-occurring species, given repeated surveys of study site S05 over different seasons show great variation in activity patterns.

I found some support for my prediction that native carnivores will alter their activity patterns at sites where exotic carnivore activity is high. For example, the strongest overlap between native and exotic carnivores occurred between ring-tail and brown-tail vontsira and dogs. I suggest this strong overlap between brown-tail vontsira and dogs may explain the absence of brown-tail vontsira from study sites S03, S04, and S05, where suitable low elevation rainforest habitat was observed but dog occupancy was extremely high. This is supported further by my findings for carnivore spatial interactions, which show a strong increase in occupancy where dogs are absent (Farris, see chapter four). Despite the strong temporal overlap between the two carnivores, I found little support for the effect of dogs on the variation in ring-tail vontsira activity across study sites, as was observed in SE Madagascar (Gerber et al. 2012a). Study site

S04, where ring-tail vontsira was strictly diurnal, and study site S05, where it exhibited more widespread activity, both had very high dog activity and occupancy (Farris Chapter 2; Appendix B).

The decrease in falanouc dusk activity from the hot-dry season and nocturnal activity during the cool-wet season may result from interactions with exotic carnivores as dogs showed more dusk activity during the hot-dry season and feral cats showed more nocturnal activity during the cool-wet season. The ultimate cause of this change in falanouc activity across these two seasons is difficult to determine given the variability in exotic carnivore capture rates across these study sites. Finally, among exotic carnivores feral cats may show evidence of avoiding temporal overlap with dogs at study sites where they co-occur (Fig. 3b and d), though this needs to be explored further. Recent research has demonstrated that increases in habitat degradation and fragmentation in Madagascar have resulted in decreases in native carnivore occupancy and density while increasing exotic carnivore occupancy (Farris Chapter 2; Gerber et al. 2012b) and this alteration of habitat is likely resulting in increased temporal overlap among native and exotic carnivores.

Overlap of Temporal Activity

My findings reveal strong temporal overlap among carnivores (both native and exotic); however, I did not find body size and niche requirements (habitat use and diet) to be strong predictors of temporal overlap as has been found in other studies of co-occurring carnivores (Sunarto et al. In press). The ecological niche of these carnivores likely encompasses more dimensions than we are currently familiar with (Goodman 2012) or were able to investigate, thus including additional niche dimensions in future analyses may help explain the temporal overlap patterns among these carnivores. The strongest temporal overlap for any species combination within this study occurred between the small-bodied, diurnal ring-tail and brown-tail vontsira, though both had little overlap with the sympatric, nocturnal broad-stripe vontsira. This study represents the first quantitative comparison of the three sympatric, smaller-bodied vontsira species (ring-tail, brown-tail, and broad-stripe vontsira), including the first study, to my knowledge, to confirm the co-existence of these three native carnivore species (Farris et al. 2012). We suggest the sympatric relationship among the three vontsira carnivores results from the division of the temporal niche (nocturnal activity by broad-stripe vontsira and diurnal activity by both ring-tail and brown-tail vontsira) and the habitat selection and potential dietary differences between ring-tail and brown-tail vontsira (Goodman 2012). I found that while ring-tail and brown-tail vontsira co-occurred at study sites S02 and S07, they rarely were captured at the same camera stations within those survey sites. These two native vontsira carnivores are sympatric in general distribution but do not appear to be at the station-level habitat level. I need additional surveys of sites in which these two carnivores co-occur to further explore their relationship; however, the overall rarity of brown-tail vontsira, including its apparent reliance on rapidly diminishing lowland rainforest habitat (Goodman 2012, IUCN 2014) makes further comparisons of the co-existence of these two species difficult. In particular, I suggest brown-tail vontsira likely faces the greatest threat given its overall rarity, limited range, preference for intact, low elevation forest, lower occupancy in the presence of dogs (Farris, unpublished data), and strong overlap in temporal activity with both dogs and feral cats. Further, I also observed temporal overlap for the crepuscular fosa and falanouc and the nocturnal spotted fanaloka and broad-stripe vontsira. I suggest the limited temporal overlap in activity and segregation in diet between the medium body-sized native carnivores spotted fanaloka and falanouc allows for their sympatric co-occurrence across eastern rainforest habitat.

This study represents the first investigation of carnivore seasonal activity patterns in Madagascar, including both the effects of season and exotic carnivore activity on native carnivore temporal activity patterns. Through this study I provide additional evidence of the burgeoning threat posed to Madagascar's native carnivores, believed to be the world's least studied and most threatened family of Carnivora (Brooke et al. 2014), from the influx of exotic carnivores across eastern rainforest habitat.

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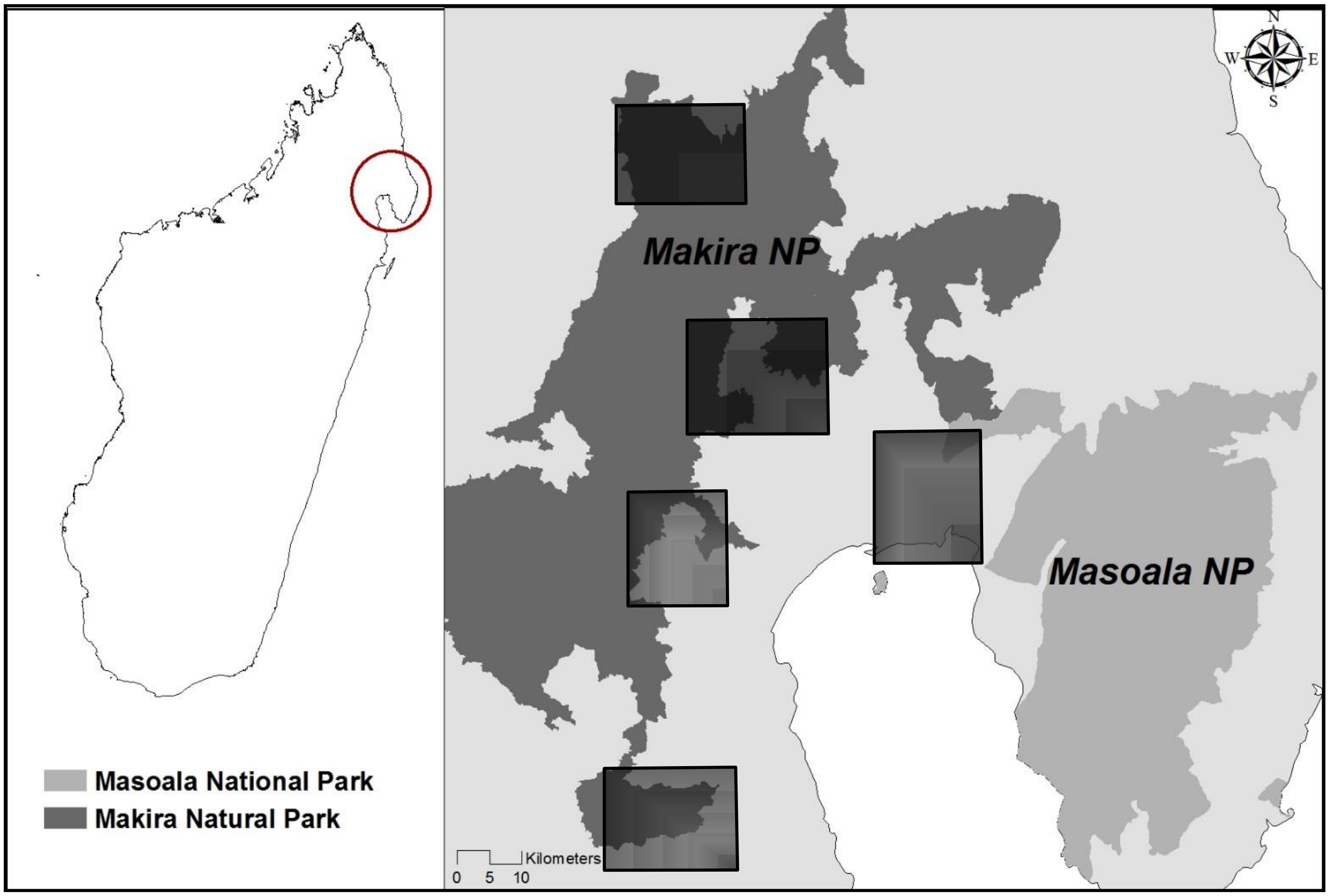
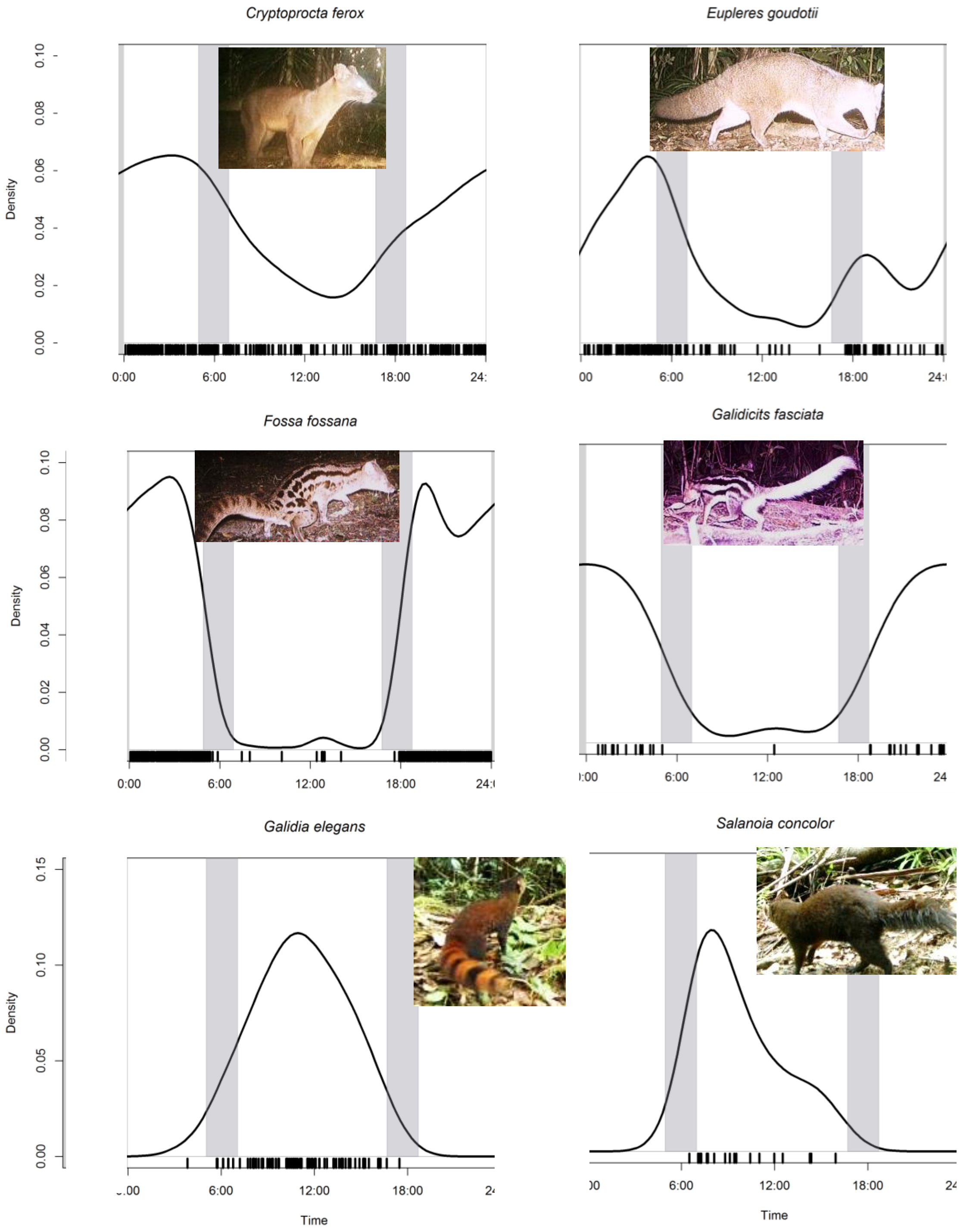


Figure 1. Map of the Masoala-Makira landscape including the outline of the regions in which the surveys were conducted at seven study sites. Photographic surveys occurred from 2008-2012.

A.)



Cryptoprocta ferox

Eupleres goudotii

Fossa fossana

Galidicits fasciata

Galidia elegans

Salanoia concolor

B.)

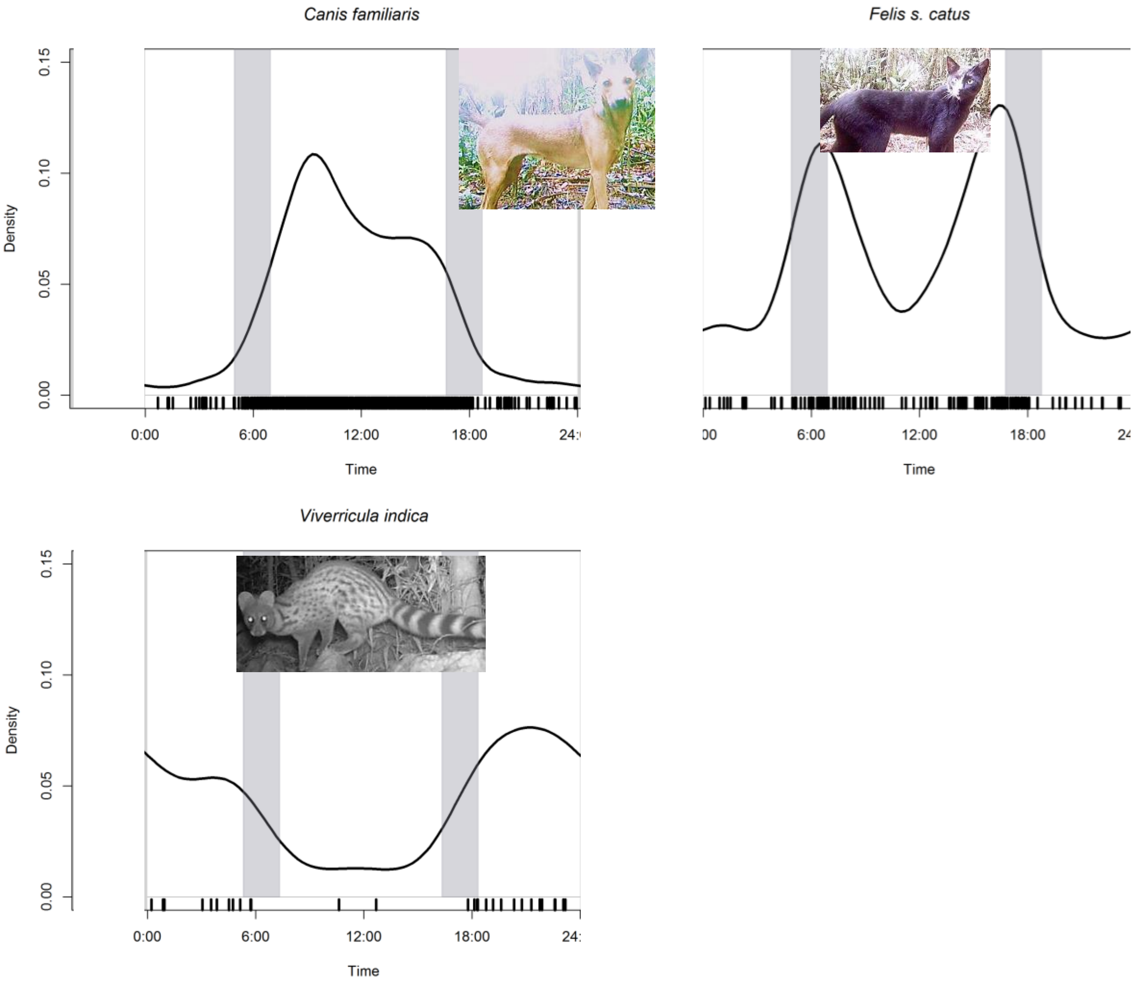
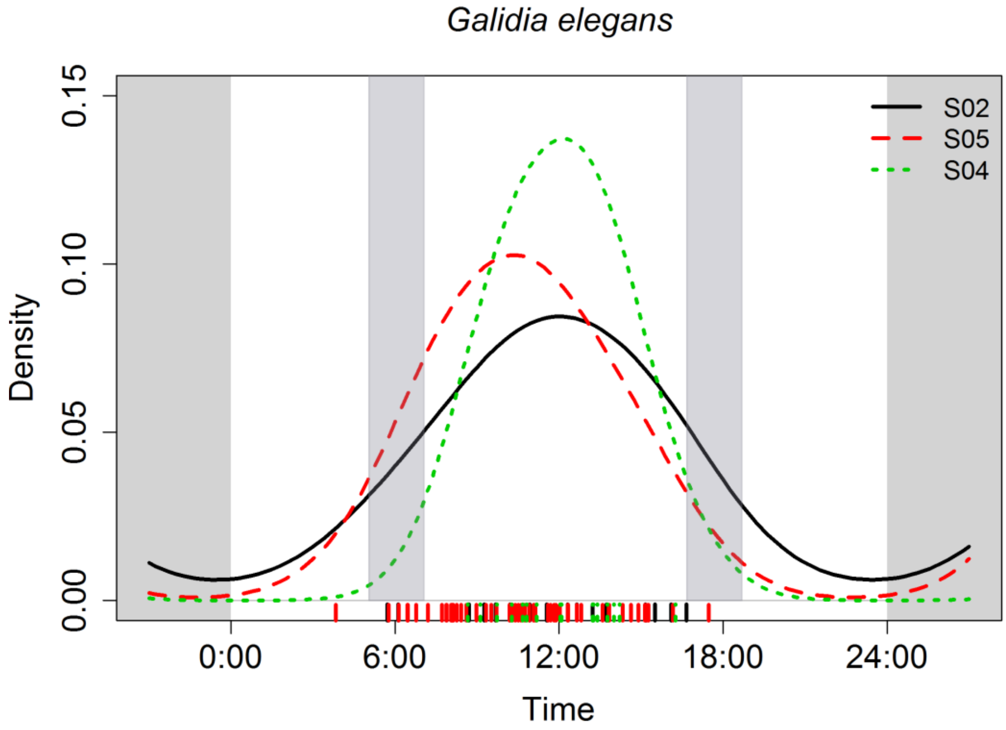
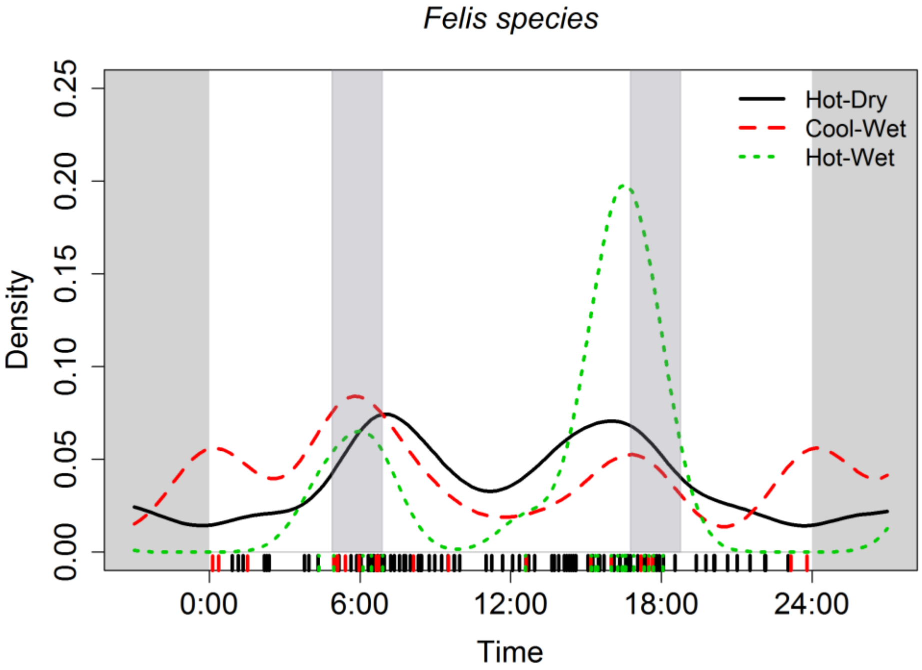


Figure 2. Temporal activity patterns resulting from Poisson regression analysis including the number of photographic captures (black bars on x-axis) across diel cycle (dawn and dusk in gray bars; day and night in white) plotted by the density of temporal activity (y-axis), where higher density represents increased activity, for A) six native and B) three exotic carnivores across the Masoala-Makira landscape. Photographic sampling occurred from 2008 to 2013.

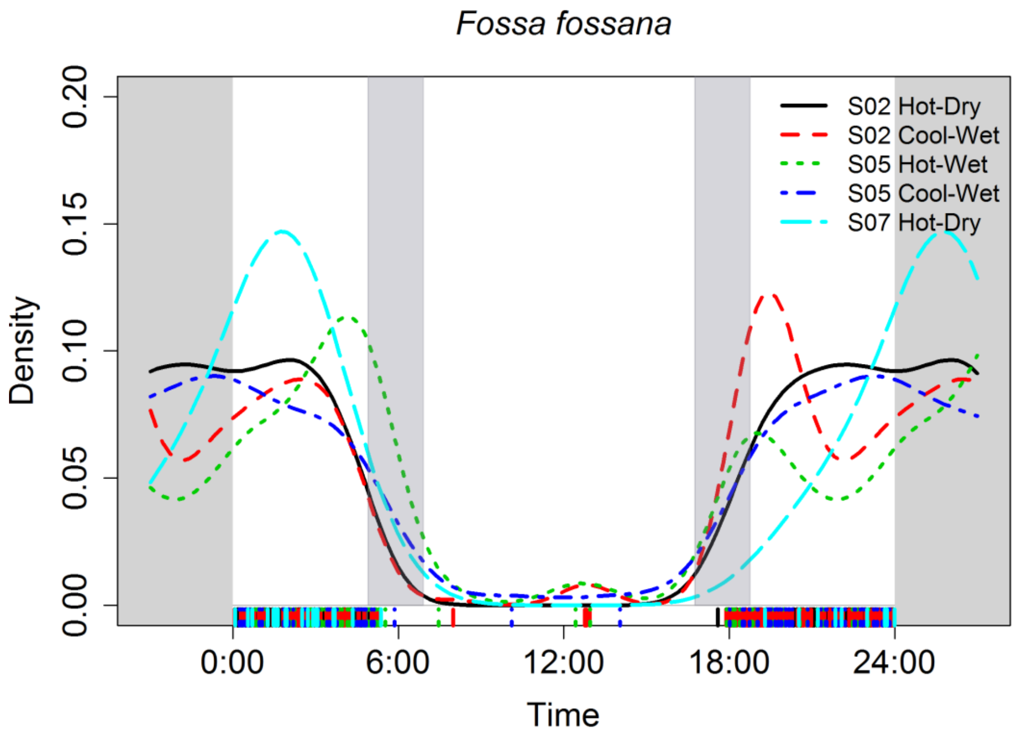
A


Galidia elegans
Density
0.00
0.05
0.10
0.15
S02
S05
S04
0:00
6:00
12:00
18:00
24:00
Time

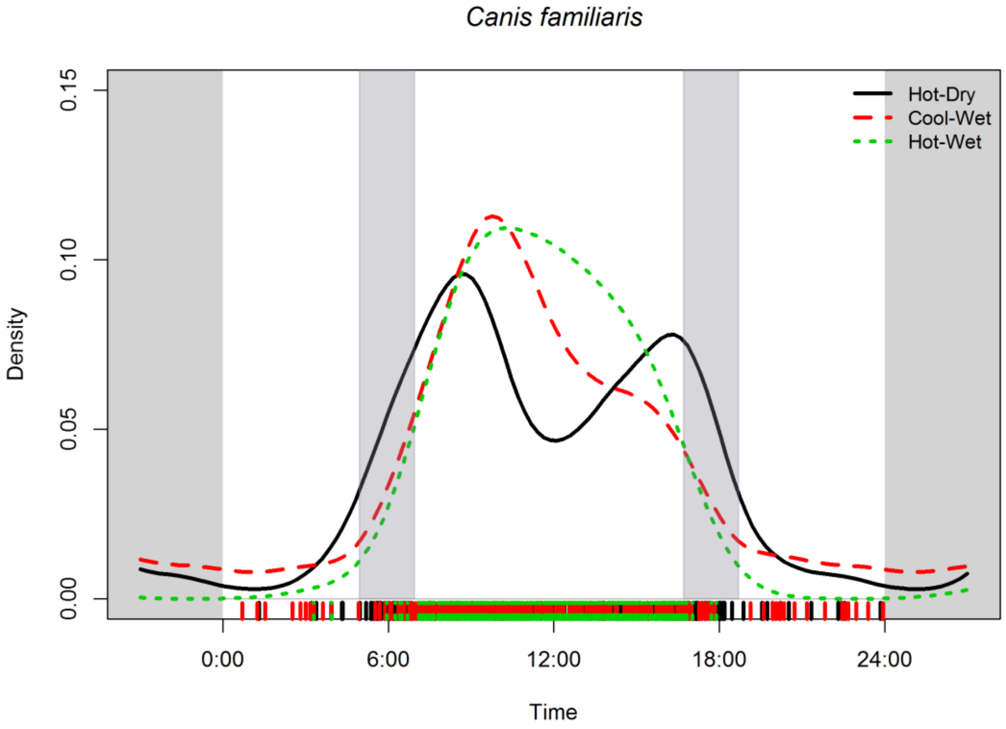
B.


Felis species
Density
0.00
0.05
0.10
0.15
0.20
0.25
Hot-Dry
Cool-Wet
Hot-Wet
0:00
6:00
12:00
18:00
24:00
Time

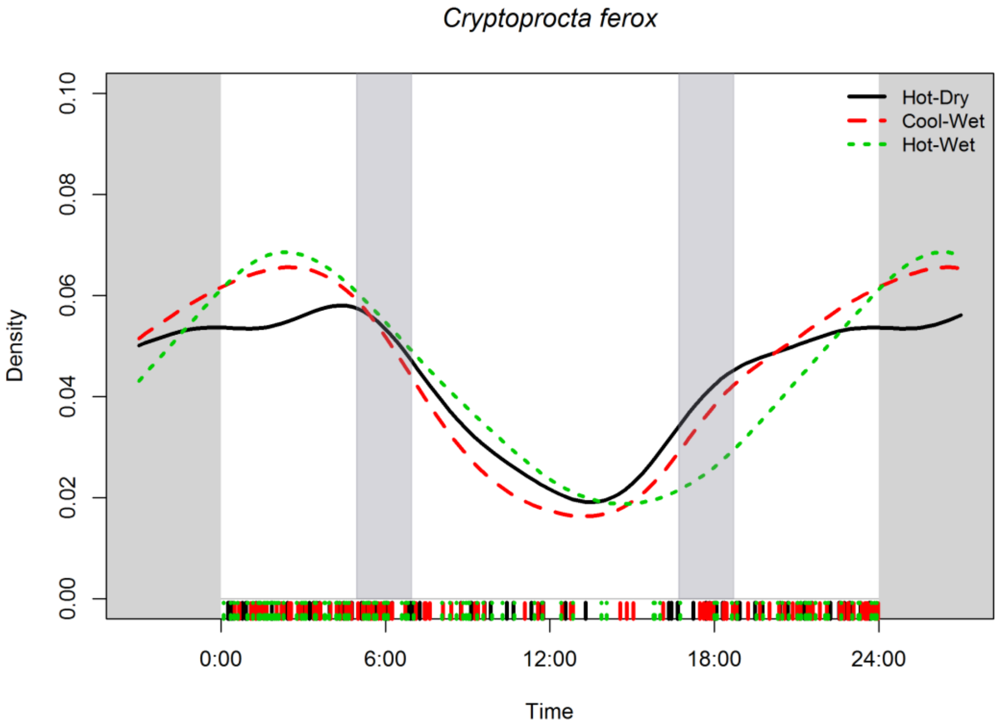
C.


Fossa fossana
Density
0.00
0.05
0.10
0.15
0.20
Time
0:00
6:00
12:00
18:00
24:00
S02 Hot-Dry
S02 Cool-Wet
S05 Hot-Wet
S05 Cool-Wet
S07 Hot-Dry

D.


Canis familiaris
Density
0.00
0.05
0.10
0.15
Time
0:00
6:00
12:00
18:00
24:00
Hot-Dry
Cool-Wet
Hot-Wet

E.


Cryptoprocta ferox
Hot-Dry
Cool-Wet
Hot-Wet
Density
0.10
0.08
0.06
0.04
0.02
0.00
0:00
6:00
12:00
18:00
24:00
Time

F.

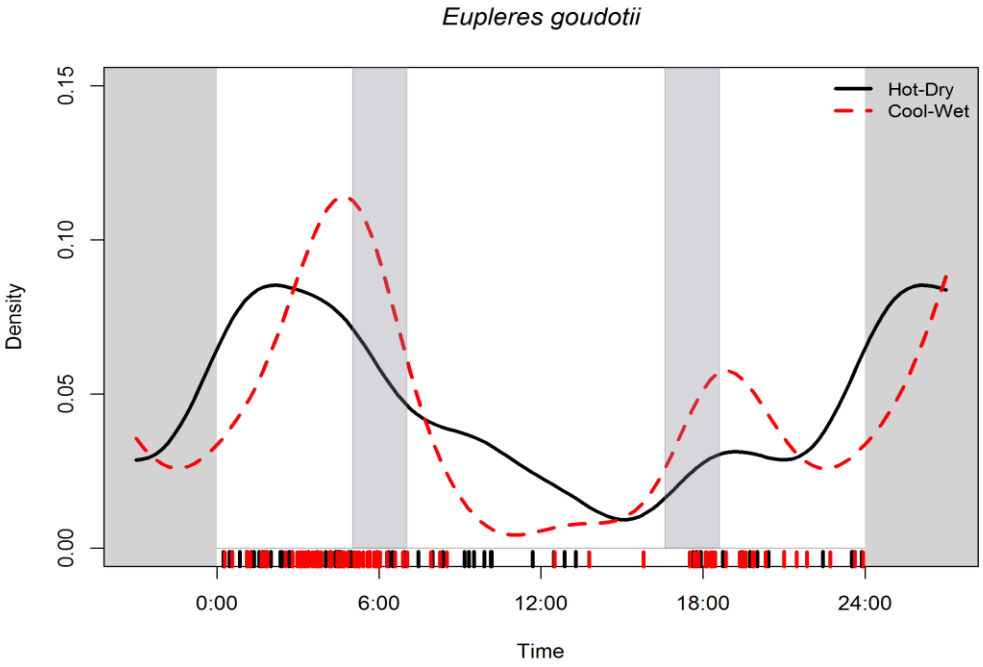

Eupleres goudotii
Hot-Dry
Cool-Wet
Density
0.15
0.10
0.05
0.00
0:00
6:00
12:00
18:00
24:00
Time

Figure 3. Temporal activity patterns revealed by number of photographic captures across diel cycle (x-axis) plotted by density of temporal activity (y-axis) for A) ring-tail vontsira *Galidia elegans* across study sites 02, 04, and 05; B) feral/wild cat *Felis species* across three seasons (hot-dry, hot-wet, and cool-wet); C) spotted fanaloka *Fossa fossana* across five site and season combinations; D) dog *Canis familiaris* across three seasons; E) fosa *Cryptoprocta ferox* across three seasons; and F) falanouc *Eupleres goudotii* across two seasons (hot-dry and cool-wet). Activity patterns for ring-tail vontsira *G. elegans,* feral/wild cat *Felis sp.*, and spotted fanaloka *F. fossana* represent the highest ranking model from the kernel density estimation. I did not estimate activity patterns for target carnivore species at individual study sites and seasons having fewer than 15 captures.

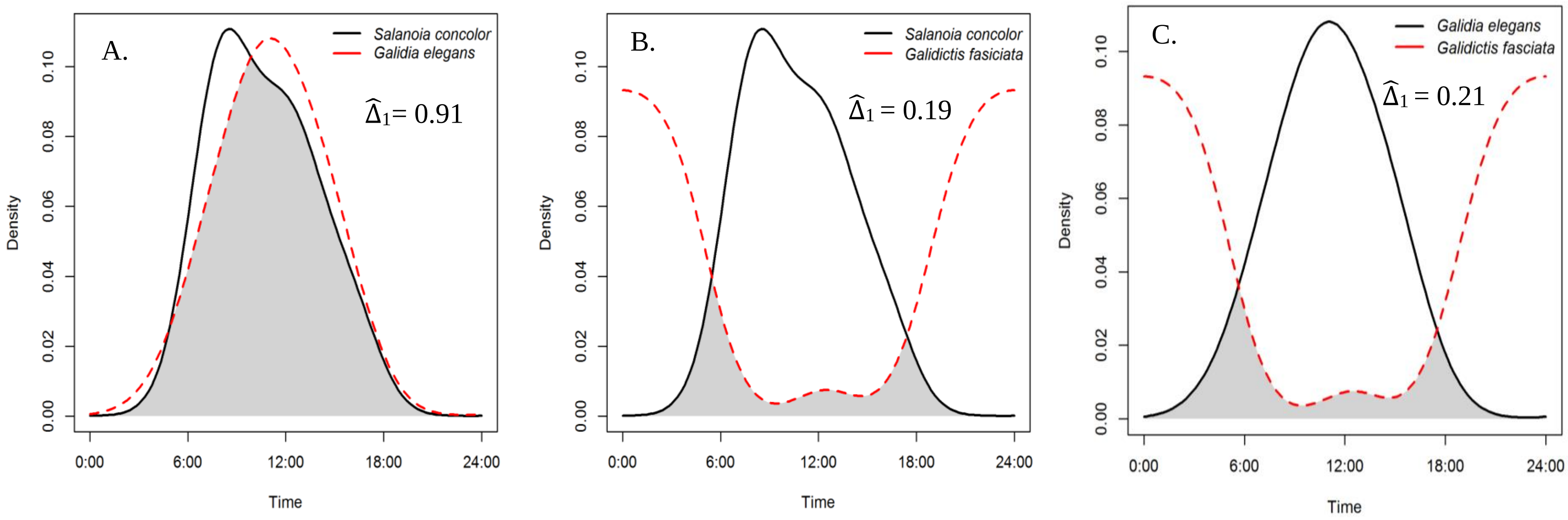


Figure 4. Level of overlap, measured by Δˆ1 estimate and shaded in gray, for activity patterns, resulting from number of photographic captures across diel cycle (x-axis) plotted by density of temporal activity (y-axis), for the similar small-bodied vontsira carnivores, measured by Δˆ1 estimate, based on kernel density estimates between A) brown-tail vontsira *S. concolor* and ring-tail vontsira *G. elegans*; B) brown-tail vontsira *S. concolor* and broad-stripe vontsira *G. fasciata*; and C) ring-tail vontsira *G. elegans* and broad-stripe vontsira *G. fasciata*.

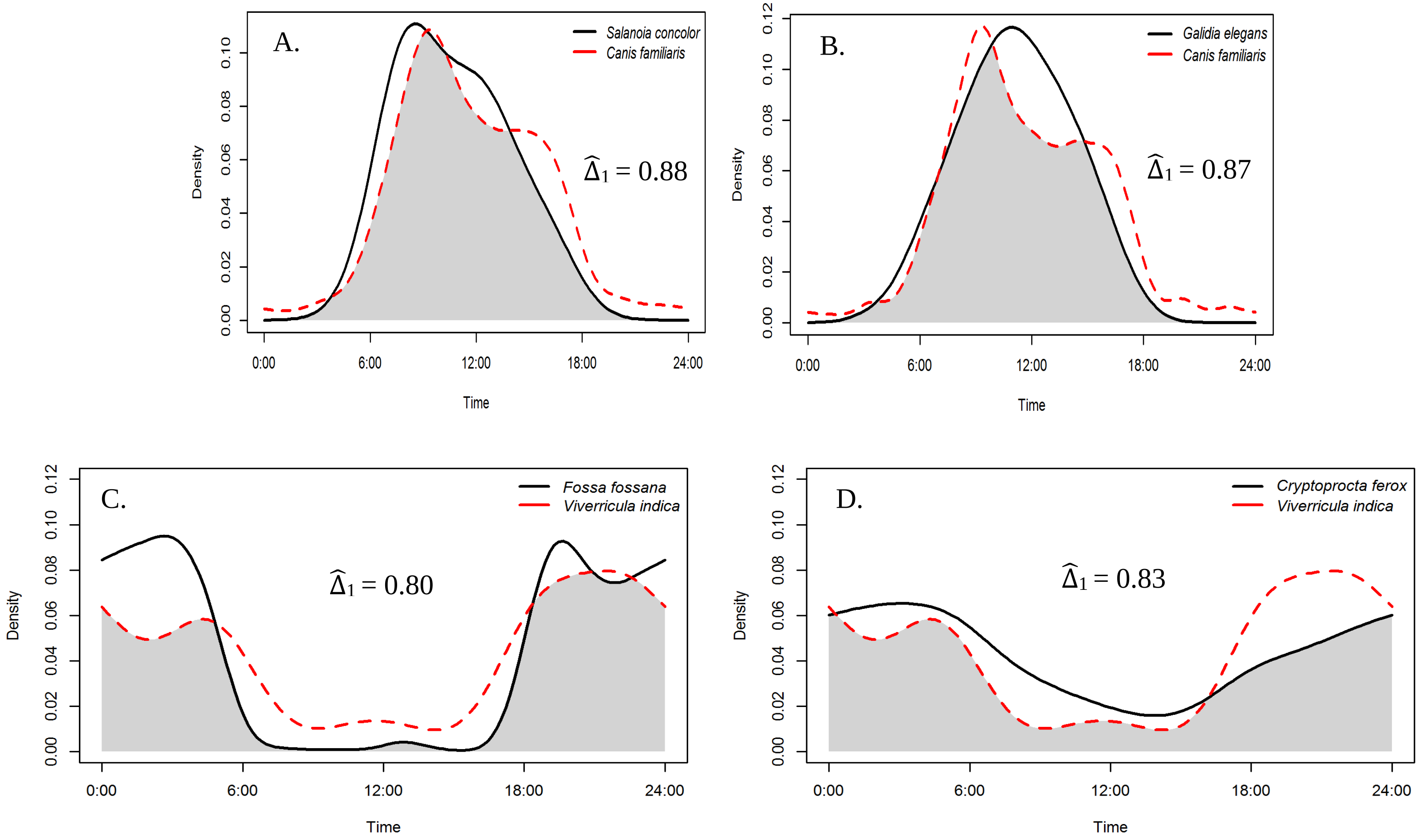

A.
Salanoia concolor
Canis familiaris
$\hat{\Delta}_1 = 0.88$
Density
0.00
0.02
0.04
0.06
0.08
0.10
0:00
6:00
12:00
18:00
24:00
Time
B.
Galidia elegans
Canis familiaris
$\hat{\Delta}_1 = 0.87$
Density
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0:00
6:00
12:00
18:00
24:00
Time
C.
Fossa fossana
Viverricula indica
$\hat{\Delta}_1 = 0.80$
Density
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0:00
6:00
12:00
18:00
24:00
Time
D.
Cryptoprocta ferox
Viverricula indica
$\hat{\Delta}_1 = 0.83$
Density
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0:00
6:00
12:00
18:00
24:00
Time

Figure 5. Level of overlap, measured by Δˆ1 estimate and shaded in gray, for activity patterns of native and exotic carnivores resulting from number of photographic captures across diel cycle (x-axis) plotted by density of temporal activity (y-axis), including A) brown-tail vontsira *S. concolor* and dog *C. familiaris*; B) ring-tail vontsira *G. elegans* and dog *C. familiaris*; C) spotted fanaloka *F. fossana* and Indian civet *V. indica*; D) fosa *C. ferox* and Indian civet *V. indica*.

Table 1. Characteristics and background of the six native and three exotic (in bold) carnivore species compared for this study. I used body weight to categorize all carnivore species as large (≥ 3.5kg), medium (1.3 – 3.5 kg), and small (≤ 1.1 kg).

Species (Common name)	IUCN Classification[a]	Weight (kg)[b,c]	Activity Pattern (Primary-Secondary)	Habitat Preference	Diet
Large carnivores					
Domestic dog *Canis familiaris*	-	Variable	Variable [b,d]	Degraded/fragmented forest, near anthropogenic areas [b,c]	Unknown in forest habitat (lemurs, small mammals likely)
Fosa *Cryptoprocta ferox*	Vulnerable	5.5-9.9	Nocturnal-Crepuscular [b,e,f,g]	Contiguous dry and humid forest [b,c]	Lemurs, small mammals, small vertebrates [c]
Feral cat *Felis species*	-	3.5-8.0	Variable [b]	Variable [b,c,d]	Unknown in forest habitat (lemurs, small mammals likely)
Medium carnivores					
Falanouc *Eupleres goudotii*	Near Threatened	1.5-4.6	Crepuscular-Nocturnal [b,e,g]	Contiguous humid forest, near marsh/aquatic areas [b,c,d]	Small vertebrates and invertebrates [c]

Table 1. Continued from previous page.

Indian civet *Viverricula indica*	Least Concern	2.0-4.0	Nocturnal [b,h]	Degraded/fragmented forest, near anthropogenic areas [b,c,d]	Unknown in forest habitat, small mammals likely
Spotted fanaloka *Fossa fossana*	Near Threatened	1.3-2.1	Nocturnal [b]	Contiguous humid forest, near marsh/aquatic areas [b,c,d]	Small mammals, amphibians, crustaceans, invertebrates [c]
<u>Small carnivores</u>					
Ring-tail vontsira *Galidia elegans*	Least Concern	0.76-1.10	Diurnal-Crepuscular[b,c,i]	Contiguous/degraded humid forests, near anthropogenic areas [b,c,d]	Highly variable (lemurs, small mammals, birds, reptiles, fish) [c]
Broad-stripe vontsira *Galidictis fasciata*	Near Threatened	0.6-1.0	Nocturnal [b,j]	Contiguous/degraded humid forest [b,c,d]	Small vertebrates (rodents, reptiles, amphibians, and invertebrates) [c]
Brown-tail vontsira *Salanoia concolor*	Vulnerable	0.55-0.75[c]	Diurnal [k,l]	Contiguous/degraded humid forest [b,c,d]	Invertebrates [c]

a (IUCN 2014); b (Gerber et al. 2012a, Goodman 2012); c (Goodman 2012); d (Farris Chapter 2); e (Albignac 1972); f (Hawkins 1998); g (Dollar 1999); h (Su and Sale 2007); i (Goodman 2003a); j (Goodman 2003b); k (Britt and Virkaitis 2003); l (Farris et al. 2012)

Table 2. Summary of independent photographic “captures” by season across the landscape from 2008 to 2013. The camera trapping sampling effort varied by season with 201, 125, and 374 trap nights during the hot-dry, hot-wet, and cool-wet, respectively.

Common Name	# Photographic Captures by Season Hot-Dry (n = 2 sites)	Hot-Wet (n = 2 sites)	Cool-Wet (n = 5 sites)	Total Photographic Captures
Fosa	98	112	142	352
Spotted fanaloka	377	88	302	767
Falanouc	76	5	121	202
Ring-tail vontsira	46	61	47	154
Broad-stripe vontsira	61	5	32	98
Brown-tail vontsira	25	0	41	66
Domestic dog	357	395	383	1135
Feral cat	3	24	146	173
Indian civet	8	2	34	44

Table 3. Relative preference of activity period (dawn, day, dusk, and night) based on number of photographic captures, mean photographic capture rate (photos/available hours) ordered from highest to lowest activity, and probability of overlap with the most active time period. The number of hours available in each time category is corrected using an offset and carnivores having < 15 captures at a given study site were excluded from analysis.

Common Name	Time period – ordered by use			
Fosa	Night	Day	Dawn	Dusk
# Captures	182	68	54	32
Photo. Rate (SE)	0.13 (0.06)	0.07 (0.02)	0.02 (0.02)	0.02 (0.01)
Prob. Overlap	-	0.48	0.09	0.05
Spotted fanaloka	Night	Dusk	Dawn	Day
# Captures	617	67	49	4
Photo. Rate (SE)	0.65 (0.49)	0.03 (0.02)	0.02 (0.02)	0.01 (0.01)
Prob. Overlap	-	0.07	0.06	0.01
Falanouc	Night	Dawn	Day	Dusk
# Captures	99	52	24	20
Photo. Rate (SE)	0.16 (0.08)	0.06 (0.04)	0.03 (0.02)	0.01 (0.01)

Table 3. Continued from previous page.

Prob. Overlap	-	0.28	0.04	0.01
Broad-stripe vontsira	Night	Dawn	Dusk	Day
# Captures	67	11	3	0
Photo. Rate (SE)	0.19 (0.04)	0.02 (0)	0 (0)	0 (0)
Prob. Overlap	-	0.09	0	0
Ring-tail vontsira	Day	Dawn	Dusk	Night
# Captures	132	13	2	0
Photo. Rate (SE)	0.24 (0.14)	0.01 (0.02)	0.01 (0.01)	0 (0)
Prob. Overlap	-	0.06	0.03	0.01
Brown-tail vontsira	Day	Dawn	Dusk	Night
# Captures	54	4	2	0
Photo. Rate (SE)	0.16 (0.09)	0.01 (0.01)	0.01 (0.01)	0 (0)
Prob. Overlap	-	0.05	0.03	0.01
Domestic dog	Day	Dawn	Dusk	Night
# Captures	851	73	61	44

Table 3. Continued from previous page.

Photo. Rate (SE)	0.32 (0.14)	0.02 (0.02)	0.02 (0.01)	0.01 (0.01)
Prob. Overlap	-	0.22	0.20	0.15
Feral cat	Day	Dusk	Night	Dawn
# Captures	73	30	33	37
Photo. Rate (SE)	0.14 (0.08)	0.08 (0.06)	0.05 (0.04)	0.04 (0.04)
Prob. Overlap	-	0.58	0.34	0.27
Indian civet	Night	Dusk	Day	Dawn
# Captures	33	4	4	2
Photo. Rate (SE)	0.33 (0.07)	0.06 (0.03)	0.05 (0.02)	0.03 (0.02)
Prob. Overlap	-	0.01	0	0

Table 4. Temporal overlap, based on $\widehat{\Delta}_1$ estimates from kernel density analyses, among native and exotic (bold) carnivore pairings with similarities (+) and differences (-) in niche (habitat use and diet) and body size listed from highest to lowest amount of temporal overlap. Photographic sampling for kernel density estimation took place from 2008 to 2013.

Species 1	Species2	Niche	Body Size	$\widehat{\Delta}_1$
Brown-tail v.	Ring-tail v.	-	+	0.91
Brown-tail v.	**Dog**	-	-	0.88
Ring-tail v.	**Dog**	+	-	0.87
Falanouc	Fosa	-	-	0.86
Broad-stripe v.	**Indian civet**	-	-	0.83
Fosa	**Indian civet**	-	-	0.82
Spotted fanaloka	**Indian civet**	-	+	0.80
Fosa	Broad-stripe v.	-	-	0.76
Falanouc	**Indian civet**	-	+	0.74
Falanouc	Broad-stripe v.	-	-	0.72
Spotted fanaloka	Fosa	-	-	0.70
Falanouc	Spotted fanaloka	+	+	0.68

Table 4. Continued from previous page.

Feral cat	**Dog**	+	+	0.67
Fosa	**Feral cat**	-	+	0.65
Falanouc	**Feral cat**	-	-	0.63
Brown-tail v.	**Feral cat**	-	-	0.61
Ring-tail v.	**Feral cat**	+	-	0.56
Feral cat	**Indian civet**	+	-	0.56
Fosa	**Dog**	-	+	0.44
Broad-stripe v.	**Feral cat**	-	-	0.42
Fosa	Ring-tail v.	-	-	0.42
Fosa	Brown-tail v.	-	-	0.41
Falanouc	**Dog**	-	-	0.39
Falanouc	Ring-tail v.	-	-	0.37
Falanouc	Brown-tail v.	-	-	0.36
Dog	**Indian civet**	+	-	0.33
Brown-tail v.	**Indian civet**	-	-	0.29

Table 4. Continued from previous page.

Ring-tail v.	**Indian civet**	+	-	0.23
Broad-stripe v.	**Dog**	-	-	0.23
Ring-tail v.	Broad-stripe v.	-	+	0.21
Brown-tail v.	Broad-stripe v.	+	+	0.19

Appendices

Appendix C.1. Photographic captures of the six native (endemic), from largest to smallest body size, and three exotic (in bold) carnivore species captured during my surveys from 2008 to 2013 across the Masoala-Makira landscape, Madagascar, including A) fosa *Cryptoprocta ferox*; B) falanouc *Eupleres goudotii*; C) spotted fanaloka *Fossa fossana*; D) ring-tail vontsira *Galidia elegans*; E) broad-stripe vontsira *Galidictis fasciata*; F) brown-tail vontsira *Salanoia concolor*; G) **domestic dog** *Canis familiaris*; H) **feral cat** *Felis species*; and I) **Indian civet** *Viverricula indica*.


G.
09/22/12 07:05 AM MT42


H.
01/13/10 04:00 PM MT22


I.
2011-08-10 9:45:24 PM M 2/3
67°F
IDFIRE PRO

Appendix C.2. Survey details for the seven study sites (camera trapping grids), ranked from least degraded (S01) to most degraded (S07), across the Masoala-Makira landscape , including the trap success and standard error (TS, SE) for each of the six endemic and three exotic carnivore species.

		Least		Level of Degradation		Most	
Study site	Site S01	Site S02	Site S03	Site S04	Site S05	Site S06	Site S07
Survey Dates	Mar 2009 – May 2009	Sept 2008 – Nov 2008	Aug 2009 – Oct 2009	Jun 2011 – Aug 2011	Mar 2011 – May 2011	Nov 2009 – Jan 2010	Dec 2010 – Feb 2011
# of Camera Stations	20	25	19	23	23	18	24
Trap Nights	1050	1257	1067	1462	1509	881	1570
Elevation (m)	1000-1400	350-690	380-550	21-385	324-786	580-820	93-507
Fosa TS*	0.41 (0.41)	3.01 (0.98)	1.19 (0.30)	1.03 (0.35)	7.15 (1.05)	0.57 (0.20)	1.96 (0.73)
Spotted fanaloka TS	1.03 (0.49)	13.91 (2.64)	0 (0)	0 (0)	5.08 (1.35)	0.18 (0.16)	2.04 (0.36)
Falanouc TS	0 (0)	3.08 (0.89)	0 (0)	2.64 (0.82)	0.33 (0.21)	0.79 (0.27)	0.48 (0.20)
Ring-tail vontsira TS	0.39 (0.18)	1.33 (0.45)	0.09 (0.09)	1.11 (0.29)	3.75 (1.63)	0.51 (0.37)	0.45 (0.20)
Broad-striped vontsira TS	0.18 (0.13)	2.57 (0.86)	0.19 (0.13)	0.13 (0.13)	0.20 (0.11)	1.31 (0.40)	1.08 (0.37)
Brown-tailed vontsira TS	0 (0)	0.98 (0.30)	0 (0)	0 (0)	0 (0)	0 (0)	0.30 (0.17)
Domestic dog TS	0.14 (0.19)	1.97 (1.15)	4.78 (1.77)	14.91 (7.41)	26.06 (4.46)	0.09 (0.08)	19.56 (7.33)
Wild/feral cat TS	0.39 (0.19)	0 (0)	0.74 (0.26)	0 (0)	1.32 (0.48)	3.13 (1.18)	0 (0)
Indian civet TS	0 (0)	0.14 (0.14)	0.10 (0.10)	1.96 (0.74)	0.13 (0.13)	0.12 (0.10)	0.40 (0.16)
Total Bird TS	13.64 (2.76)	62.85 (9.26)	9.22 (1.78)	24.07 (3.93)	23.35 (5.04)	22.61 (3.58)	31.18 (5.48)

Appendix C.2. Continued from previous page.

Total Small Mammal TS	40.05 (5.30)	42.31 (6.84)	15.15 (3.52)	4.34 (1.20)	4.34 (1.24)	31.59 (4.31)	6.86 (1.50)
Lemur species richness	9	7	3	3	6	NA	4
Total Lemur Abundance**	1.52 (0.11)	0.89 (0.10)	0.45 (0.04)	0.98 (0.17)	0.93 (0.05)	NA	0.45 (0.03)

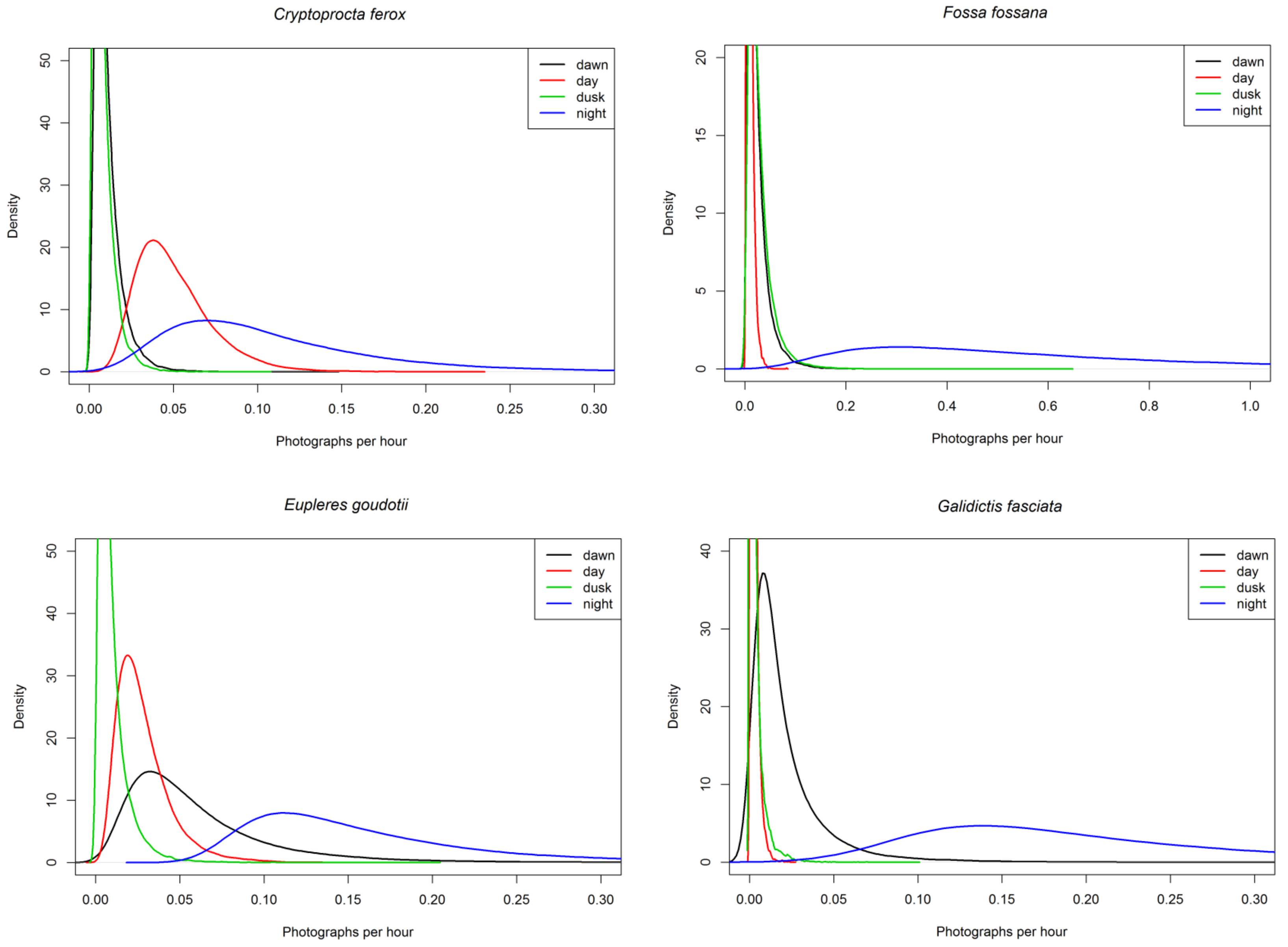
* TS: trap success is the number of independent photos of a target species divided by the trap nights multiplied by 100

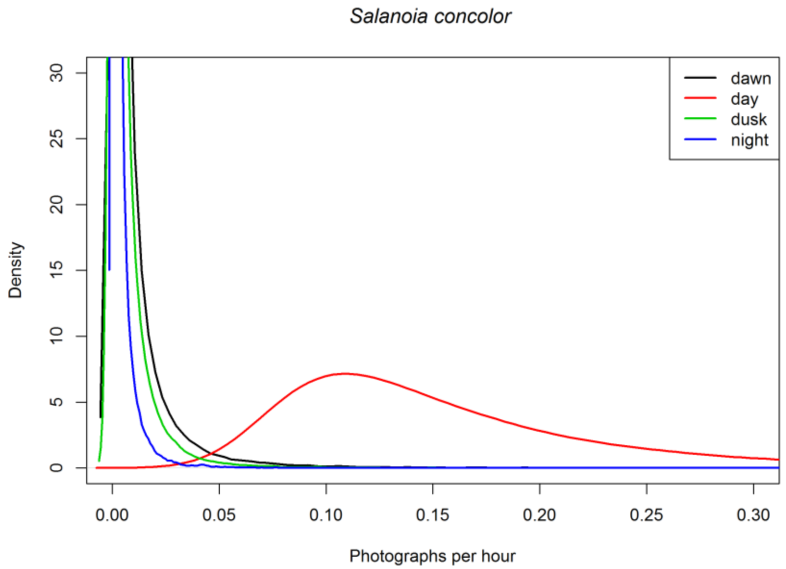
** Relative abundance = number of lemur species (diurnal and nocturnal) observed per km

Appendix C.3. I modeled temporal activity of carnivores using a hierarchical Bayesian poisson model of daily counts (*i*) of capture events in four time categories (*j*, day, night dawn, dusk) from remote cameras across study sites (*k*). An offset (log (Hours$_{ijk}$) is used to correct for different availability of time within each category. Modified from Ridout and Linkie (2009).

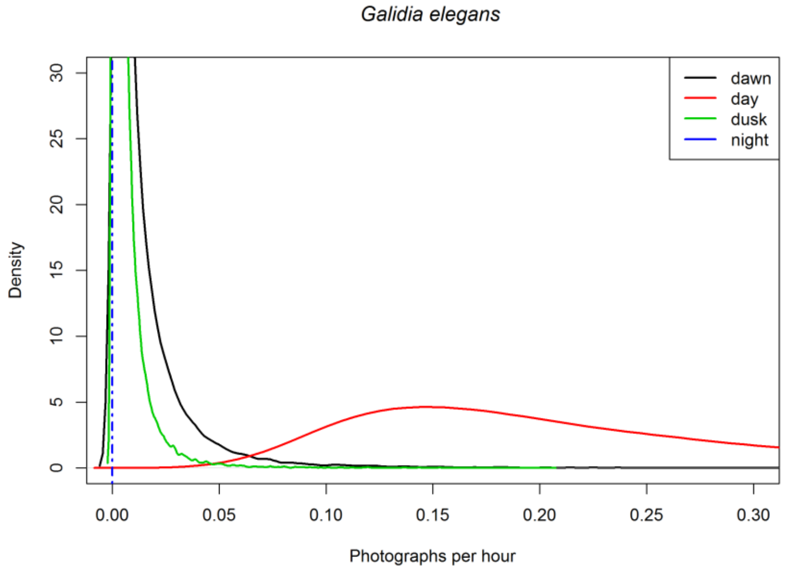
$$
\begin{array}{rl}
\text{Observation Model:} & y_{ijk} \sim Poisson\,(\lambda_{ijk}) \\
\text{Ecological Process:} & log(\lambda_{ijk}) = log(Hours_{ijk}) + \mathbf{x}'_{jk}\beta_{jk} \\
 & \beta_k \sim N\left(\boldsymbol{\mu}, \sigma^2\boldsymbol{I}\right) \\
 & \\
\text{Prior Information:} & \boldsymbol{\mu} \sim N(\mathbf{0}, 100\text{x}\boldsymbol{I}), \qquad log(\sigma^2) \sim N\,(0, 100) \\
 & \beta_k \sim N(\mathbf{0}, 100\text{x}\boldsymbol{I}) \\
 & \\
\text{Joint Posterior Distribution:} & [\beta, \boldsymbol{\mu}, \sigma^2|\boldsymbol{y}] \propto [\boldsymbol{y}|\beta][\beta|\boldsymbol{\mu}, \sigma^2][\boldsymbol{\mu}][\sigma^2][\beta]
\end{array}
$$

Appendix C.4. Posterior distribution graphs demonstrating the temporal activity patterns for six native and three exotic carnivore species across dawn, day, dusk, and night time periods. Temporal data result from photographic sampling across seven study sites from the Masoala-Makira landscape from August 2008 to November 2013.

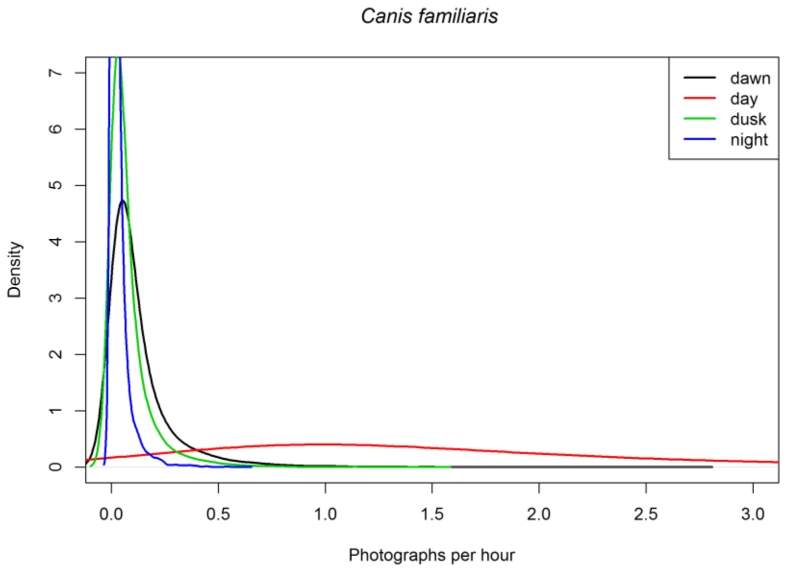




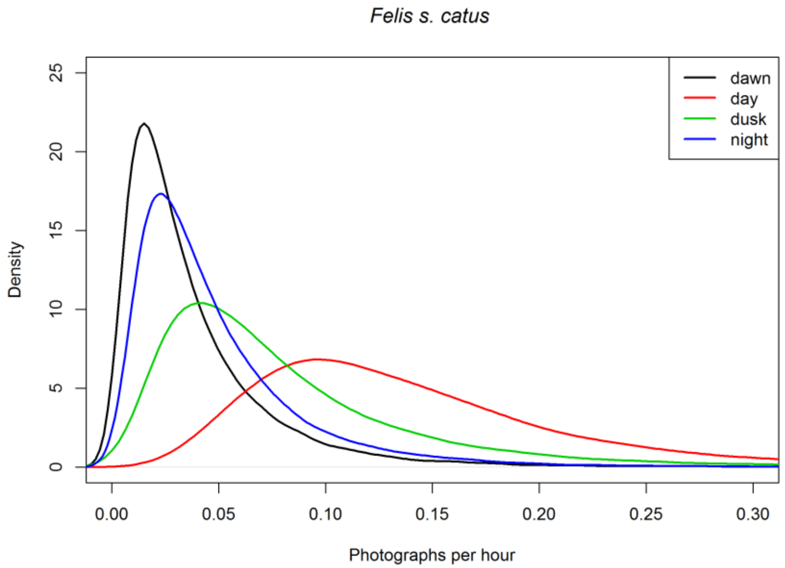
Salanoia concolor



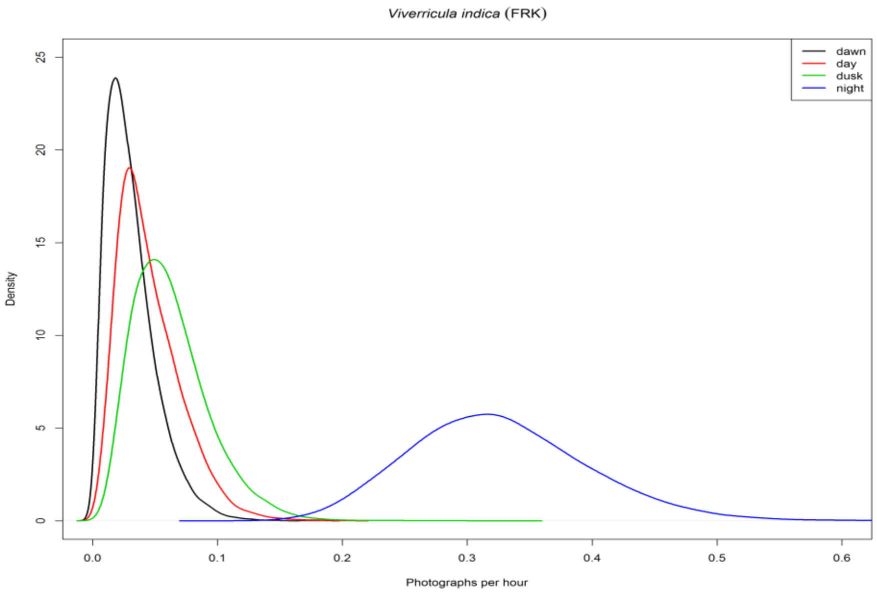
Galidia elegans



Canis familiaris



Felis s. catus


Viverricula indica (FRK)
dawn
day
dusk
night
Density
0
5
10
15
20
25
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Photographs per hour

Appendix C.5. Kernel density estimation model results including AIC value, delta AIC, model likelihood, AIC weight, and number of parameters (K). Species broad-stripe vontsira *G. fasciata*, brown-tail vontsira *S. concolor,* and Indian civet *V. indica* had < 15 captures for all study sites which excluded them from analysis. Photographic sampling for kernel density estimation took place across seven study sites (Site) and three seasons (Season) from 2008 to 2013.

Species	MODEL	AIC	Delta AIC	Model Likelihood	AIC weight	K
Fosa	Null	-63.36	0.00	1.00	0.66	1
	Season	-61.27	2.08	0.35	0.23	3
	Site	-59.21	4.15	0.13	0.08	4
	Season*Site	-56.03	7.32	0.03	0.02	6
Spotted fanaloka	Season*Site	-648.70	0.00	1.00	0.85	5
	Season	-643.99	4.70	0.10	0.08	3
	Site	-643.74	4.95	0.08	0.07	3
	Null	-633.02	15.68	0.00	0.00	1
Falanouc	Null	-48.30	0.00	1.00	0.50	1
	Site	-46.64	1.66	0.44	0.22	2
	Season	-46.38	1.91	0.38	0.19	2
	Season*Site	-44.65	3.65	0.16	0.08	3
Ring-tail vontsira	Site	-104.17	0	1	0.51	3
	Null	-104.08	0.09	0.96	0.49	1
Dog	Null	-608.78	0.00	1.00	0.72	1
	Season	-606.29	2.49	0.29	0.21	3
	Site	-603.27	5.51	0.06	0.05	5
	Season*Site	-601.23	7.55	0.02	0.02	7
Feral/wild cat	Season	-14.47	0.00	1.00	0.62	3
	Season*Site	-13.01	1.46	0.48	0.30	7
	Null	-9.28	5.19	0.08	0.05	1
	Site	-9.00	5.47	0.07	0.04	5

Chapter 4

PATTERNS OF SPATIAL CO-OCCURRENCE AMONG ENDEMIC AND EXOTIC CARNIVORES, NE MADAGASCAR

Abstract

As human populations continue to increase and encroach on remaining natural habitats, commensal exotic carnivores such as dogs and cats will likewise increase in number and range and increasingly interact with native carnivores and other wildlife. We know relatively little about the effects of domestic and/or feral dogs and cats on native carnivore populations. Two-species occupancy models are a tool that enable investigations of spatial interactions among exotic carnivores and native wildlife. I combined photographic sampling and two-species occupancy modeling to provide the first assessment of the spatial co-occurrence of native and exotic carnivores in Madagascar along with an examination of habitat characteristics that might explain observed relationships across a diverse rainforest landscape in NE Madagascar. My photographic surveys from 2008 to 2013 resulted in 2,991 captures of native and exotic carnivores across 8,854 trap nights. My estimates of co-occurrence among native and exotic carnivores in rainforest habitat reveal that native and exotic carnivores occur together less often than expected and that exotic carnivores may be replacing native carnivores, particularly in forests nearest villages. Six of the native carnivores within this study reveal higher occupancy in the absence of exotic carnivores (psiNe > psiNE; where N is native and E is exotic) while their corresponding species interaction factors (SIF) revealed a lack of co-occurrence (i.e. occurred together less than expected than if independent; SIF < 1.0). I found that nocturnal and/or crepuscular native carnivores (i.e. falanouc *Eupleres goudotii*, spotted fanaloka *Fossa fossana*, and broad-stripe vontsira *Galidictis fasciata*) were less likely to co-occur with exotic carnivores

compared to diurnal native carnivores (i.e. ring-tail vontsira *Galidia elegans* and brown-tail vontsira *Salanoia concolor*). Further, I found that native carnivores were less likely to co-occur with exotic carnivores in patchy forest located nearest villages. I demonstrate the effectiveness of combining photographic sampling with co-occurrence models to investigate the effects of exotic carnivores on an entire community of native carnivores. I recommend a combination of targeted educational and removal programs to combat the influx of exotic carnivores and their replacement of native carnivores.

Introduction

Understanding spatial interactions (i.e. level of co-occurrence and behavioral responses to co-occurring species) is of great importance to community ecologists. Spatial interactions are important for addressing questions of community membership, including how communities are shaped and structured (via biotic interactions or random assembly), why some species become members of a community and some do not (i.e. inclusion vs. rejection), and which selection criteria are most important for community assembly (Diamond 1975, Lazenby and Dickman 2013, Ritchie et al. 2009, Weiher and Keddy 1999, Wootton and Emmerson 2005). Investigating co-occurrence and asymmetrical interactions among species, particularly between predator-prey, different sized predators, competitors, and native-exotic species, allows researchers to investigate concepts, such as competitive exclusion, resource partitioning, predator-prey dynamics, and ecological constraints (Lazenby and Dickman 2013, Lockwood et al. 1999, Luiselli 2006, MacKenzie et al. 2004, Waddle et al. 2010).

As exotic carnivores (primarily domestic/feral dogs and cats) continue to increase worldwide in number and range, their interactions with native wildlife species continue to mount. Recent work has highlighted the negative impacts of these exotic carnivores, particularly feral dogs (Hughes and Macdonald 2013), on wildlife populations worldwide. Moreover, recent work in Madagascar has highlighted the influx of exotic carnivores and, for the first time, estimated population parameters for these exotic species (Farris Chapter 2, Chapter 3; Farris et al. 2014; Gerber et al. 2012a, b). This research has demonstrated the overlap in temporal activity, habitat use, diet, and body size among native and exotic carnivores; however, the spatial interactions of native and exotic carnivores, including the variables influencing these interactions, remain little studied for Madagascar and similar habitats worldwide. In fact, to my knowledge, the co-occurrence and spatial interactions among multiple, sympatric native and exotic carnivores has yet to be investigated for any habitat worldwide.

Spatial co-occurrence, or two-species interaction occupancy, models provide a framework to investigate asymmetrical interactions and/or behavioral responses for co-occurring species (Bailey et al. 2009, MacKenzie et al. 2004, Richmond et al. 2010, Waddle et al. 2010). In particular, these models provide an estimate of co-occurrence between two or more species within a maximum likelihood framework while accounting for imperfect detection (MacKenzie et al. 2004), thus allowing the investigation of various ecological interactions, such as competition, predator-prey dynamics, community assembly, and native and exotic species interactions. As a result, these models have been used to investigate interactions among a variety of taxa, including mammals (Farris et al. 2014, Lazenby and Dickman 2013, Santulli et al. 2014, Williamson and Clark 2011), birds (Bailey et al. 2009, Haynes et al. 2014, Richmond et al. 2010, Sauer et al. 2013), reptiles (França and Araújo 2007, Luiselli 2006, Steen et al. 2014), and amphibians (MacKenzie et al. 2004, Olson et al. 2012, Waddle et al. 2010). However, the use of this spatial modeling approach to investigate the influence of exotic carnivores on native wildlife is currently limited (Krauze-Gryz et al. 2012, Santulli et al. 2014).

My goal was to provide the first assessment of the spatial co-occurrence of native and exotic carnivores within a complex native-exotic carnivore community. To achieve this goal I photographically sampled carnivores across a diverse rainforest landscape and estimated the co-occurrence and/or co-detection, with the inclusion of station-level habitat and landscape variables, prey species, and human presence as covariates, among all native (fosa *Cryptoprocta ferox*, falanouc *Eupleres goudotii*, spotted fanaloka *Fossa fossana*, ring-tail vontsira *Galidia elegans*, broad-stripe vontsira *Galidictis fasciata*, and brown-tail vontsira *Salanoia concolor*) and exotic (domestic dog *Canis familiaris*, feral cat *Felis species,* and Indian civet *Viverricula indica*) carnivore pairings having sufficient captures for model convergence. I expected to find a lack of co-occurrence among native and exotic carnivores as contiguous, non-anthropogenic forest increased and strong co-occurrence where forest became more degraded, patchy, and/or fragmented and where exotic carnivore and human activity has been shown to increase.

Methods

Study site

The Masoala-Makira landscape, consisting of the newly designated (2013) Makira Natural Park (372,470 ha of protected area and 351,037 ha of community management zone), as well as Masoala National Park (240,000 ha), represents the largest protected area landscape in Madagascar (Holmes 2007, Kremen 2003). This landscape is estimated to have the highest levels of biodiversity in Madagascar, but faces numerous anthropogenic threats, including exotic carnivores, poaching, human encroachment, and fragmentation (Farris et al. 2014, Golden 2009, Golden et al. 2014, Holmes 2007). I photographically sampled carnivores from 2008 to 2013 at seven sites having various levels of degradation and fragmentation across the Masoala-Makira landscape (Appendix A). These seven study sites were selected as part of an on-going research project investigating the effects of habitat fragmentation and degradation, exotic species, and human encroachment on Madagascar's native carnivores and lemurs (Farris et al. 2012, Farris et al. 2014, Farris and Kelly 2011). At two of the seven study sites I conducted repeat surveys, providing a total of thirteen surveys across the landscape.

Photographic Sampling

I established camera grids, consisting of 18-25 camera stations per grid, at each of the seven study sites across the Masoala-Makira landscape (Figure 1) and surveyed each site an average of 67 days ± SD 8.10. I placed two digital (Reconyx PC85 & HC500, Wisconsin, USA; Moultrie D50 & D55, Alabama, USA; Cuddeback IR, Wisconsin, USA) and/or film-loaded (DeerCam DC300) remote sensing cameras at each camera station, spaced approximately 500m apart, within the camera grid. I placed cameras on opposing sides of human (0.5-2.0 m wide) and game (< 0.5 m wide) trails (establishing newly cut trails was avoided whenever possible) to capture both flanks of passing wildlife. I offset cameras to prevent mutual flash interference and I paired each camera with an opposing brand or model of camera to compensate for inefficiency in detection speed, flash, or photo quality of various camera models. I checked cameras every 5-10 days to change batteries, memory cards and/or film, and to ensure proper functioning. I placed cameras 20-30 cm off the ground, allowed them to run 24 h/day, and I used no bait or lure.

Station-level habitat and Landscape Sampling

To measure station-level habitat features (Appendix A) for use in occupancy models I sampled vegetation at each camera station by walking a 50 m transect in three directions (0, 120, and 240 degrees) starting at each individual camera station. At 25 m and 50 m on each transect I used the point-quarter method (Pollard 1971) to estimate tree density and basal area, recording DBH for any stem/tree with ≥ 5 cm diameter. At 20 m and 40 m I established a 20 m transect running perpendicular to the established 50 m station-level habitat transect and I measured understory cover at three levels (0-0.5 m, 0.5-1.0 m, and 1.0-2.0 m) by holding a 2 m pole perpendicular to the ground at one meter intervals and recording presence (1 = vegetation touching pole) or absence (0 = no vegetation touching pole) of understory cover (Davis et al. 2011). Finally, at each 10 m interval along each transect I estimated the canopy height and percent cover. I used this sampling array, including the sampling scale, to provide station-level habitat sampling covariates for Madagascar's small-bodied native carnivores for use in my landscape and site-specific occupancy models.

To understand how landscape features (Appendix A) influence carnivore co-occurrence I used Landsat satellite imagery (2004, 2006, and 2009) and classified the following cover types using Erdas Imagine (Intergraph Corporation): rainforest, degraded forest, and matrix (non-forest area exhibiting early succession, cultivation, or open fields for cattle). I placed a 500 m (landscape level) buffer around individual camera stations, dissolved these individual buffers, and clipped the classified imagery for each of the resulting seven camera grid buffers (each providing an approximately 10 – 15 km^2 area) for analysis in program FragStats (McGarigal et al. 2012). For fosa I used a 2000 m buffer around individual camera stations, rather than the initial 500m buffer, to extract more meaningful, species-specific landscape covariates given the estimated home range of this larger carnivore species (Hawkins and Racey 2005).

Using program FragStats I created the following landscape level covariates and clipped imagery from each camera grid buffer (~10 - 15 km^2) for use in my occupancy models: 1) number of patches: total number of rainforest, degraded forest, and matrix patches (based on habitat classifications from satellite imagery) within the buffer; 2) largest patch index: the percentage of total buffered area comprised by the largest rainforest patch; 3) LSI: landscape shape index or the standardized measure of total edge adjusted for the size of the buffered area (McGarigal et al. 2012); 4) percent rainforest within the buffered area; 5) percent matrix or non-forest, cultivated area within the buffered area; 6) total rainforest core area: the sum of the core areas (accounting for edge of depth of 500m) of each rainforest patch within the buffer; and 7) total edge (in meters per hectare); (McGarigal et al. 2012). Further, I provided an average distance of each camera station to the nearest forest edge (Avg. Dist. to Edge) and to the nearest village (Avg. Dist to Village; Appendix A) using satellite imagery.

Co-Occurring Species Activity

I defined a 'capture event' as all photographs of a given species within a 30 min time period (Di Bitetti et al. 2006). Further, I defined a trap night as a 24 h period during which at least one of the two cameras at a camera station is functioning properly. I calculated the trap success (TS) for each species by dividing the number of capture events by the number of trap nights at each camera station, minus malfunctions, and multiplied by 100. I calculated TS to provide a measure of activity for co-occurring humans and/or prey species (birds, small mammals) for use as covariates in my co-occurrence models.

Co-occurrence analysis and modeling

I created capture histories for each of the six native and three exotic carnivore species using daily capture events to determine the presence or absence of each species at each camera station. Using these capture histories I investigated the spatial interactions between native and exotic carnivores via co-occurrence modeling. I used the psiBa parameterization for the single-season, two-species occupancy model presented by Richmond et al. (2010) and modeled co-occurrence using program PRESENCE (Hines 2006). This parameterization provides eight estimable parameters, including the occupancy of the dominant species (psiA), occupancy of the subordinate species where the dominant is present (psiBA) and absent (psiBa), the probability of detection for the dominant species (pA) and subordinate (pB) given the other is absent, the probability of detecting dominant given both present (rA), and the probability of detecting subordinate where dominant is present (pBA) and absent (pBa). Madagascar's exotic carnivores have been shown to negatively influence the occupancy and density of native carnivores (Gerber et al. 2012a, b). Further, these exotic carnivores have a larger body size than the majority of the native carnivores (Farris, see chapter three). As a result, I used the exotic (E) carnivores as the dominant and the native (N) carnivore as the subordinate for all carnivore pairings, which in turn allowed us to investigate how the occupancy of native carnivores change in the presence (psiNE) and absence (psiNe) of exotic carnivores. In addition to these parameters, I derived a species interaction factor (SIF) for each carnivore pairing based on the formula provided by Richmond et al. (2010). This SIF is a measure of interaction between the two species to determine if habitat use and selection are due to random processes (SIF = 1.0) or if co-occurrence is greater (SIF < 1.0) or less (SIF > 1.0) than if they were independent (Steen et al. 2014). I used the "deltamethod" function in the msm package in program RStudio version 0.98.507 (Jackson 2011, RStudio 2014) to calculate the SIF and corresponding confidence intervals for each carnivore pairing. To evaluate the effect of station-level habitat and landscape features, prey species, and human presence on native-exotic carnivore co-occurrence and co-detection I used the most influential covariates from existing single-season, single species occupancy modeling for each individual carnivore (Farris Chapter 2). I created *a priori* models for each native-exotic carnivore pairing and I used Akaike Information Criterion, corrected for small sample sizes (AICc), and model selection to rank models (Akaike 1973). For each carnivore pairing I reported all top-ranking models (deltaAIC < 2.0).

For any carnivore pairing having insufficient captures to estimate co-occurrence using the single-season, two-species occupancy modeling I used single-season, single-species occupancy models to estimate the occupancy and detection of the native carnivore species and I used the capture history of the exotic carnivore as a covariate to assess the effect of exotic carnivore presence on native carnivore occupancy and detection. I combined all surveys across the seven study sites to estimate native-exotic carnivore co-occurrence. At sites having repeat surveys across years, I used the survey having the highest cumulative total of native-exotic carnivore captures for the carnivore pair being assessed. This provided a total of 152 camera stations across the Masoala-Makira landscape to estimate native-exotic carnivore co-occurrence.

Results

From 2008 to 2013, I captured all six native and three exotic species of carnivore known to occupy the Masoala-Makira landscape (Farris et al. 2012, Goodman 2012). I surveyed an average of 1,264 trap nights per site providing a total of 8,854 trap nights across my seven study sites for a total of 2,991 captures of native and exotic carnivores. Of the 18 native-exotic carnivore pairings, I was unable to estimate the spatial co-occurrence and/or co-detection for six pairings due to insufficient captures. For these six carnivore pairings, I attempted the use of single-season, single-species occupancy models to assess the influence of the exotic predator on native carnivore occupancy; however, due to insufficient captures these models did not converge or models revealed poor fit (c-hat > 3.0).

My results revealed several native carnivores co-occur less often than expected with exotic carnivores than if they were independent (psiNe > psiNE; Table 1). In particular, native carnivores had lower or equal occupancy in the presence of dogs and lower occupancy in the presence of Indian civet. Only one native carnivore, falanouc, had a higher occupancy in the presence of an exotic carnivore, feral/wild cat (Table 1; Figure 2). In addition, the corresponding species interaction factors (SIF) provide further evidence of these negative relationships (SIF < 1.0) for these carnivore pairings (Table 1). Six of the native-exotic carnivore pairings revealed a lack of co-occurrence (i.e. occurred together less than expected than if independent). Of those six pairings, four occurred between the exotic Indian civet and native carnivores and two between dogs and native carnivores, while feral/wild cat had the one co-occurrence relationship with falanouc (Figure 2). Nocturnal and/or crepuscular native carnivores were more likely to show lack of co-occurrence with exotic carnivores (n = 5 pairings; Table 1; Figure 2-4). In particular, falanouc and broad-stripe vontsira were the least likely native carnivores to co-occur with exotic carnivores (Table 1; Figure 3 and 4).

I found five native-exotic carnivore pairings that co-occurred independently (psiNE = psiNe; SIF = 1.0) across the landscape. Dog and feral/wild cat were the two exotic carnivores with the highest independent co-occurrence relationships (n = 3, n = 2; respectively) while fosa and brown-tail vontsira were the two native carnivores with the highest independent relationships (2 each; Table 1). These independent relationships occurred among the three largest bodied and most wide-ranging species in this study (dog, feral/wild cat, and fosa; Farris Chapter 2), as well as the most rare and elusive carnivore (brown-tail vontsira; Farris et al. 2012).

I found that landscape variables, particularly number of patches (n = 5) and distance to nearest village (n = 3), were most important for explaining the spatial co-occurrence for native and exotic carnivores (Appendix B). Bird trap success, percent rainforest, and percent matrix were the only other variables present in top-ranking models (Appendix B). My results revealed native carnivores are less likely to co-occur with exotics within patchy forest nearest villages (Figure 2-4). Finally, I found co-detection probabilities were independent (rNE = rNe) for the majority of my native-exotic carnivores pairings (Table 1). However, I did find that falanouc, whose detection was positively influenced by bird activity, were more difficult to detect when dogs were present. Conversely, fosa, whose detection increased with increasing patchiness, had an increase in detection when feral/wild cat were present (Table 1).

Discussion

The negative impacts of exotic carnivores (particularly dogs) as competitors, predators, and disease vectors on native wildlife have been documented in a variety of habitats worldwide (Hughes and Macdonald 2013), thus drawing attention to this trend threatening native species worldwide. However, we still lack sufficient knowledge of the spatial interactions between these exotic carnivores and co-occurring native wildlife, particularly across rainforest habitat. This study contributes to this body of knowledge by providing the first investigation of the spatial co-occurrence among multiple co-occurring native and exotic carnivores, including identifying important variables explaining these relationships. I provide strong evidence of native carnivores being negatively influenced by exotic carnivores across the landscape. Specifically, I found that the presence of exotic carnivores results in decreased occupancy of native carnivores revealing evidence of exotics replacing natives across the landscape. Further, these negative relationships are linked to anthropogenic disturbance and/or presence (distance to nearest village and increased patchiness). My on-going research shows that native carnivores have moderate probabilities of occupancy within degraded, fragmented forest and that exotic carnivores have a widespread occupancy across the landscape, including a higher occupancy than half the native carnivore species, even in contiguous, non-degraded forest (Farris, Chapter 2). These results suggest my findings are not simply habitat-mediated relationships and that native carnivores avoid or are excluded from sites where dogs and Indian civets are present. These findings provided confirmation of my hypothesis that native carnivores would exhibit limited co-occurrence with exotic carnivores in contiguous, non-degraded forest where prey activity is highest and exotic carnivore and human activity were lowest (Farris, Chapter 2). As exotic carnivores increase their presence and/or range across both degraded and non-degraded, contiguous forest, we are likely to see further decreases in native carnivore occupancy which may result in the extirpation of some native carnivores across this landscape.

These co-occurrence models do not allow us to contrast between direct or indirect effects from exotic carnivores, thus additional work is needed to explore further the causality of these negative relationships between native and exotic carnivores. I suggest the strong co-occurrence between feral/wild cat and falanouc is habitat mediated given the higher occupancy of both carnivores across degraded forest (Farris, Chapter 2). I found no evidence of prey activity explaining the relationships among native and exotic carnivores across the landscape. However, my models incorporated bird and small mammal trap success only and did not adequately incorporate the diverse prey base for Madagascar's native carnivore community (Goodman 2012). Additional work is needed to improve our understanding of the diet of Madagascar's native and exotic carnivores before we can adequately assess their importance on explaining these co-occurrence relationships.

Recent research on Madagascar's carnivore community has revealed a decrease of native carnivores as degradation and/or exotic carnivore activity increase, as well as negative relationships between native carnivores and a host of anthropogenic variables, including distance to edge and village, human presence, and hunting/poaching rates (Farris et al. 2012, Gerber et al. 2012b). Additionally, my long-term surveys at one site reveal considerable decreases in native carnivore occupancy and strong increases in feral/wild cat occupancy over a six-year period (Farris, unpublished data). My work to date on Madagascar's carnivore community points to diminishing native carnivore populations as these exotic carnivore species increase. In addition, my work has recently highlighted the level of temporal activity overlap among native and exotic carnivores across rainforest landscape in Madagascar. For the three exotic carnivores, the greatest temporal overlap occurred between Indian civet and native carnivores. The culmination of strong temporal overlap and the spatial co-occurrence highlighted by this study between Indian civet and falanouc, spotted fanaloka, and broad-stripe vontsira represents an alarming conservation issue that demands attention. However, the hunting data revealed Indian civet to be the most consumed carnivore species across this region (Farris, Chapter 2), thus this augmenting anthropogenic pressure may serve to diminish the effects of this carnivore on the native carnivore community. We need additional information on population estimates, home range, and diet of Indian civet to evaluate better their influence on native carnivore populations.

These findings draw attention to the need for targeted management strategies to address the growing presence of exotic carnivores, and their resulting interactions with native wildlife, in Madagascar and similar habitats worldwide. In particular, I found a strong correlation between humans and dogs across my survey sites (Farris, unpublished data) and suggest that education of local people on the negative interactions between dogs and native wildlife and encouraging local people to leave their pets at home when traveling to the forest may greatly diminish these negative interactions. I strongly propose removal programs for feral/wild cat across Madagascar’s forests, particularly across the Masoala-Makira landscape where their occupancy is high and strong negative associations between feral/wild cat and multiple native carnivore and lemur species exist (Farris, Chapter 2; Farris et al. 2014). However, trap-removal programs have proven costly and have been met with mixed results in a wide-range of habitats (Campbell et al. 2011, Foley et al. 2005, Longcore et al. 2009, Winter 2004), thus such programs carried out over a large landscape like Masoala-Makira may not be attainable or effective. The opportunity exists to introduce a bounty program for feral/wild cat; however, the unsustainable hunting of native carnivores and lemurs occurring across this region (Golden 2009) further complicates the effectiveness of this approach as the increased presence of locals and/or hunting traps within forest habitat in response to this program may result in an increase in direct or indirect killing of native species as well.

My findings provide valuable insight to conservationists and managers working worldwide to address the influx of exotic carnivores and their impact on native wildlife. In particular, I highlight the successful use of these co-occurrence or single-season, two-species occupancy models for investigating the effects of elusive exotic carnivores on multiple native carnivore species. While studies investigating the spatial interactions between exotic carnivores and co-occurring native carnivores do exist (e.g. Vanak and Gompper 2010) these studies are confined to a single exotic-native carnivore pairing while many ecosystems struggle with synergistic effects from multiple, sympatric introduced or exotic carnivores (Glen and Dickman 2005). Here I demonstrate the effectiveness of combining photographic sampling with co-occurrence models to monitor changes in the occupancy of native wildlife in relation to the presence of exotic carnivores. Additionally, I bring attention to the importance of anthropogenic landscape variables, particularly distance to village and number of patches, in explaining these negative relationships across the landscape. My findings from this study, as well as from my on-going surveys of carnivores across Madagascar, shed light on the connection between human encroachment upon contiguous forest and increasing human-carnivore conflicts, such as increasing exotic carnivores, spatial and temporal interactions among native and exotic carnivores, and unsustainable hunting of native carnivores. I suggest these human-carnivore conflicts in similar habitats worldwide, particularly as they relate to exotic carnivores, are similarly linked to these anthropogenic variables and working to address human encroachment upon contiguous forest is necessary to effectively address these conservation issues.

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Table 1. Probability of spatial co-occurrence between exotic and native carnivores, including the probability of occupancy (psi) and detection (r) with (NE) and without (Ne) the co-occurring exotic predator. The spatial interaction between each exotic and native predator is revealed by the species interaction factor (SIF) where lack of co-occurrence is revealed by SIF < 1.0 and co-occurrence by SIF > 1.0. Photographic sampling of carnivores occurred across the Masoala-Makira landscape from 2008 to 2013.

Species	psiNE (SE)	psi Ne (SE)	rNE (SE)	rNe (SE)	SIF (SE)
C.familiaris & *C.ferox*	0.51 (0.06)	0.51 (0.06)	0.22 (0.02)	0.22 (0.02)	0.95 (0.09)
C.familiaris & *F.fossana*	0.43 (0.05)	0.43 (0.05)	0.29 (0.03)	0.29 (0.03)	1.0
C.familiaris & *E.goudotii*	0.23 (0.05)	0.69 (0.11)	0.07 (0.03)	0.22 (0.04)	0.51 (0.11)
C.familiaris & *G.fasciata*	0.24 (0.06)	0.90 (0.15)	0.08 (0.02)	0.08 (0.02)	0.59 (0.09)
C.familiaris & *S.concolor*	0.31 (0.05)	0.31 (0.05)	0.01 (0.005)	0.01 (0.005)	0.91 (0.002)
F.s.catus & *C.ferox*	0.85 (0.03)	0.85 (0.03)	0.14 (0.04)	0.07 (0.01)	0.98 (0.05)
F.s.catus & *E.goudotii*	0.43 (0.03)	0.07 (0.03)	0.04 (0.01)	0.04 (0.01)	1.90 (0.21)
F.s.catus & *S.concolor*	0.13 (0.04)	0.13 (0.04)	0.02 (0.01)	0.02 (0.01)	1.0
V.indica & *F.fossana*	0.33 (0.11)	0.72 (0.31)	0.36 (0.05)	0.36 (0.05)	0.50 (0.26)
V.indica & *E.goudotii*	0.11 (0.05)	0.64 (0.19)	0.33 (0.05)	0.33 (0.05)	0.22 (0.06)
V.indica & *G.elegans*	0.14 (0.06)	0.86 (0.27)	0.25 (0.04)	0.25 (0.04)	0.26 (0.01)

Table 1. Continued from previous page.

V.indica & *G.fasciata*	0.11 (0.08)	0.89 (0.22)	0.06 (0.03)	0.06 (0.03)	0.21 (0.01)

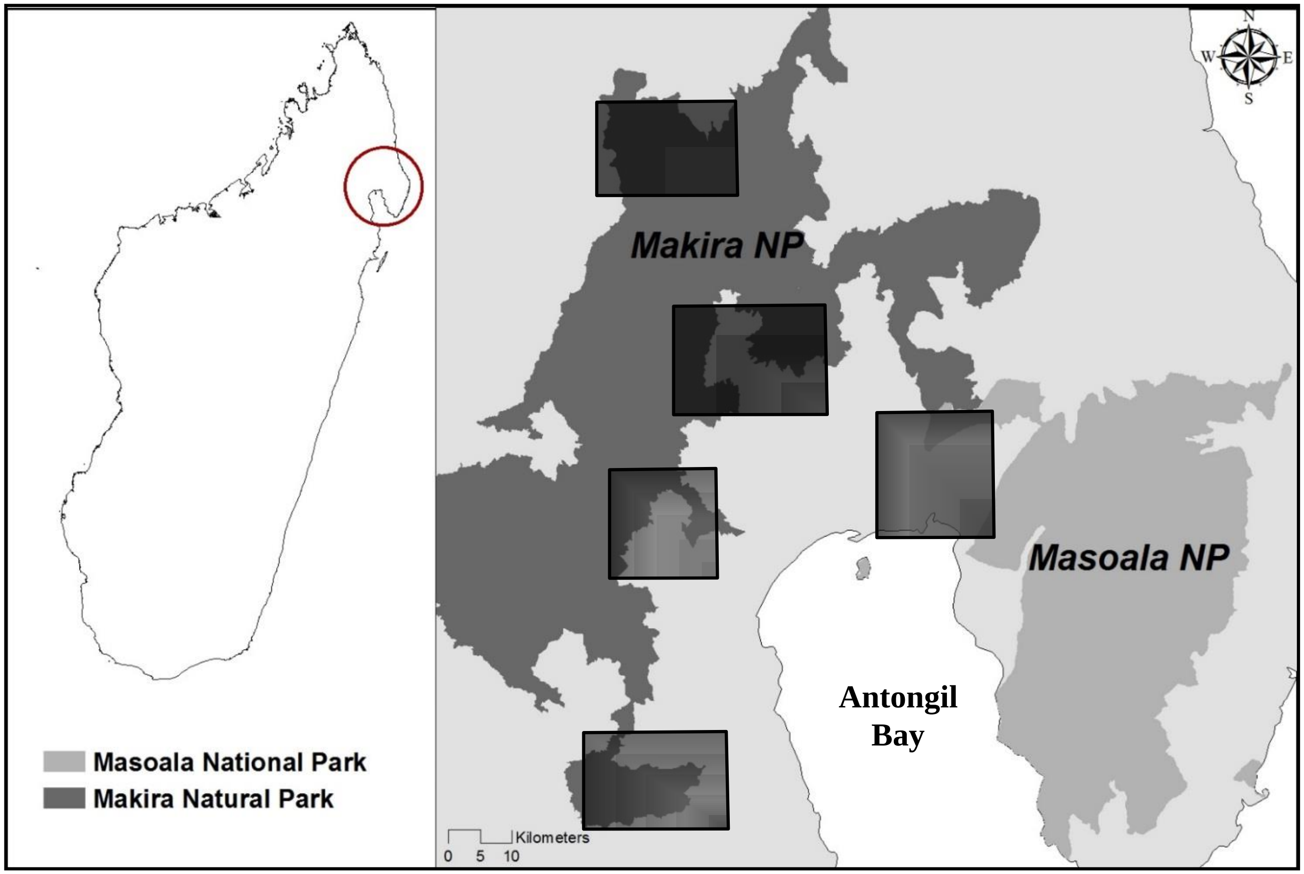
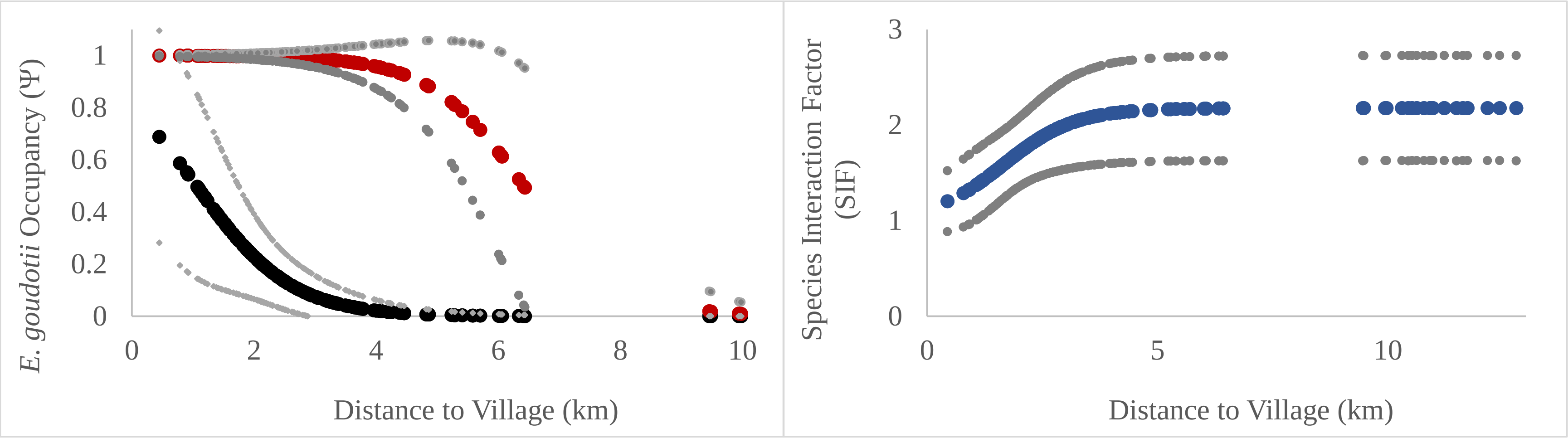


Figure 1. Map of the Masoala-Makira landscape including the outline of the regions in which the surveys were conducted at seven study sites. Photographic surveys occurred from 2008-2012.



A.

B.

Figure 2. Level of co-occurrence between the native falanouc and exotic feral/wild cat, including A) the probability of occupancy (Ψ) for falanouc with (NE; red line) and without (Ne; black line) feral/wild cat as a function of distance to village (km) and B) the species interaction factor (SIF) revealing strong co-occurrence between feral/wild cat and falanouc as distance to village increases. Gray lines show the 95% confidence intervals. Photographic sampling of carnivores occurred across the Masoala-Makira landscape from 2008 to 2013.

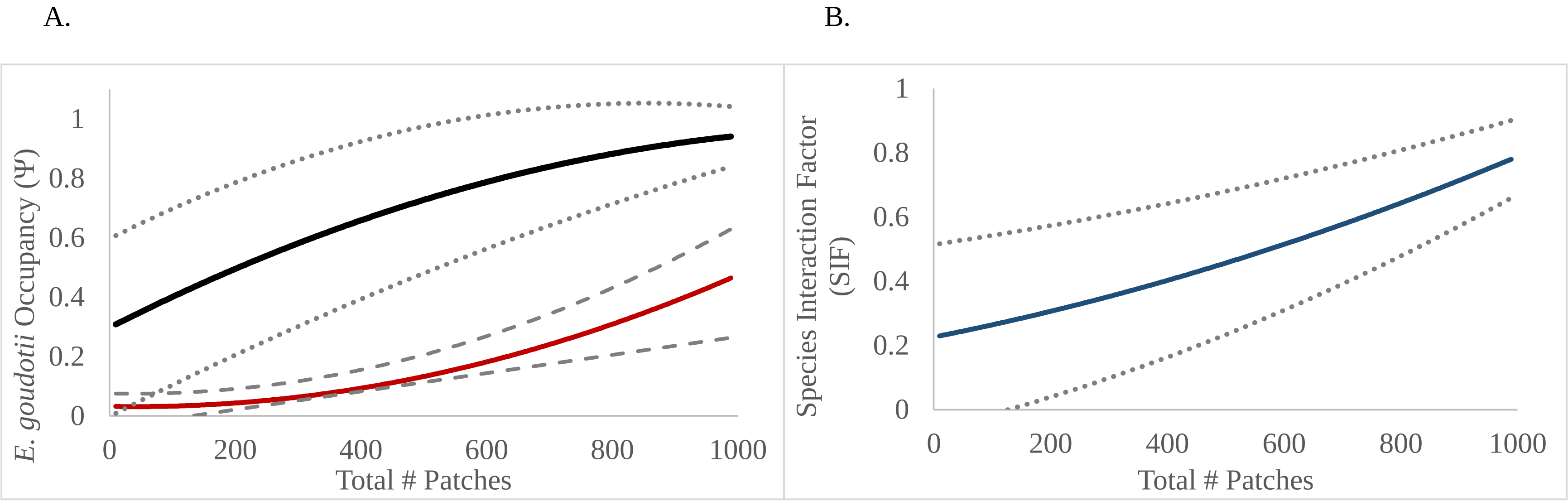
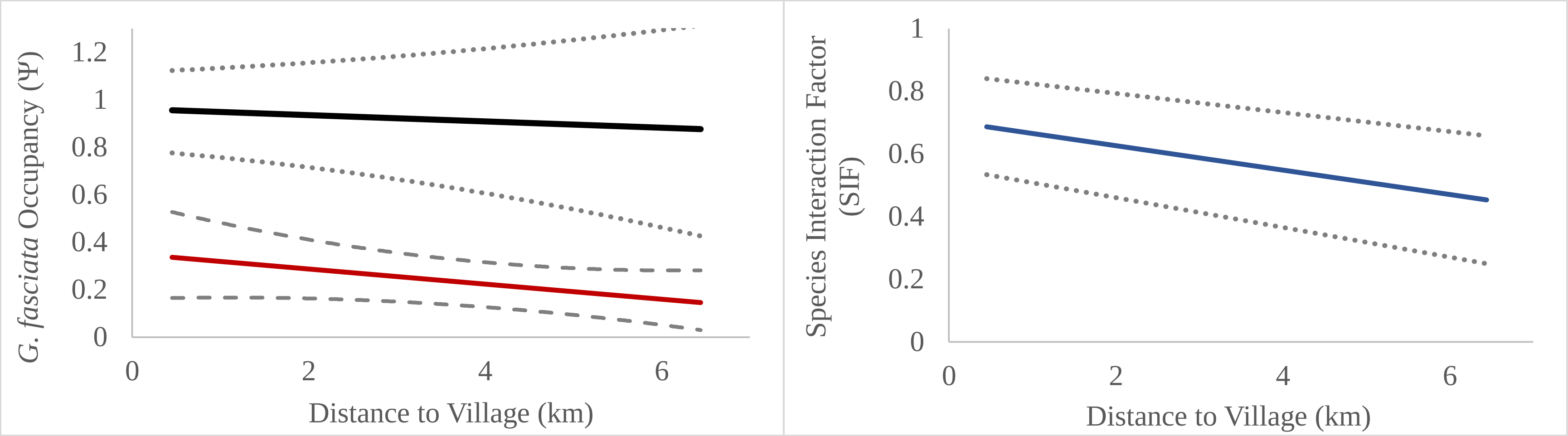


Figure 3. Level of co-occurrence between the native falanouc and exotic dog, including A) the probability of occupancy (Ψ) for falanouc with (NE; red line) and without (Ne; black line) dogs as a function of total number of patches and B) the species interaction factor (SIF) revealing evidence of spatial segregation of falanouc by dogs in forest habitat where number of patches is low. Gray lines show the 95% confidence intervals. Photographic sampling of carnivores occurred across the Masoala-Makira landscape from 2008 to 2013.



A.

B.

Figure 4. Level of co-occurrence between the native broad-stripe vontsira and exotic Dog, including A) the probability of occupancy (Ψ) for broad-stripe vontsira with (NE; red line) and without (Ne; black line) dogs as a function of distance to village (km) and B) the species interaction factor (SIF) revealing evidence of spatial segregation of broad-stripe vontsira by dogs as distance to village increases. Gray lines show the 95% confidence intervals. Photographic sampling of carnivores occurred across the Masoala-Makira landscape from 2008 to 2013.

Appendices

Appendix D.1. Station-level habitat (camera station) and landscape (500 m grid buffer) features (SE) for the seven study sites, ranked from least degraded (S01) to most degraded (S07), across the Masoala-Makira landscape (Farris, Chapter 2).

		←	Least		Level of Degradation		Most	→
Level	Study site	Site S01	Site S02	Site S03	Site S04	Site S05	Site S06	Site S07
Station-level habitat	TreeDen (stems ≥5cm / ha) [a]	1,200 (300)	3,500 (900)	4,100 (1,600)	4,600 (1,700)	4,400 (1,100)	-	3,000 (700)
	BA (stems ≥5cm, m^2/ha) [b]	82.00 (10.22)	57.4 (6.11)	22.85 (4.59)	73.54 (13.03)	76.54 (8.48)	-	49.85 (6.35)
	Can Ht (m) [c]	16.97 (1.95)	12.50 (0.96)	7.48 (0.67)	10.55 (1.23)	12.89 (1.08)	-	9.75 (1.27)
	% Can Cover [d]	64.15 (5.58)	57.05 (4.89)	62.75 (3.17)	43.52 (6.82)	60.84 (4.09)	-	42.45 (5.14)
	% Understory Cover (0-2 m)	0.50 (0.05)	0.44 (0.04)	0.53 (0.03)	0.46 (0.04)	0.44 (0.05)	-	0.52 (0.04)
Landscape	# Patches [e]	3	10	22	21	31	116	190
	Largest Patch Index [f]	60.38	52.33	44.88	51.30	39.90	43.72	50.36
	LSI [g]	1.04	1.34	2.12	1.95	2.02	3.11	6.76
	%Rainforest	99.94	98.89	94.48	95.19	96.87	96.06	81.07
	%Matrix [h]	0.05	0.66	4.38	0.59	0.76	0.19	4.07
	Tot Core Rainforest (ha) [i]	0.88	0.99	0.85	0.87	1.14	0.72	0.59
	Tot Edge (m per ha)	0.03	0.59	1.85	1.53	2.13	3.51	7.89
	Avg. Dist. to Village (km)	10.96	2.80	3.33	2.08	4.82	2.71	1.45
	Avg. Dist. to Edge (km)	1.14	0.68	0.29	0.36	0.34	0.60	0.18

[a] TreeDen = tree density averaged across all camera stations (*n* = 18-25) for each study site; [b] BA = average basal area; [c] Can Ht = average canopy height; [d] % Can Cover = average percent canopy cover; [e] #Patches: total number of rainforest, degraded forest, and matrix patches within the camera grid buffer; [f] Largest patch index: the percentage of total

landscape area comprised by the largest rainforest patch; [g] LSI: landscape shape index or the standardized measure of total edge adjusted for the size of the landscape; [h] %Matrix: percent matrix defined as non-forest land cover consisting of cultivation, open field, or early succession; [i] Tot Core Area: total core area defined as the sum of the core areas within the camera grid buffer (accounting for 500m edge depth) of each rainforest patch

Appendix D.2. Top ranking models from my single-season, two-species occupancy models for exotic (E; dominant) and native (N; subordinate) carnivore pairings having sufficient captures for model convergence.

Species (Dominant & Subordinate)	Model	AIC	AIC wt	K
C.familiaris & *C.ferox*	psiE(Human), psiNE=psiNe(#Patches), pE(Human) pN(Matrix) rE, rNE=rNe	2095.44	0.38	10
	psiE(Human), psiNE*psiNe(#Patches), pE(Human) pN(Matrix) rE, rNE=rNe	2096.34	0.25	11
	psiE(Human), psiNE=psiNe(#Patches), pE(Human) pN(Matrix) rE, rNE*rNe	2096.61	0.21	11
	psiE(Human), psiNE*psiNe(#Patches), pE(Human) pN(Matrix) rE, rNE*rNe	2097.54	0.13	12
C.familiaris & *F.fossana*	psiE(Human), psiNE=psiNe(#Patch), pE(Human), pN(TotEdge), rE, rNE=rNe	2101.45	0.69	10
	psiE(Human), psiNE=psiNe(#Patch), pE(Human), pN(TotEdge), rE, rNE*rNe	2103.02	0.31	11
C.familiaris & *E.goudotii*	psiE(.), psiNE*psiNe(#Patches), pE(Human), pN(TotEdge), rE, rNE*rNe	1676.53	0.79	11
	psiE(.), psiNE*psiNe(Village), pE(Human), pN(TotEdge), rE, rNE*rNe	1679.5	0.18	11
C.familaris & *G.fasciata*	psiE(.), psiNE*psiNe(Village), pE(Human), pN(.), rE, rNE=rNe	1555.5	0.71	9
	psiE(.), psiNE*psiNe(Village), pE(Human), pN(.), rE, rNE*rNe	1557.3	0.29	10
C.familaris & S.concolor	psiE(.), psiNE=psiNe(#Patches), pE(Human), pN(.), rE, rNE=rNe	1237.48	0.46	8
	psiE(.), psiNE=psiNe(#Patches), pE(Human), pN(.), rE, rNE*rNe	1238.99	0.22	9
	psiE(.), psiNE * psiNe(#Patches), pE(Human), pN(.), rE, rNE=rNe	1239.06	0.21	9

Appendix D.2. Continued from previous page.

F.s.catus & *C.ferox*	psiE(Bird), psiNE = psiNe(Village), pE(TotEdge), pN(%Matrix), rE, rNE*rNe	1306.41	0.55	11
	psiE(Bird), psiNE * psiNe(Village), pE(TotEdge), pN(%Matrix), rE, rNE*rNe	1308.27	0.22	12
	psiE(Bird), psiNE = psiNe(village), pE(TotEdge), pN(%Matrix), rE, rNE=rNe	1308.45	0.20	10
F.s.catus & *F.fossana**	psi(#Patches+Cat),p(%Matrix)	733.69	0.64	5
	psi(#Patches+Cat),p(%Matrix+Cat)	735.54	0.25	6
F.s.catus & *E.goudotii*	psiE(.), psiNE*psiNe(Village), pE(TotEdge), pN(Village), rE, rNE=rNe	1069.99	0.50	10
	psiE(.), psiNE*psiNe(Village), pE(TotEdge), pN(Village), rE, rNE*rNe	1070.55	0.38	11
F.s.catus & *S.concolor*	psiE(Bird), psiNE=psiNe, pE(TotEdge), pN(.), rE, rNE=rNe	696.57	0.13	8
	psiE(Bird), psiNE=psiNe(%Matrix), pE(TotEdge), pN(.), rE, rNE=rNe	696.72	0.12	9
	psiE(Bird), psiNE*psiNe(%Matrix), pE(TotEdge), pN(.), rE, rNE=rNe	696.78	0.12	10
V.indica & *F.fossana*	psiE(.), psiNE*psiNe(#Patches), pE(%Rain), pN(TotEdge), rE, rNE=rNe	1067.94	0.34	10
	psiE(Village), psiNE*psiNe(#Pathces), pE(%Rain), pN(TotEdge), rE, rNE=rNe	1068.35	0.28	11
	psiE(.), psiNE*psiNe(#Patches), pE(%Rain), pN(TotEdge), rE, rNE*rNe	1069.29	0.18	11
	psiE(Village), psiNE*psiNe(#Patches), pE(%Rain), pN(TotEdge), rE, rNE*rNe	1069.48	0.16	12
V.indica & *E.goudotii*	psiE(Village), psiNE*psiNe(%Rain), pE(%Rain), pN(%Matrix), rE, rNE=rNe	707.24	0.35	11
	psiE(Village), psiNE*psiNe(%Rain), pE(%Rain), pN(%Matrix), rE, rNE*rNe	709.23	0.13	12

Appendix D.2. Continued from previous page.

V.indica & *G.elegans*	psiE(.), psiNE*psiNe(Bird), pE(%Rain), pN(TotEdge), rE, rNE=rNe	779.98	0.61	10
	psiE(.), psiNE*psiNe(Bird), pE(%Rain), pN(TotEdge), rE, rNE*rNe	780.99	0.37	11
V.indica & *G.fasciata*	psiE(.), psiNE*psiNe(%Matrix), pE(.), pN(.), rE, rNE=rNe	606.84	0.41	8
	psiE(.), psiNE=psiNe(TotEdge), pE(.), pN(.), rE, rNE=rNe	607.39	0.31	7

Chapter 5

PREDATOR-PRIMATE DISTRIBUTION, ACTIVITY, AND CO-OCCURRENCE IN RELATION TO HABITAT AND HUMAN ACTIVITY ACROSS FRAGMENTED AND CONTIGUOUS FORESTS IN NORTHEASTERN MADAGASCAR.

Abstract

Predator-primate interactions are under-studied yet predators have been shown to influence primate behavior, population dynamics, and spatial distribution. The dearth of information stems from difficulty in observing such interactions, especially in dense forest with cryptic species. Novel approaches are needed to better understand the spatial relationships between predators and primates across changing landscapes. I combined photographic surveys of predators and humans (locals; non-researchers) with line transect sampling of lemurs across contiguous and fragmented forests in Madagascar to: 1) compare relative activity; 2) estimate probability of occupancy and detection; 3) estimate predator-primate and local-primate co-occurrence; and 4) assess which variables influence occupancy, detection, and co-occurrence for predators, locals, and lemurs across contiguous and fragmented forests. In fragmented (compared to contiguous) forest sites endemic predator and lemur activity were lower while introduced predator and local activity were higher. My two-species interaction occupancy models revealed a higher number of interactions among species across contiguous forest where predator and lemur occupancy were highest. Mouse lemurs show evidence of ‘avoidance’ with all predator species (endemic and introduced) in contiguous forest while white-fronted brown lemurs show ‘attraction’ with feral cats and locals in contiguous forest. Distance to forest edge and distance to nearby villages were important in predicting predator occupancy and detection. These results highlight the growing threat to endemic predators and lemurs as habitat loss and fragmentation increase throughout

Madagascar. I demonstrate the effectiveness of a novel combination of techniques to investigate how predator species impact primate species across a gradient of forest fragmentation.

Introduction

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. Forest loss and fragmentation negatively impact a host of primate species in various regions of the world (Arroyo-Rodríguez and Dias 2010, Boyle and Smith 2010, Estrada et al. 2012, Ganzhorn et al. 2003, Gilbert 2003, Harcourt and Doherty 2005, Johns and Skorupa 1987, Kankam and Sicotte 2013, Onderdonk and Chapman 2000, Schwitzer et al. 2011, Yanuar and Chivers 2010). 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 introduced predators impact primate populations in disturbed and fragmented forests is critical for conservation and management of these populations. This also includes an understanding of how human (non-researcher; hereafter "locals") presence impacts primate populations across these forest types.

Local presence and/or activity may pose a significant threat to primate populations resulting from disturbance, forest loss, poaching, or other anthropogenic pressures (Blom et al. 2004, Golden 2009, Goudie 2013, Griffiths and van Schaik 1993, Yamagiwa 2003). As predators and primates are increasingly forced into isolated fragments of forest, natural or exacerbated predation rates by predators may negatively impact primate populations that are simultaneously being limited by declining habitat quality and human encroachment. For example, predation by fosa (*Cryptoprocta ferox*), Madagascar's largest carnivore, was found to lead to the extirpation of sifakas (*Propithecus diadema*) from disturbed, fragmented forest sites in Madagascar and the consumption of primates by fosa (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 predator and primate interactions across fragmented and contiguous forests is still lacking.

Predator-primate interactions remain understudied as a result of the challenges associated with investigating these relationships. Predation influences primate behavior, population dynamics, spatial distribution, and group size (Colquhoun 2006, Goodman 2003c, Hart 2007, Hill and Lee 1998, Irwin et al. 2009, Isbell 1994, Karpanty 2006, Miller 2002, Miller and Treves 2007, Shultz et al. 2004, Terborgh and Janson 1986, Willems and Hill 2009, Zuberbühler and Jenny 2002). 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 to primate populations and the researchers studying them (Creel 2011, Lima 1998). 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 chance sightings of predation attempts or events, 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 predator scat and investigation of prey remains [lethal interactions] (Braczkowski et al. 2012, Burnham et al. 2013, Hart 2007, Henschel et al. 2011, Isbell 1994, Jooste et al. 2013, Morino 2011). 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 combination of camera trapping and line-transect sampling presents a unique approach to investigate these interactions to further our knowledge of how predator-primate dynamics are impacted by forest loss and fragmentation.

To achieve my objectives, I quantified the spatial distribution and occupancy of predators, locals, and lemurs in both contiguous and fragmented forests across the Masoala-Makira landscape in northeastern Madagascar, and assessed patterns of co-occurrence (interactions) between locals and lemurs, as well as predators and their potential lemur prey. Specifically we: 1) compared the relative activity and/or trap success of predators and lemurs between contiguous and fragmented forest sites; 2) determined the landscape and habitat variables impacting predator and lemur occupancy and detection across the landscape; 3) quantified the distributional relationship (co-occurrence) between predator-lemur and local-lemur occupancy in contiguous and fragmented forest sites; and 4) assessed the level of convergence among variables impacting predator-lemur and local-lemur occupancy, detection, and co-occurrence. Through these analyses I provide valuable insight on the spatial interactions or co-occupancy (i.e. random assemblages vs. species attraction/avoidance) among predators, locals, and lemurs, and the variables influencing these relationships.

Methods

Study site

I surveyed predators and lemurs by 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 my contiguous forest sites (Table 1). There are six species of endemic predators (Eupleridae), three species of introduced predators, and 22 species of lemurs that are known to occur across the Masoala-

Makira landscape [Table 2] (Farris et al. 2012, Garbutt 2007). Madagascar's endemic predators have generalist diets (Garbutt 2007); however, the following endemic and introduced predators are known lemur predators (Goodman 2003c) 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, local activity and disturbance is prevalent across this region, including the poaching of predators and lemurs (Golden 2009). To understand how human activity/presence is impacting primate populations I included photographic capture events of locals (all local activity given I could not distinguish between poachers and non-poachers) in my analyses.

The two contiguous (C) forest study sites, Anjanaharibe (AJB-C) and Mangabe (MGB-C), were located inside the Makira Natural Park (NP), which is a combination of a 3,724 km^2 park and 3,510 km^2 community-managed buffer zone. Makira NP, protects the largest remaining tract of contiguous rainforest in Madagascar and is thought to contain the highest levels of biodiversity in Madagascar (Holmes 2007, Kremen 2003). The AJB-C and MGB-C study sites consisted of intact, primary rainforest with varying degrees of degraded, secondary rainforest present near the forest edge (Figure 1). MGB-C was bisected by a heavily-traveled local trail that connected the western and eastern portions of Makira NP. For my fragmented (F) forest sites, the Farankarina site (FRK-F) was located inside the Farankarina forest reserve, a 16.5 km^2 reserve and was separated by at least 5 km from intact forest (Figure 1). This site consisted of primary, undisturbed rainforest in the southern portion of the protected area (~15 km^2) and highly degraded forest with extensive forest loss in the northern portion and extending beyond the protected area (~23.5 km^2). My final site, Lohan'sanjinja, (SLJ-F) was located 9.3 km from the nearest protected area and no community management system existed for this site. This site consisted 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 I established a camera-trapping grid consisting of 23 to 25 camera stations spaced approximately 500 m apart to photographically sample wildlife (Table 1). I used both digital (Moultrie D40, Reconyx PC85 and Cuddeback IR) and film-loaded camera-traps (DeerCam DC300) which were operational 24 hour/day and positioned about 20–30 cm above the ground. I placed two cameras on opposing sides of existing human trails (0.5-2.0 m wide) and game trails (< 0.5 m wide). I checked cameras every 5–10 days to change batteries, memory cards, and/or film and to ensure proper functioning due to the high levels of rain and humidity. I took every effort to minimize the time spent at each camera station during camera checks so as to reduce our impact on wildlife detection. Cameras were operational for an average of 67 days per survey and I used no bait or lure at camera stations to attract wildlife.

Lemur surveys

I 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 my photographic surveys of predators. At each study site I surveyed lemur transects five to six times diurnally, between 07:00 and 11:00, and five to six times nocturnally, between 18:30 and 0:00. For all lemur observations I 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-occurrence I 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 I 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 I used the point-quarter method (Pollard 1971) to estimate tree density and basal area, recording DBH for any stem/tree > 5 cm diameter. Finally, at 20 m and 40 m I measured understory cover at three levels (0-0.5 m, 0.5-1.0 m, and 1.0-2.0 m) by placing a 2 m pole on the ground at one meter intervals and recording presence (1) for vegetation touching the pole and absence (0) when no vegetation was touching. Understory sampling was conducted on a 20 m transect running perpendicular to the established 50 m habitat transect (Davis et al. 2011).

Analyses

Predator Trap Success and Lemur Activity

I defined a single ‘capture event’ for predators as all photographs of a distinct individual of particular species within a 30 minute time period. This 30 minute sampling period aims to remove temporal dependence between consecutive photographs and has become a standard in camera trap surveys (Di Bitetti et al. 2006). For predators and locals I 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, I calculated trap success (TS) by dividing the number of capture events by total number of trap nights, minus malfunctions, multiplied by 100. I defined a trap night as a 24 hour period during which at least one of the two cameras at a given camera station was functioning properly. For lemurs I 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 observation occurring within 250 m of the camera station (based on the 500 m spacing between camera stations) was considered a detection (1) for that particular camera site. For each study site I used lemur transect surveys to construct detection histories (0’s and 1’s) for each lemur species. To compare lemur activity across camera sites and study sites, I divided the number of lemur captures by the total number of kilometers surveyed within 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, Gerber et al. 2014; this special selection, Thompson 2004). The collection of detections (1s) and non-detections (0s) over a given survey 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). In addition, this modeling approach allows for the inclusion of covariates that may influence occupancy and/or detection of the target species.

To investigate how predator, locals, and lemur occupancy and detection vary across the landscape I combined detection histories across all four study sites (AJB-C, MGB-C, FRK-F, SLJ-F) and analyzed single-season, single-species occupancy models with covariates in program PRESENCE (Hines 2006). I used only one survey of the AJB study site (1AJB-C 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 I constructed a detection history using camera stations that overlapped with lemur transects, which provided 11-13 camera stations per study site and 48 sites overall. To estimate occupancy for predators I constructed a detection history using the location of all individual camera stations, which provided 20-25 camera stations per study site and 95 sites overall. Detection histories for both predators and lemurs were collapsed to 6-day intervals (encounter occasions) to improve maximum likelihood convergence. I hypothesized that predator, locals, and/or lemur occupancy and detection may be influenced by these variables: distance to forest edge, distance to nearest village, canopy height, percent canopy cover, tree density, basal area, understory cover, and the trap success of locals, domestic dogs, feral cats, fosa, and ring-tail vontsira. To improve maximum likelihood convergence with covariates and ensure covariates were on the same scale, all variables with values > 2.0 were Z-scored (Ragazzini and Zadeh 1952).

For each target species (predators, locals, and lemurs), I first generated a list of *a priori* models. To assess model fit I used a Pearson's goodness-of-fit test (P = 0.05) and to assess over-dispersion I used a measure of c-hat. For any species investigated, if the model did not fit the observed data (based on my goodness-of-fit test and/or showed evidence of severe over-dispersion, c-hat value > 3.0) occupancy was not estimated, unless otherwise noted. I used

Akaike Information Criterion (Akaike 1973) to rank models and perform model selection to determine the highest ranking covariates and top ranking models, based on AIC score, and competing models based on ΔAIC < 2.0. In addition to analyzing all *a priori* models I also generated one to three *post hoc* models based on the highest ranking covariates for occupancy and detection. For each target species I reported the highest ranking model, and the estimates of occupancy and detection with standard errors.

Two-species Co-occurrence Interaction Models: Predators-Lemurs

In addition to the single-season, single-species occupancy modeling, the two-species interaction (co-occurrence) modeling approach provides a unique framework to investigate biological interactions between two species, including competitive exclusion, predator-prey interactions, and community assemblages (MacKenzie et al. 2004). These co-occurrence models take into account imperfect detection of all target species, estimate the occupancy of two or more species, and determine if the presence of one species impacts the occupancy or detection of the other (MacKenzie 2006). The co-occurrence model provides nine estimable parameters (see MacKenzie et al. 2004) including a "species interaction factor" (SIF), a measure of interaction to determine if two target species co-occur independently (SIF = 1.0), if co-occurrence is less than it would be if independent (SIF < 1.0, 'avoidance'), or if co-occurrence is greater than it would be if independent (SIF > 1.0, 'attraction').

To evaluate whether the presence of a particular predator species influenced the occurrence of a particular lemur species I used a single-season, two-species interaction occupancy model (MacKenzie 2006, MacKenzie et al. 2004) and modeled these interactions in Program PRESENCE (Hines 2006). I combined all surveys of contiguous forest (1AJB-C, 2AJB-

C, 3AJB-C, MGB-C), and all surveys of fragmented forest (SLJ-F, FRK-F) to provide a comparison of interactions across these two forest types. Given that the two-species interaction occupancy models investigate the probability of co-occurrence of two species at a given site, I could only use lemur transects which overlapped with camera stations. As a result, I used a total of 23 camera stations in fragmented forest and 72 stations in contiguous forest to estimate predator-primate co-occupancy. I 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 I created two models for each predator-lemur species comparison: 1) a 'full model' in which occupancy of species A and B, and 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.

Ethical Note

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

Results

My photographic and line transect surveys documented a total of six endemic predators, two introduced predators, and 12 lemur species (Table 2); however, for this manuscript I focused solely on confirmed lemur predators (fosa *Cryptoprocta ferox*, ring-tail vontsira *Galidia elegans*, feral dog *Canis familiaris*, feral cat *Felis silvestris catus*, and humans 'locals' *Homo sapiens*) and lemur species having adequate captures for model convergence for my two-species interaction occupancy models (white-fronted brown lemur *Eulemur albifrons*, eastern wooly lemur *Avahi laniger*, and mouse lemur *Microcebus sp.*).

My results highlight the difference in predator and lemur trap success or relative activity between contiguous and fragmented forests across the Masoala-Makira landscape. In particular, endemic predator trap success was higher across contiguous forest while introduced predator and locals trap success was higher in fragmented forest sites (Table 3). Feral cats were not detected at any fragmented forest sites but were present in all surveys of contiguous forest. For lemurs, wooly lemur and mouse lemur relative activity (number of observations per transect) was highest in the fragmented FRK-F site while white-fronted brown lemur activity was highest in the contiguous 1AJB-C survey (Table 3).

Understory cover had the greatest impact (both positive and negative depending on the species) on the majority of my endemic and introduced predator occupancy and detection probabilities (Table 4). Distance to village and distance to forest edge were important variables for occupancy and survey period (time) was important for detection. I found strong positive associations between locals and domestic dog occupancy. Locals show the most wide-ranging occurrence across the landscape ($\widehat{\Psi}$ = 0.82 ± SE 0.06) while feral cats show the lowest occurrence ($\widehat{\Psi}$ = 0.30 ± SE 0.08) for introduced predators (Table 4). Canopy height had the greatest influence on mouse lemur occupancy (Table 4), whereas locals trap success and fosa trap success had the greatest impact on wooly lemur occupancy and detection (respectively). Both wooly lemur ($\widehat{\Psi}$ = 0.90 ± SE 0.09) and mouse lemur ($\widehat{\Psi}$ = 0.53 ± SE 0.14) had high occupancy across the landscape (Table 4). I was unable to provide estimates of white-fronted brown lemur occupancy and detection as a result of the limited number of captures.

As a result of the limited number of lemur surveys in relation to photographic surveys of predator species, lemur ‘captures’ were low leading to difficulty in convergence of co-occurrence models when estimating detection probabilities. To address this problem I used single season, single species occupancy and estimated the detection rate of each predator and lemur species in both contiguous and fragmented forest. For any predator-lemur comparison in which captures were too low to estimate detection probabilities for my co-occupancy models (n = 8) I fixed the detection rate in my two-species interaction occupancy models for these predator-lemur species combinations which allowed my interaction models to converge and provide estimates of the species interaction factor (SIF) between species. Using fixed detection rates should have minimal impact on the final SIF and occupancy estimates as they simply provide an estimate of detection based on the capture history of this species resulting from a less complex modeling framework (single season, single species modeling) and fixed detection rates were similar (± 0.03) to estimated detection from other species combinations where models did converge.

Species interaction models indicated a strong contrast in predator-primate co-occurrence in contiguous versus fragmented forest sites. In particular, I found a higher number of species interactions (n = 8) in contiguous forest where both predator and lemur occupancy were higher (Figure 3; Appendix A). Mouse lemurs show evidence of ‘avoidance’ (SIF < 1.0; Figure 2) of all predator species across contiguous forest (Figure 3; Appendix A). White-fronted brown lemurs show evidence of ‘avoidance’ with fosa (Figure 2) in both contiguous and fragmented forest (Figure 3; Appendix A). Further, this cathemeral lemur species also shows evidence of ‘attraction’ (SIF > 1.0; Figure 2) with both feral cats and locals in contiguous forest (Figure 3; Appendix A). Ring-tail vontsira demonstrated the greatest number of interactions with lemurs for all predator species (Figure 3; Appendix A).

In contiguous forest feral cats show an interaction with each lemur species (though weak in the case of wooly lemurs) while locals show an interaction with only white-fronted brown lemur and domestic dogs with only mouse lemur (Figure 3; Appendix A).

Discussion

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

My analyses highlight the differences in activity and distribution of endemic and introduced predators, as well as locals, between contiguous and fragmented forests. Fragmented forest had considerably higher trap success for locals and domestic dogs; however, I found no captures of feral cats across my two fragmented sites. Recent studies by Gerber et al. (2011, 2012b) from the south-eastern Ranomafana NP differ from results presented here. While I found feral cats only in contiguous forest, Gerber et al. (2012b) found a strong increase in feral cat occupancy in fragmented forest. The difference in feral cat captures between these two studies may be related to differences in management strategies between two areas, the sampling method used by Gerber et al. (2010; 2012), which included the use of bait, or even the hunting and consumption of feral cats by locals in this region (Chris Golden, personal communication). While capture rates and distribution of feral cats differed between the two sites, occupancy estimates of domestic dogs and locals were similar between the two studies.

For lemurs the difference in activity between contiguous and fragmented forest is less striking. The high activity of lemur species at the fragmented FRK-F site, however, likely results from the presence of primary rainforest cover in the southern protected part of the FRK-F reserve. In addition, this study incorporates only the three most common lemur species observed. I found a strong decrease in total lemur species richness from contiguous to fragmented forest (Table 3), including an absence of all diurnal species (excluding white-fronted brown lemurs) in all fragmented forest sites surveyed (Farris, unpublished data). This outcome is alarming given the on-going patterns of forest loss and fragmentation throughout Madagascar.

Single-Season, Single-Species Occupancy Across the Landscape

My low numbers of captures, primarily for lemurs, prevented the comparison of contiguous and fragmented forests using occupancy estimation with covariates; however, my single-season, single-species occupancy and detection estimates across all sites provide insight into how predators and lemurs are impacted by changes across the landscape. The extremely high occupancy for both locals and domestic dogs across the landscape may represent an important conservation/management issue. The strong positive association between locals and dogs is expected given the use of domestic dogs by locals to perform various tasks such as herding and hunting. The relatively high occupancy of fosa across the landscape is similar to recent research conducted by Gerber et al. (2011, 2012b) in south-eastern Madagascar on carnivores, and is perhaps not surprising given the large areas across which this species roams.

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 introduced predator occupancy also draws attention to the on-going trends in fragmentation, edge effects, and human encroachment and their impacts on endemic and introduced wildlife species across eastern rainforest habitat. For example, the strong inverse relationship between distance to village and fosa occupancy may stem from the killing of fosa by farmers (Kotschwar et al. 2014)across the Masoala-Makira region due to the depredation of chickens and ducks by fosa (Farris, personal observation and communication with locals). In fact, I suspect this mortality resulting from hunting is likely one of the biggest conservation concerns for fosa in this region of Madagascar.

For lemurs, the high occupancy estimates and similarly high relative activity of both wooly lemurs and mouse lemurs in fragmented forest appears to be indicative of their widespread presence across eastern rainforest habitat (Garbutt 2007). Further, mouse lemurs increased in detection nearer forest edge while wooly lemurs show a positive relationship with locals' activity. These results support the supposition that wooly lemurs and mouse lemurs may be more common in disturbed, secondary forest compared to primary forest (Ganzhorn 1988, 1995). The inability to provide estimates of occupancy for white-fronted brown lemurs resulted from low capture rates in both contiguous and fragmented forest sites. Longer transects and more repeat surveys may be required to estimate occupancy for this, and other larger bodied, gregarious lemur species, including the more than nine other species observed across this landscape.

Two-species Co-occurrence Interaction Models: Contiguous and Fragmented Forests

Mouse lemur's negative relationship with all predators in contiguous forest may result from predator avoidance behavior by this small nocturnal lemur, as individuals of this genus are preyed upon by fosa, ring-tail vontsira, and domestic dog (Goodman 2003c). Feral cats prey on multiple lemur species (Goodman 2003c) and endemic rodents (Farris, personal observation) and are believed to be an important *Microcebus sp.* predator. Mouse lemurs are wide-ranging and common throughout eastern rainforest habitat (Garbutt 2007); however, my surveys found their distribution to be limited, particularly in contiguous forest (Figure 3a-c), and my low sample size may have led to the ‘avoidance’ results with the more wide-ranging predators. Alternatively, this ‘avoidance’ result may be habitat mediated since mouse lemur occupancy was positively related to canopy height while predators were positively influenced by understory cover, and these two habitat variables were negatively correlated with each other. Higher sample sizes would enable incorporating habitat covariates into the co-occurrence models to better understand the interplay between habitat and co-detection in influencing species interactions (Bailey et al. 2009, Waddle et al. 2010).

Both fosa and ring-tail vontsira are confirmed lemur predators and my two-species interaction models demonstrate evidence of multiple lemur species ‘avoiding’ these two endemic predator species. Moreover, these negative relationships occur in both contiguous and fragmented forests. In particular, both white-fronted brown lemur and mouse lemur show ‘avoidance’ with fosa. In recent years attention has been placed on the diet of fosa, particularly as it relates to their hunting of lemurs, as they have been shown to prey upon numerous lemur species (Goodman 2003c), have significant impact on lemur population dynamics (Irwin et al. 2009), and have been suggested to be a lemur specialist (Wright et al. 1997). I found no interactions with any predator-lemur or local-lemur across fragmented forest; however, the high level of occupancy and widespread distribution of locals and domestic dog across the entire camera grid in fragmented forest (see locals distribution in Figure 2) may be the cause for lack of pattern in co-occurrence. High occupancy of domestic dog and locals across fragmented forests, as well as the increased patchiness and limited habitat availability, are likely creating more encounters between these species. The impact on lemurs from these potential increased encounters across fragmented forest remains unknown, but I assume domestic dog and local encounters will be damaging for all three lemur species (Daszak et al. 2000, Golden 2009, Koster 2008, Lenth et al. 2008). Surveys by my team of other highly fragmented sites with exceptionally high trap rates of locals and domestic dog have shown very low numbers and/or a complete absence of all lemur species (Farris, unpublished data). Furthermore, the training of domestic dogs by locals to hunt various wildlife species, including lemurs, is common for this region (anecdotal accounts and personal observation) and this is likely contributing to the diminished species richness we have observed across fragmented forests. Additional research on the use of domestic dogs by locals to hunt wildlife is needed to fully understand the pressure this places on lemur populations across this region. To my knowledge, this is the first attempt to model domestic dog and lemur interactions in Madagascar.

The lack of feral cat 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. My co-occurrence models indicate a strong ‘avoidance’ between feral cats and mouse lemurs in contiguous forest, despite both species having narrow distributions and low capture rates in these forest sites. During my surveys I obtained photographic evidence of feral cats killing endemic rodents; however, I know of no available information on the rate of take or capture efficiency of various lemur species in the diet of either feral cats or the more abundant and wide ranging domestic dog. A complete diet analysis of these two introduced predators and a better understanding of the factors associated with their occupancy are needed to assess the impact of these predators on endemic wildlife, particularly lemurs, throughout Madagascar.

My work highlights a novel approach in combining camera trapping and line transects for investigating predator-lemur interactions; however, my data collection was designed specifically for the goal of estimating predator population parameters (which requires a large number of trap nights). I recommend future studies investigating predator-primate dynamics place greater effort on increasing the number of primate line-transect surveys across the site to improve convergence in occupancy and detection estimation. Further, if camera resources are limited so that expanding the grid size using two cameras per site is not possible, then using only a single camera per camera station and expanding both the extent of the camera grids and line-transects will allow for the estimation of occupancy and detection over a broader area and include more covariate data for analyses. Using existing trails for camera placement is important to obtain adequate captures of carnivores (Dillon and Kelly 2007, Maffei et al. 2004); however, the location of highly accessible and heavily traveled trails may bias results for some target species, particularly my lemur species, such as at my MGB-C site. Furthermore, this high level of domestic dog and local activity at the MGB-C site may have also impacted lemur observations as line-transects were placed along existing trails to overlap with photographic sampling data. As a result, the placement of cameras and line-transects is a vital part of study design for similar studies using these methods. I recommend increased sampling to include more “sites” to simultaneously model habitat variables with the two-species interaction model framework.

The challenges associated with collecting data on elusive predators and primates have resulted in a dearth of information on predator-primate interactions. The importance of and potential uses of these novel, non-invasive techniques to the field of primatology are 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 introduced) that are influencing the occupancy and detection of numerous rare, endangered, and/or elusive primate species. Finally, combining these methods with other non-invasive methods (such as scat analysis including molecular scatology) 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.

Finally, this research highlights the need to expand our knowledge of carnivore-primate dynamics and interactions. In particular, we need thorough density analyses across each forest type, which incorporate numerous landscape and habitat covariates, to better understand the effects of fragmentation and forest loss on carnivore and lemur species across Madagascar. Further, this research points to the need for an increased understanding of the variables influencing the presence and/or absence of domestic dogs and feral cats, both confirmed lemur predators, across eastern rainforest habitat in Madagascar. More specifically, we need additional research on the population dynamics and diet of these wide-ranging predators throughout Madagascar to better understand their impact on lemur populations, particularly in fragmented forest sites. Finally, while data exist 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 carnivore and lemur home range and daily activity patterns are critical to explore further the impact of poaching on these species. This additional research on carnivore-primate dynamics and interactions across contiguous and fragmented forests will increase our understanding of these relationships and greatly improve conservation and management efforts throughout Madagascar.

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Table 1. Sampling details and survey effort for photographic and lemur surveys performed across the Masoala-Makira landscape in NE Madagascar, including elevation range and distance to nearest village from edge of study site.

Study site	Forest Type	Survey Dates	# of Camera Stations	Trap Nights	Elevation (m)	Dist. to Nearest Village (km)
Anjanaharibe (1AJB)	Contiguous (C)	Sept – Nov, 2010	25	1257	350-690	2.8
Anjanaharibe (2AJB)	Contiguous (C)	Aug – Oct, 2011	24	1383	350-690	2.8
Anjanaharibe (3AJB)	Contiguous (C)	Aug – Oct, 2012	24	1536	350-690	2.8
Mangabe (MGB)	Contiguous (C)	Mar – May, 2011	24	1509	324-786	4.8
Lohan’sanjinja (SLJ)	Fragmented (F)	Dec – Feb, 2010	24	1570	93-507	1.5
Farankarina (FRK)	Fragmented (F)	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. The total number of observations (line-transect sampling) and/or captures (photographic surveys) of endemic predators, introduced predators, and lemurs during my surveys across the Masoala-Makira landscape, NE Madagascar. Species included in analyses for this manuscript are in bold.

Scientific Name	Common Name	Total Observations/Captures
Endemic Predators		
Cryptoprocta ferox	**Fosa**	244
Fossa fossana	Spotted fanaloka	486
Eupleres goudotii	Falanouc	141
Galidia elegans	**Ring-tail vontsira**	112
Galidictis fasciata	Broad-striped vontsira	53
Salanoia concolor	Brown-tail vontsira	44
Introduced Predators		
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	Black & white-ruffed lemur	2

Table 2. Continued from previous page.

Propithecus candidus	Silky sifaka	1
Indri indri	Indri	25
Microcebus sp.	**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.

Table 3. Trap success (SE) or relative activity (number of captures / total km surveyed) of endemic predators, introduced predators, and locals (non-researcher humans) and the number of detections per survey for each lemur species at each survey site across the Masoala-Makira landscape. 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 distinct individual of a species within a 30-minute time period.

		Contiguous Forest Sites				Fragmented Forest Sites	
Scientific Name	Common Name	1AJB-C	2AJB-C	3AJB-C	MGB-C	SLJ-F	FRK-F
Cryptoprocta ferox	Fosa	2.2 (0.7)	1.3 (0.5)	1.7 (0.5)	7.2 (1.0)	2.0 (0.7)	1.0 (0.4)
Galidia elegans	Ring-tail vontsira	1.5 (0.4)	1.0 (0.3)	0.4 (0.2)	3.8 (1.6)	0.5 (0.2)	1.1 (0.3)
Canis familiaris	Domestic dog	1.0 (0.5)	1.1 (0.6)	0.7 (0.3)	26.1 (4.5)	19.6 (7.3)	14.9 (7.4)
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)
Homo sapiens (Locals)	Human (non-researcher)	2.2 (0.9)	11.8 (10.6)	2.4 (1.3)	165.4 (33.2)	170.5 (57.9)	119.3 (52.3)
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 sp.	Eastern mouse lemur	0.71	0.69	0.49	0.29	0.53	1.61
Number of Lemur Species		7	7	7	6	5	4
Total Lemur Observations		60	41	38	66	27	68

Table 4. Top single-season, single-species occupancy model results (model likelihood > 0.125) for each target species across the Masoala-Makira landscape, including estimates for occupancy (Ψ) and probability of detection (p) with standard error.

Species	Model	AIC	AIC wgt	k	Ψ (SE) [*]	p (SE) [*]
Fosa	Ψ (.)[1], p(Under) [2]	762.35	0.25	3	0.63 (0.06)	0.18 (0.02)
	Ψ (Locals)[3], p(Under)	762.74	0.21	4	0.63 (0.08)	0.18 (0.02)
	Ψ (.), p(Village)[4]	763.05	0.18	3	0.67 (0.07)	0.16 (0.02)
Ring-tail vontsira [‡]	Ψ (Under), p(Dog)[5]	459.11	0.64	4	0.58 (0.10)	0.10 (0.02)
	Ψ (Under), p(.)	462.19	0.14	3	0.56 (0.11)	0.11 (0.02)
Domestic dog	Ψ (Under), p(Time)[6]	1063.81	0.14	15	0.64 (0.06)	0.37 (0.06)
Feral cat	Ψ (Under), p(Time)	312.46	0.97	15	0.30 (0.08)	0.12 (0.05)
Human (Locals)	Ψ (Dog), p(Under,Time)	1139.11	0.99	16	0.82 (0.06)	0.41 (0.05)

Table 4. Continued from previous page.

Wooly lemur	Ψ (Locals), p(Fosa)[7]	292.28	0.17	4	0.90 (0.09)	0.20 (0.03)
	Ψ (.), p(Fosa)	292.34	0.16	3	0.90 (0.10)	0.20 (0.04)
Mouse lemur	Ψ (Can ht.)[8], p(.)	188.79	0.10	3	0.53 (0.14)	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 familiaris* trap success; 6 Time – survey specific rate of occupancy and/or detection; 7 Fosa – Fosa 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.

[‡] 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

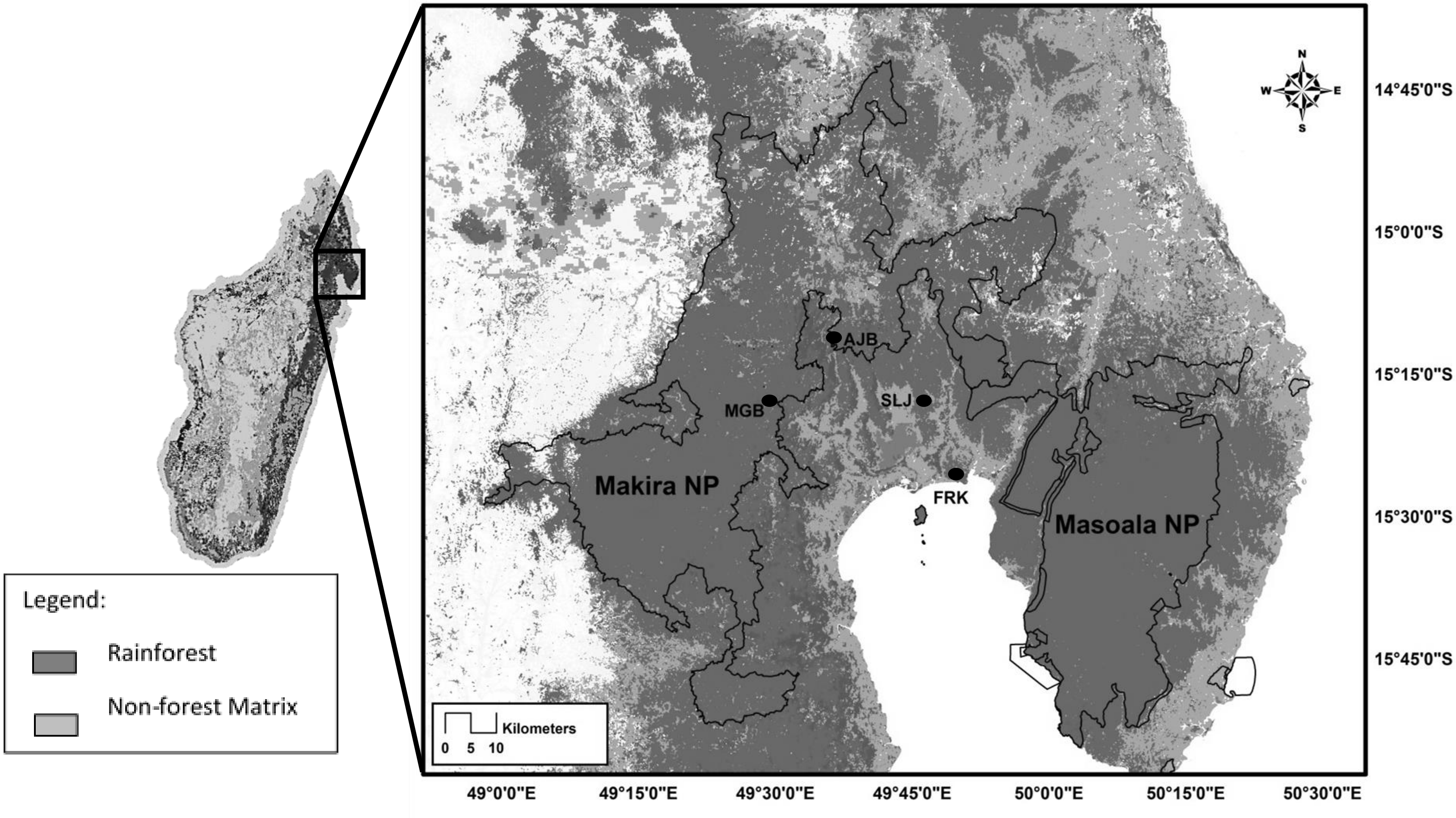


Figure 1. Map of study sites across the Makira Natural Park highlighting the location of Masoala National Park, Makira Natural Park, as well as the two contiguous study sites: Anjanaharibe (AJB) and Mangabe (MGB) and the two fragmented study sites: Lohan'sahanjinja (SLJ) and Farakarina (FRK).

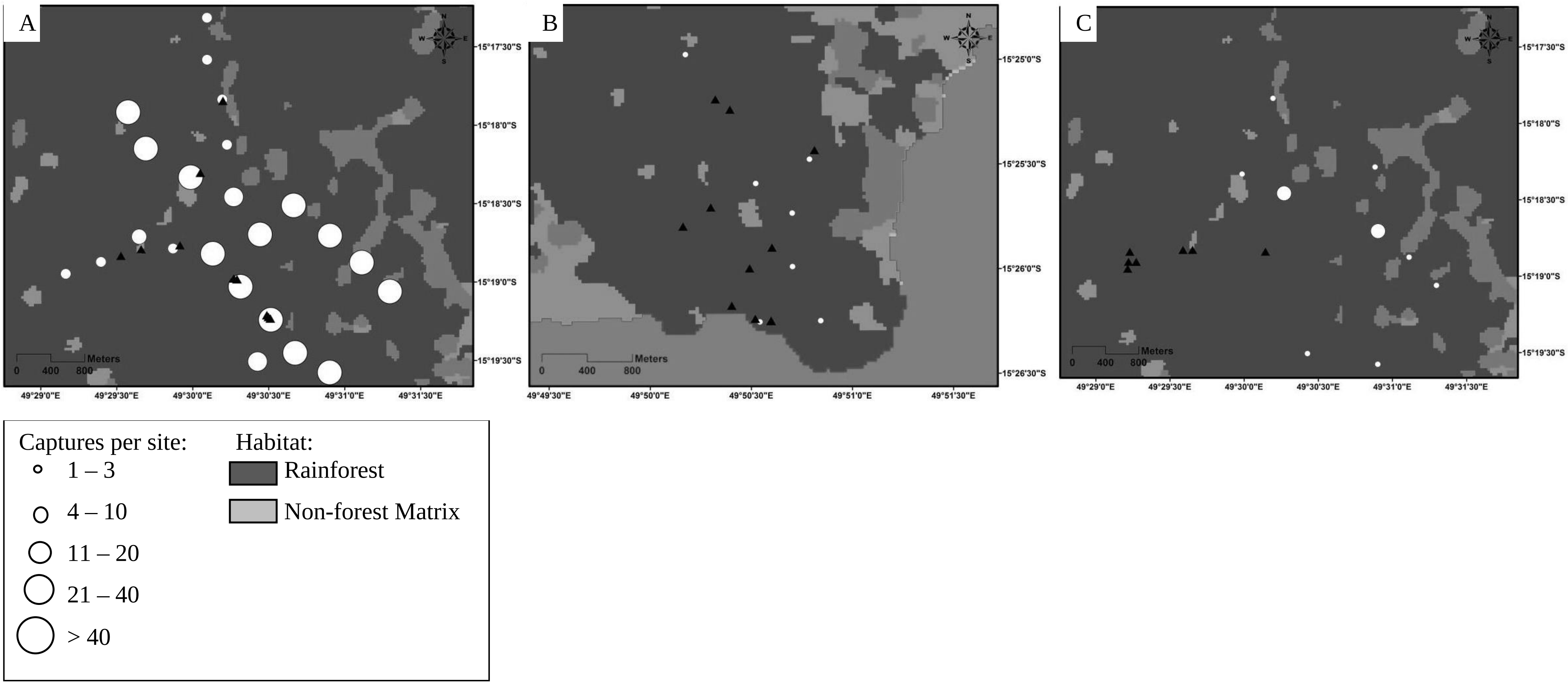
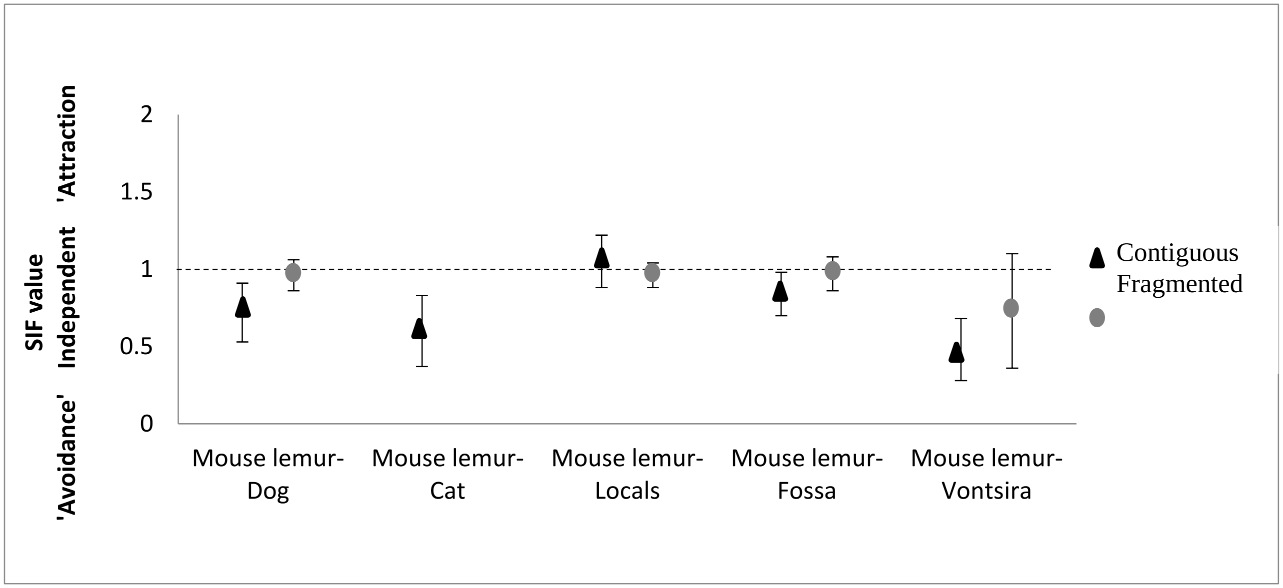
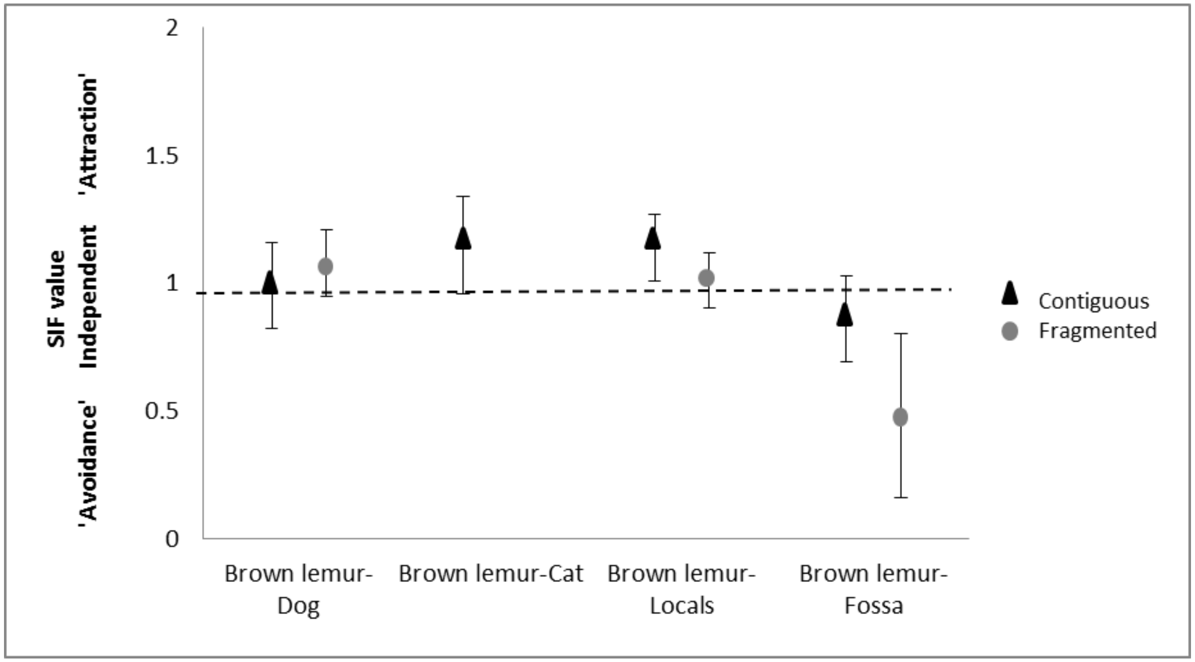


Figure 2. Capture locations for A) Locals (White circles) and *Eulemur albifrons* (Black triangles) highlighting the species “attraction” [SIF = 1.14 (0.13)] at the Mangabe study site (MGB) in contiguous forest; B) Fosa (White circles) and *Eulemur albifrons* (Black triangles) highlighting the species “avoidance” [SIF = 0.48 (0.32)] at the Farankarina study site (FRK) in contiguous forest; and C) Ring-tail vontsira (White circles) and *Microcebus sp.* (Black triangles) highlighting the species “avoidance” [SIF = 0.48 (0.20)] at the MGB study site in contiguous forest.

A.


SIF value
'Avoidance' Independent 'Attraction
2
1.5
1
0.5
0
Mouse lemur-Dog
Mouse lemur-Cat
Mouse lemur-Locals
Mouse lemur-Fossa
Mouse lemur-Vontsira
▲ Contiguous
● Fragmented

B.


2
1.5
1
0.5
0
SIF value
'Avoidance' Independent 'Attraction'
Brown lemur-Dog
Brown lemur-Cat
Brown lemur-Locals
Brown lemur-Fossa
Contiguous
Fragmented

C

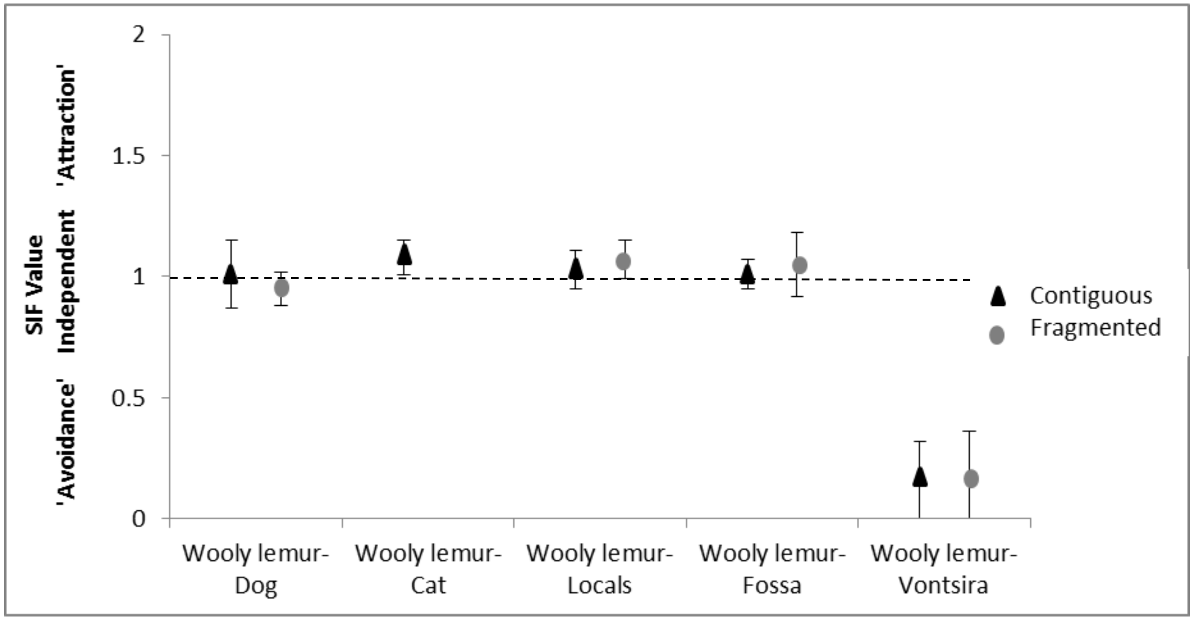

2
1.5
1
0.5
0
SIF Value
'Avoidance' Independent 'Attraction'
Wooly lemur-Dog
Wooly lemur-Cat
Wooly lemur-Locals
Wooly lemur-Fossa
Wooly lemur-Vontsira
Contiguous
Fragmented

Figure 3. Species Interaction Factor (SIF), or the level of co-occurrence between species(where SIF = 1.0 is independent; dashed line), in contiguous and fragmented forest between A) Mouse lemur (*Microcebus sp.*) and predators; B) White-fronted brown lemur (*Eulemur albifrons*) and predators; and C) Wooly lemur (*Avahi laniger*) and predators.

Appendices

Appendix E.1. Best model results for single season, two-species interaction occupancy models for each predator(A)-lemur(B) species comparison, including the occupancy (Ψ), detection (p), and predator-lemur species interaction factor (SIF).

Species:	Forest Type	Model	ΨA (SE)	ΨB (SE)	pA (SE)	pB (SE)	SIF (SE) [1]
A B							
Dog-Brown lemur	Contig	NI & E[2], p(fixed) [3]	0.56 (0.06)	0.56 (0.06)	0.21	0.16	0.99 (0.17)
	Frag	NI & NE[4], I & NE[5]	0.94 (0.04)	0.79 (0.12)	0.94 (0.06)	0.05 (0.10)	1.08 (0.13)
Dog-Mouse lemur	Contig	NI & NE, p(.)	0.48 (0.05)	0.48 (0.05)	0.18 (0.02)	0.18 (0.02)	0.72 (0.19)
	Frag	NI & E, p(.)	0.87 (0.09)	0.58 (0.11)	0.17 (0.04)	0.17 (0.04)	0.96 (0.10)
Dog-Wooly lemur	Contig	NI & NE, p(fixed)	0.54 (0.09)	0.95 (0.04)	0.64	0.16	1.01 (0.14)
	Frag	NI & NE, p(.)[6]	0.84 (0.08)	0.62 (0.10)	0.29 (0.02)	0.29 (0.02)	0.95 (0.07)
Locals-Brown lemur	Contig	NI & E, p(.)	0.56 (0.06)	0.56 (0.06)	0.25 (0.02)	0.25 (0.02	1.14 (0.13)
	Frag	NI & NE, p(.)	0.87 (0.07)	0.35 (0.10)	0.46 (0.02)	0.46 (0.02)	1.01 (0.11)
Locals-Mouse lemur	Contig	NI & E, p(fixed)	0.56 (0.08)	0.40 (0.07)	0.27 (0.02)	0.27 (0.02)	1.05 (0.17)
	Frag	NI & NE, p(.)	0.87 (0.07)	0.52 (0.10)	0.45 (0.02)	0.45 (0.02)	0.96 (0.08)

Appendix E.1. Continued from previous page.

Locals-Wooly lemur	Contig	NI & NE, p(.)	0.56 (0.08)	0.81 (0.07)	0.25 (0.02)	0.25 (0.02)	1.03 (0.08)
	Frag	NI & NE, p(.)	0.87 (0.07)	0.61 (0.10)	0.44 (0.02)	0.44 (0.02)	1.07 (0.08)
Cat-Brown lemur	Contig	NI & NE, p(.)	0.59 (0.14)	0.83 (0.15)	0.08 (0.02)	0.08 (0.02)	1.15 (0.19)
Cat-Mouse lemur	Contig	NI & E, p(.)	0.53 (0.08)	0.53 (0.08)	0.10 (0.02)	0.10 (0.02)	0.60 (0.23)
Cat-Wooly lemur	Contig	NI & NE, p(fixed)	0.48 (0.10)	0.91 (0.07)	0.19	0.16	1.08 (0.07)
Fossa-Brown lemur	Contig	NI & NE, NI & NE	0.70 (0.09)	0.67 (0.11)	0.09 (0.04)	0.07 (0.03)	0.86 (0.17)
	Frag	NI & E, p(fixed)	0.65 (0.14)	0.43 (0.13)	0.13	0.13	0.48 (0.32)
Fossa-Mouse lemur	Contig	NI & NE, p(.)	0.77 (0.08)	0.44 (0.08)	0.16 (0.02)	0.16 (0.02)	0.84 (0.14)
	Frag	NI & NE, p(fixed)	0.88 (0.13)	0.69 (0.15)	0.12	0.36	0.97 (0.11)
Fossa-Wooly lemur	Contig	NI & E, p(.)	0.85 (0.06)	0.85 (0.06)	0.16 (0.01)	0.16 (0.01)	1.01 (0.06)
	Frag	NI & NE, NI & NE	0.87 (0.13)	0.89 (0.13)	0.45 (0.11)	0.45 (0.11)	1.05 (0.13)
Vontsira-Mouse lemur	Contig	NI & E, p(fixed)	0.45(0.05)	0.45 (0.05)	0.09	0.21	0.48 (0.20)
	Frag	NI & NE, NI & E	0.40 (0.13)	0.67 (0.15)	0.11 (0.04)	0.11 (0.04)	0.73 (0.37)
Vontsira-Wooly lemur	Contig	NI & NE, p(.)	0.48 (0.10)	0.84 (0.07)	0.13 (0.01)	0.13 (0.01)	0.85 (0.16)
	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

CHAPTER 6

MOVING FORWARD: ADDRESSING THE FUTURE OF ENDEMIC WILDLIFE IN MADAGASCAR

Introduction

Madagascar has received much conservation attention over the last decade as a result of its high levels of biodiversity and endemism, as well as the increasing anthropogenic pressures threatening that unique biodiversity (Brooks et al. 2006, Goodman and Benstead 2005, Harper et al. 2007, Kremen et al. 2008, Rakotomanana et al. 2013). Of the unique wildlife in Madagascar, top carnivores are critically important as they may exert significant influence on ecosystem structure and serve as “umbrella species” due to their large home ranges (Gittleman et al. 2001, Noss 1990). My dissertation has contributed substantially to the existing knowledge base on these unique carnivores, although more work surely needs to be done and is described below, to best conserve these carnivores and the diverse species that fall under their ‘umbrella.’ My research was conducted in the context of the recognition that Madagascar’s carnivores arguably are both the least studied and most threatened Family of Carnivora in the world (Brooke et al. 2014). Madagascar’s carnivores and co-occurring endemic wildlife face numerous threats relating to increasing anthropogenic disturbance, including forest loss and fragmentation (Allnutt et al. 2008, Green and Sussman 1990, Harper et al. 2007), exotic species (Brockman et al. 2008, Farris et al. 2012, Farris et al. 2014, Farris and Kelly 2011, Gerber 2011, Gerber et al. 2012a, b, Goodman 2012, Kolby 2014), and unsustainable hunting rates (Barrett and Ratsimbazafy 2009, Golden 2009, Golden et al. 2014, Kotschwar et al. 2014). The goal of my research as detailed in the preceding chapters was to provide the first long-term assessment of Madagascar's eastern rainforest carnivore community, including how these various forms of anthropogenic pressure influence fosa *Cryptoprocta ferox*, falanouc *Eupleres goudotii*, spotted fanaloka *Fossa fossana*, ring-tail vontsira *Galidia elegans,* broad-stripe vontsira *Galidictis fasciata,* and brown-tail vontsira *Salanoia concolor* across Madagascar's largest protected landscape, the Masoala-Makira landscape.

From 2008 to 2013 I utilized photographic sampling for carnivores and line-transect sampling for lemurs across seven study sites, including repeat surveys at two sites for a total of 13 surveys. These surveys provided a total of 245 camera stations (average = 23 stations per site) and spanned across all three eastern Madagascar seasons: hot-dry (n = 4), hot-wet (n = 2), and cool-wet (n = 7). I surveyed a total of 824 days (average = 64 ± SE 8 days per site), providing a total of 16,431 trap nights (average = 1,264 ± SE 221 days per site). I used 48 station-level habitat, landscape, and co-occurring species covariate variables to determine their influence on carnivore population parameters. My surveys provided more than 120,000 photographs, including 3,555 photo captures of carnivores, 3,843 captures of birds, and 2,463 captures of small mammals. The carnivore captures consisted of 1,795 captures of the six native carnivore species and 1,760 captures of the three exotic carnivore species. From these extensive surveys, and the subsequent analyses described in this dissertation, I summarize here my major findings, management implications, and research needs that remain.

Major findings

This extensive, long-term assessment of carnivores across Madagascar's largest protected area highlights numerous striking trends between Madagascar's native and exotic carnivores, and their relationships to habitat fragmentation and subsistence-level hunting, including:

- A strong increase in human and exotic species activity and occupancy as degradation and fragmentation increase, as well as a higher probability of occupancy for dogs *Canis familiaris* and cats *Felis species* than half of the native carnivores and a higher probability of occupancy of humans than all carnivores across the entire Masoala-Makira landscape surveyed.
- Decreases in native carnivore, lemur, small mammal, and bird activity and/or occupancy, including an absence of all diurnal lemur species (except white-fronted brown lemur *Eulemur albifrons*) as degradation, as well as human and exotic carnivore activity increase.
- A strong positive association between bird and small mammal trap success and native carnivore occupancy, but strong negative association with exotic carnivores.
- Indian civet *Viverricula indica* and cats *Felis sp.* constrain the occupancy of spotted fanaloka *F. fossana*.
- Intense hunting rates across the landscape, including evidence that hunters are focusing their efforts where native carnivore and lemur populations are most abundant.
- Evidence of high temporal overlap between native and exotic carnivores indicating the potential for increased interactions and competition.
- Fosa *Cryptoprocta ferox* altering their temporal activity patterns during their breeding season and avoiding humans and dogs *C. familiaris* across all seasons.

- Strong evidence that native and exotic carnivores occur together less often than expected and that exotic carnivores may be replacing native carnivores.
- Six of the native carnivores within this study reveal higher occupancy in the absence of exotic carnivores (psiNe > psiNE) while their corresponding species interaction factors (SIF) reveal a lack of co-occurrence.
- Co-occurrence among native and exotic carnivore pairings decreases rapidly at sites nearest villages or with high number of patches.
- Predator and primate interactions, including interactions with exotics, are more likely to occur in contiguous forest where predator and lemur occupancy were highest.
- Mouse lemurs *Microcebus sp.* fail to co-occur with all predator species (native and exotic) in contiguous forest while white-fronted brown lemurs *Eulemur albifrons* co-occur with feral cats and locals in contiguous forest.

In addition to this summarized list of findings I have also organized the major findings for each species in Appendix A-F, which was also recently used to update the IUCN Red List species classifications.

Successes, Deficiencies, & Recommendations

These findings highlight an alarming negative trend in endemic carnivore populations and I hypothesize these trends are not unique to the Masoala-Makira landscape, but are widespread across forests throughout Madagascar. To address these issues across the Masoala-Makira landscape I have: 1) identified a handful of approaches that the Wildlife Conservation Society Madagascar Program is currently doing to address these issues; 2) highlighted the shortcomings or deficiencies of these approaches in regards to the major conservation issues addressed by my study; and 3) provided recommendations on how to better address these pressing conservation issues across this region.

First and foremost, I would like to acknowledge the Wildlife Conservation Society Madagascar Program and the tireless efforts of their staff and researchers to protect and conserve the diverse, endemic wildlife and its habitat across this important ecoregion. Without their presence none of this research would have been possible and the numerous benefits to conservation and development across this region would not exist. Any shortcomings and deficiencies that exist are simply a result of their limited resources and do not reflect a lack of passion or intense work ethic on their part.

Currently the WCS program is overseeing numerous community managed zones surrounding the Makira Natural Park that were created to relieve pressure from over-extraction of natural resources from within the protected area. These community managed zones are overseen and managed by a community management association, which is a collection of individuals from the villages located within each community managed zone. The role of these community management associations is to provide record and accountability of the resource use by families occupying these managed areas. These community managed areas/associations have had a mix of success across the Makira Natural Park and the over-extraction of resources from forested areas both within and buffering the protected area has likely been diminished as a result of these efforts by WCS to establish and oversee these community managed associations. However, to my knowledge, these records and accountability do not take into account bushmeat use or hunting either within the buffer areas or within the protected area. My results clearly demonstrate the high rates of carnivore consumption across this region and highlight the conservation and management issues that are likely to follow if these trends continue. These consumption rates and how they vary for each species across the entire region need to be accounted for. I would recommend these community management associations take into account the number of each wildlife species consumed by each household to help in our efforts to monitor and quantify the consumption rates across this region.

The WCS program has continued to purchase satellite imagery across the Makira Natural Park in the hopes of monitoring rates of forest loss and land conversion. This satellite imagery and the researchers/staff working to classify and quantify it will be a vital part of helping to understand the rate at which available habitat is being lost, monitoring important conservation sites, and assisting with targeted education and reforestation programs for the long-term protection of this important conservation area. However, despite having almost a decade worth of imagery and permanent staff devoted to analyzing and classifying this imagery the data and results gathered on these changing landscapes are not being translated or converted into programs that help to diminish forest loss, nor are they being made publicly accessible or converted into peer reviewed manuscripts that disseminate these important findings to the scientific community. I highly recommend that WCS move towards making this imagery available through some form of public access data base, encourage collaborations with various conservation organizations and academic institutions to analyze these data, and work towards publishing these important findings on the rates of forest loss and conversion over the last decade across the Makira Natural Park.

Through a collaboration with Chris Golden (WCS HEAL program) the WCS Madagascar Program is initiating a new livestock program to attempt to alleviate the pressures of bushmeat hunting and consumption across this region by providing vaccinated chickens and ducks to local villages where hunting pressures are greatest. This program is likely to have great success in alleviating these pressures for the village areas where the program will be carried out. However, the results of my research demonstrate that not only are the consumption of carnivores very high across this region, but the hunters appear to disproportionately focus their efforts on forests, located far from villages, where carnivores and co-occurring wildlife are most abundant. As a result, my results indicate that these negative effects on carnivores and co-occurring wildlife may persist as a result of intense hunting pressures from nearby areas not participating in this program. In other words, livestock programs, unless they are expansive enough to cover the majority of the Makira Natural Park, are likely to fail to adequately reduce the negative effects from this widespread hunting. Expanding these livestock programs/introductions across very broad areas and coupling these efforts with targeted education programs that inform locals of the risk of disease and pathogen transfer from handling and consuming bushmeat, as well as the long-term consequences of un-sustainable killing of wildlife from these forests may prove more effective than localized livestock programs alone.

Over the last decade the WCS program has conducted wide-spread socio-economic and education programs across the Makira Natural Park. These programs have provided valuable services, materials, and knowledge to local populations on topics such as family planning, sanitation, disease prevention, economic development, and wildlife conservation. These programs and services are often very well received and welcomed by these local communities. However, as a result of the limited staff and resources of the WCS program, these programs and services have a very limited distribution and resulting impact across the expansive region. In turn, we continue to see an increase in human population growth with corresponding encroachment upon protected areas which results in increases in human-wildlife conflict, increased hunting pressures, an influx of exotic carnivores, and an increase in habitat and landscape characteristics (distance to edge, distance to village, increasing degradation, increasing fragmentation) that are negatively associated with carnivore and lemur populations. Further, the influence of these anthropogenic pressures on wildlife populations (ex. human presence, exotic species, bushmeat hunting) do not appear to be monitored, nor are there programs in place to attempt to diminish their influence. Targeted education programs that: 1) inform local people of the importance of native carnivores and the dangers of exotic carnivores for ecosystem health and function; 2) encourage local people to leave their dogs at home when traveling to or within the forest; 3) propose alternative strategies for feeding zebu other than transporting them into the forest; and 4) introduce new economic opportunities that alleviate resource extraction from forested areas, as well as additional opportunities and programs may help to reduce human and exotic carnivore presence within forest habitat.

In addition to these various recommendations I also believe that additional work is needed to effectively address the numerous conservation and management concerns highlighted by my research project. In particular, additional work is needed to diminish the clearing of large patches of forest habitat within contiguous forest sites. This may be carried out through various incentive programs, such as improving school facilities and programs or expanding and improving health care availability in established villages/towns located far from contiguous forest to incentivize local people to live nearest these areas. In addition, I strongly recommend aggressive removal programs for feral cats *F. species* and Indian civets *V. indica*, particularly at sites where their occupancy is high, where strong negative associations or interactions are known to exist (Farris, Chapter 2; Farris et al. 2014), and at sites protecting endangered local wildlife. An opportunity exists to introduce a bounty program for feral cats *F. species*; however, the unsustainable hunting of native carnivores and lemurs occurring across this region (Golden 2009) further complicates the effectiveness of this approach as the increased presence of locals and/or hunting traps within forest habitat in response to this program may result in an increase in direct or indirect killing of native species as well.

Finally, I suggest that the strong inverse relationship between distance to village and fosa occupancy may stem from the killing of this carnivore by farmers (Kotschwar et al. 2014) across the Masoala-Makira region due to the depredation of chickens and ducks by fosa (Farris, personal observation and communication with locals). In fact, due to the widespread occurrence of this opportunistic killing of fosa and the unsustainable consumption rates of fosa (Golden 2009) I suspect this mortality resulting from hunting is likely one of the biggest conservation concerns for fosa in this region of Madagascar. I recommend widespread dissemination of educational materials informing locals of how to protect their domestic fowl from fosa and ring-tail vontsira *G. elegans* predation, including a trial program to build communal fowl housing for villages where this form of predation is extensive as this may greatly diminish loss of chickens and ducks and protection of native carnivores (Kotschwar et al. 2014).

Additional Research across the Masoala-Makira Landscape

These findings on native and exotic carnivore populations across the Masoala-Makira landscape bring to light additional research needs to effectively address these widespread, alarming threats to Madagascar's diverse, endemic wildlife. In particular, there is a great need to continue with the on-going repeat surveys of two sites across the Makira Natural Park as this study represents the only long-term investigation of carnivore populations in Madagascar and these findings on how both native and exotic carnivore populations are responding to various forms of anthropogenic disturbance will be vital for the effective conservation and management of carnivores moving forward. Further, a great need exists to expand our knowledge of the natural history, including the diet, home range, and behavior of Madagascar's native and exotic carnivores. I suggest expanding our studies of carnivores through the use of GPS and/or radio telemetry studies to investigate native and exotic carnivore home range and activity patterns, scat analysis and molecular scatology studies to investigate the diet and pathogen loads of both native and exotic carnivores and a robust investigation of genetic diversity across the landscape, and expansive village-based questionnaire/surveys to improve our understanding of poorly understood human-wildlife conflicts, such as chicken and duck predation by fosa and ring-tail vontsira *G. elegans* and/or the role of domestic dogs *C. familiaris* and their widespread use by locals across Madagascar's forests.

Additional modeling of carnivore population parameters will continue to expand our knowledge of how humans and exotics are affecting native carnivore populations, including which habitat and landscape variables are most important for predicting these relationships. In particular, through my dissertation work I demonstrate the effectiveness of using two-species occupancy models to investigate interactions among species. With expanded surveys and additional modeling on these parameters, for both carnivores and lemurs, we will be able to effectively identify those co-occurring species relationships having the greatest negative effect on native wildlife species and improve our targeted efforts to control exotic carnivore populations and improve the long-term conservation efforts of various organizations working throughout Madagascar. This is particularly true for the repeat survey sites across Makira where I could incorporate two-species, multi-season occupancy modeling which will inform us of how these interactions change across years as exotic carnivores increase in number. Additionally, these expanded surveys will allow us to utilize additional modeling approaches that will provide accurate, necessary carnivore population parameters, such as density of non-individually identifiable carnivores via mark-resight modeling (McClintock et al. 2011), modeling and predicting species richness across the Madagascar landscape (Dorazio et al. 2006), or abundance estimation of carnivores, lemurs, birds, and small mammals using repeat presence-absence data (Royle and Nichols 2003).

Finally, I suggest the brown-tail vontsira *Salanoia concolor* is one of the world's most threatened carnivores given its overall rarity, limited range, preference for intact, low elevation forest, its high rate of consumption by local people, its negative association with feral cats, and the strong overlap in temporal activity with both dogs and feral cats. Very little is known about the natural history or range of this threatened carnivore, despite this extensive list of disconcerting traits, as evidenced by the current IUCN Red

List assessment for this carnivore (Hawkins et al. 2008). While my surveys expanded the known range of this threatened carnivore (Farris et al. 2012), the Masoala-Makira protected landscape likely remains the last strong-hold for sustaining the brown-tail vontsira. I suggest, based on the findings of my research and the dearth of information surrounding this rare carnivore, that the brown-tail vontsira faces the greatest threat of extirpation, and potential extinction, of all carnivores occupying the Masoala-Makira landscape. Additional research is needed to further our knowledge of its natural history, range, and interactions with co-occurring carnivores and humans if we are to ensure the protection of this carnivore for the foreseeable future.

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Appendices

Appendix A. Summary of findings on fosa *Cryptoprocta ferox* from my dissertation research across the Masoala-Makira landscape in NE Madagascar. Prepared for recent updates by the IUCN specialist group for red list classifications.

Cryptoprocta ferox (Fosa)

Curent classification: Vulnerable

Geographic range

Range Description:

No new information learned on their geographic range.

Population:

Population:

Gerber et al. (2012) estimated the total population of Fosa in Madagascar at between 2,635 (the population estimated to occur in protected areas) and 8,626 adults. Of the upper estimate, 4,476 are estimated to be in 32 populations in rainforest, and 4,150 in 38 populations in dry forest. In their estimation, 95% of the rainforest population occurred in forest blocks north of Andasibe-Perinet; the only protected areas in this region capable of holding more than 300 adult Fosa are Vohidrazana-Zahamena and Makira-Masoala. Around 95% of the dry forest population was in 9 large forest blocks, of which only two could hold more than 300 individuals.

Gerber et al. (2012) found densities of Fosa around Ranomafana NP to be similar in primary forest (0.12± SE0.05 individuals per square kilometer) and logged forest (0.09 ±

SE 0.04), and found the species present in forest fragments 2.5 km from intact forest, although absent from fragments 15 km from intact forest.

In NE Madagascar, camera trap surveys found a high probability of occupancy (0.68 SE ± 0.08) for fosa across the Masoala-Makira landscape. Fosa were found at similar levels of probability of occupancy in non-degraded forest (0.66 SE ± 0.06) and degraded forest (0.68 SE ± 0.13). Surveys at one contiguous forest site shows little to no change in fosa occupancy (0.79 to 0.85) from 2008-2013 (trap success changed from 3.04 in 2008 to 3.42 in 2013). However, at another repeat survey site trap success decreased from 7.16 (2011) to 3.43 (2013) over a three year period. Fosa occurred in forest fragments at Farankarina managed area which is separated by > 5 km from both Makira and Masoala NP, as well as additional smaller fragmented forest patches. The smallest fragmented forest patch fosa were captured in was the Farankarina managed area (-15.422, 49.837) which was 8 sq km and located 5 km or farther from both Masoala and Makira forests. Fosa were also observed moving through anthropogenic landscapes.

Habitat and Ecology:

In NE Madagascar, camera trap surveys show fosa presence in in contiguous, non-degraded, fragmented, and highly degraded forest sites and evidence that fosa may have a lower activity and probability of occupancy in contiguous, core rainforest areas. The most intact, contiguous forest surveyed by my team across the Makira region had the fewest number of captures (n = 4) and resulting trap success (0.38) compared to the average number of captures per site (n = 30) and average trap success (2.43). In degraded forest fosa were often captured on trails near the forest edge, which they likely used at night to travel to villages to hunt for chickens and ducks (Farris and Kelly 2011; Farris, Chapter 2).

Fosa were solitary for the majority of the year; however, pairs were often photographed near the breeding season (Oct-Dec). I observed what appeared to be an adult traveling with a juvenile in May and a very small fosa (possibly infant or very early juvenile) in September.

My temporal activity analyses reveal that fosa demonstrate primarily nocturnal behavior; however, they did exhibit some diurnal behavior throughout the year (Farris, Chapter 3). Fosa demonstrated strict nocturnal behavior at sites having high human and dog activity, suggesting these species may influence fosa activity. Fosa also altered their temporal activity, demonstrating more diurnal behavior, during the peak breeding season (Oct-Dec.; Farris, Chapter 3)

Threats:

I found 99 fosa were consumed within four villages (n = 144 households surveyed) from 2005 to 2011 across the Makira Natural Park. Hunting rates were highest in non-degraded forest and were positively associated with fosa occupancy, meaning hunters appear to be focusing their efforts in non-degraded forest where fosa are most abundant (Farris, Chapter 2).

Golden et al (in review) report 4 fosa hunted in one year at Betampona SNR, two hunted opportunistically (presumably with dogs).

Fosa altered their temporal activity by exhibiting strict nocturnal activity when diurnal humans and dogs were highly active. Further, they show high nocturnal temporal activity overlap with both Indian civets and feral/wild cats, revealing the potential for increased interactions and competition (Farris, Chapter 3).

Many camera-trap photos of fosa were obtained with nooses from make-shift traps which have failed and photos of fosa with numerous scars and missing body parts (ears, lip, tail) which reportedly result from locals trying to kill them with machetes when they raid their chickens and ducks.

Deforestation and forest disturbance across the range of the Fosa has increased significantly since 2009. R. Rajaonson (pers comm) estimates that deforestation in eastern forest increased from 0.5% per annum between 2005-2010 to 0.94% per annum in 2010- 2013. Allnut et al. (2009) estimate that in Masoala NP, annual rates of deforestation in the study area increased to 1.27% per annum in 2011. High levels of illegal settlement in protected areas, especially around the Bay of Antongil, are linked to artisanal mining (for quartz) and logging of rosewood, and hunting for food using dogs has increased greatly in these areas as a result. Some villages have seen increases in populations of between 200 and 300% (C.Golden pers. comm.).

In western Madagascar, Zinner et al. (2014) show that for central Menabe, one of the most important centres of distribution of Fosa, deforestation rates of 0.78 km2/yr between 2003-2006 increased to 1.09 km2/yr between 2006-2008, and to 2.55 km2/yr by 2008-2010. There is ample evidence that the recent trend has continued in 2010-2104, with in addition increased illegal logging and hunting in the core forest areas, which will undoubtedly negatively impact populations of all native carnivores, especially through the increased presence of dogs.

Appendix B. Summary of findings on falanouc *Eupleres goudotii* from my dissertation research across the Masoala-Makira landscape in NE Madagascar. Prepared for recent updates by the IUCN specialist group for red list classifications.

Eupleres goudotii (Eastern falanouc)

Current classification: Near threatened

Geographic range:

Range Description:

No new information learned on their geographic range.

Population:

Population:

Gerber et al. (2012) found Eastern falanouc to be present at 7% of camera trap stations in primary forest and 31% of trap stations in selectively logged forest at Ranomafana NP. The species was absent from forest fragments more than 2.5 km from intact forest.

In NE Madagascar, camera trap surveys revealed a low probability of occupancy (0.31 SE ± 0.07) for Eastern falanouc across the Masoala-Makira landscape (Farris, Chapter 2). This included a similar probability of occupancy in non-degraded (0.24 SE ± 0.08) and degraded (0.30 SE ± 0.07) rainforest. Their occupancy had a strong positive association with bird camera trap success, possibly an indication that large birds of the kind that set off camera traps are subject to similar threats (Farris and Kelly 2011; Farris, Chapter 2). In addition to these similar estimates of occupancy Eastern falanouc was also found in all degraded, fragmented forest sites (including at the Farankarina site at > 5km from contiguous forest) providing evidence they may be less dependent upon contiguous forest than originally proposed.

Surveys over a six year period (2008-2013) and resulting multi-season occupancy analyses at one contiguous forest site shows falanouc occupancy decreased significantly from 0.79 (2008) to 0.20 (2013) (trap success during this time changed from 3.11 in 2008 to 1.09 in 2013) which resulted in a probability of local extirpation of 0.31 (0.10), while trap success at an additional repeat site remained low over a three year period from from 2011 (0.33) to 2013 (0.25) (Farris et al. 2014).

Habitat and Ecology:

Falanouc were positively associated with bird activity and, to a lesser extent, with distance to village. These are both likely habitat mediated relationships that are likely correlated with slightly degraded area which may have more open, wet, or muddy areas; however, these relationships need to be explored further.

Falanouc were almost exclusively solitary; however, I did photograph a female traveling with her single juvenile (January). My temporal activity analyses show falanouc appear to exhibit crepuscular activity with a preference for nighttime periods just prior to dawn and just after dusk. However, during the hot-dry season falanouc demonstrated more variable activity across the diel cycle rather than primarily crepuscular activity (Farris, Chapter 3).

Threats:

Deforestation and forest disturbance across the range of the Eastern falanouc has increased significantly since 2009. R. Rajaonson (pers comm) estimates that deforestation in eastern forest increased from 0.5% per annum between 2005-2010 to 0.94% per annum in 2010- 2013. Allnut et al. (2009) estimate that in Masoala NP, annual rates of deforestation in the study area increased to 1.27% per annum in 2011. High levels of illegal settlement in protected areas, especially around the Bay of Antongil, are linked to artisanal mining (for quartz) and logging of rosewood, and hunting for food using dogs has increased greatly in these areas as a result. Some villages have seen increases in populations of between 200 and 300% (C.Golden pers. comm.).

In NE Madagascar, I found 28 falanouc were consumed from 2005 to 2011 across four villages (n = 143 households surveyed) near the Makira Natural Park. Hunting rates were highest in non-degraded forest and were positively associated with falanouc occupancy, meaning hunters appear to be focusing their efforts in non-degraded forest where falanouc are most abundant (Farris, Chapter 2).

Eastern falanouc demonstrate strong temporal activity overlap with Indian civets, revealing the potential for increased interactions and competition (Farris, Chapter 4).

My co-occurrence models demonstrate that Eastern falanouc have strong co-occurrence with the exotic feral/wild cat, meaning falanouc are detected more at sites where cat activity is very high. Further, falanouc probability of occupancy is higher at sites where cats are most active. This may be a habitat mediated relationship; however, it almost certainly translates into increased interactions between these two carnivore species (Farris, Chapter 4). However, I found the opposite relationship between falanouc and dogs. Falanouc probability of occupancy increases dramatically when dogs are not present at a site and the two occur together less than expected across the landscape, meaning falanouc do not use sites where dogs are highly active (Farris, Chapter 4) possibly as dogs kill falanouc.

Appendix C. Summary of findings on spotted fanaloka *Fossa fossana* from my dissertation research across the Masoala-Makira landscape in NE Madagascar. Prepared for recent updates by the IUCN specialist group for red list classifications.

Fossa fossana (spotted fanaloka)

Current classification: Near threatened

Geographic range:

Range Description:

No new information learned on their geographic range.

Population:

Population:

Gerber et al. (2012) found around Ranomafana NP that spotted fanaloka was found at lower density (1.38+\- SE 0.22 individuals per square kilometer) in logged forest compared to unlogged (3.19+\- SE 0.55) and were absent from forest fragments greater than 2.5 km from intact forest.

In NE Madagascar, camera trap surveys revealed a high probability of occupancy of 0.70 (SE ± 0.07) across the Masoala-Makira landscape, the highest of any native carnivore. However, spotted fanaloka occupancy was significantly higher in non-degraded forest (0.73 SE ± 0.08) compared to degraded forest (0.50 SE ± 0.08). Spotted fanaloka were not detected in forest fragments located ≥ 5 km from contiguous forests (Farris and Kelly 2011; Farris, Chapter 2). Spotted fanaloka are constrained by the presence of both exotic feral/wild cats (*Felis sp.*) and exotic Indian civets (*Viverricula indica*) (Farris, Chapter 2; Gerber et al. 2012). Photographic surveys over a six year period (2008-2013) and resulting multi-season occupancy analyses at one contiguous forest site shows spotted fanaloka occupancy decreased from 1.0 (2008) to 0.80 (2013) (trap success decreased from 14.0 in 2008 to 3.59 in 2013) which resulted in a moderate probability of local extirpation of 0.14 (0.05), while at another repeat survey site I found trap success changed only from 5.04 in 2011 to 4.46 in 2013 (Farris et al. 2014).

Habitat and Ecology:

My surveys revealed a much lower probability of occupancy and significantly fewer captures in degraded forest sites. Further, spotted fanaloka had a negative association with distance to villages (Farris and Kelly 2011; Farris et al. 2012; Farris, Chapter 2). Spotted fanaloka were almost exclusively solitary; however, I photographed an adult and juvenile traveling together in March. My temporal activity analyses revealed spotted fanaloka were exclusively nocturnal; however, I have a handful of photographs of spotted fanaloka active during daylight hours. My analyses reveal evidence of spotted fanaloka shifting peak activity from cool season to hot season; however, this may have resulted from increased human and dog activity (Farris, Chapter 3).

Threats:

Deforestation and forest disturbance across the range of the Eastern falanouc has increased significantly since 2009. R. Rajaonson (pers comm) estimates that deforestation in eastern forest increased from 0.5% per annum between 2005-2010 to 0.94% per annum in 2010- 2013. Allnut et al. (2009) estimate that in Masoala NP, annual rates of deforestation in the study area increased to 1.27% per annum in 2011. High levels of illegal settlement in protected areas, especially around the Bay of Antongil, are linked to artisanal mining (for quartz) and logging of rosewood, and hunting for food using dogs has increased greatly in these areas as a result. Some villages have seen increases in populations of between 200 and 300% (C.Golden pers. comm.).

Hunting and/or bushmeat consumption appear to be less of a concern for spotted fanaloka compared to other carnivores across the Masoala-Makira landscape. My research showed only 11 spotted fanaloka were consumed within four villages (n = 143 households surveyed) from 2005 to 2011 near the Makira Natural Park. However, hunting rates were still positively associated with spotted fanaloka occupancy, demonstrating increased efforts in non-degraded forest where their abundance/activity is highest.

Spotted fanaloka appear to alter their temporal activity when human and dog activity are very high. Further, spotted fanaloka have strong temporal overlap with Indian civets, revealing the potential for increased interactions and competition (Farris, Chapter 3). Single-season, landscape occupancy analyses showed that spotted fanaloka probability of occupancy decreases dramatically when feral cat and Indian civet were present (Farris, Chapter 4).

Appendix D. Summary of findings on ring-tail vontsira *Galidia elegans* from my dissertation research across the Masoala-Makira landscape in NE Madagascar. Prepared for recent updates by the IUCN specialist group for red list classifications.

Galidia elegans (Ring-tailed Vontsira)

Current classification: Least concern

Geographic range:

Range Description:

No new information learned on their geographic range.

Population:

Population:

Gerber et al. (2014) found Ring-tailed Vontsira to be recorded in 100% of camera traps in intact and logged forest around Ranomafana NP, in 77% (±10%) of fragments less than 2.5 km from intact forest, in 19% (± 12%) of forest matrix around these fragments, in 77% (±10%) of fragments more than 15 km from intact forest, and also 19% (± 12%) of forest matrix around these forest fragment sites. Similarly, in Makira/ Masoala, Ring-tailed vontsira were detected in all degraded, fragmented sites surveyed (Farris, Chapter 2).

In NE Madagascar, camera trap surveys revealed a moderate probability of occupancy (0.48 SE ± 0.08) for this carnivore across the Masoala-Makira landscape, although this estimate is likely biased by my survey efforts being highest in forest habitat located far from anthropogenic areas. This is further supported by the higher rates of activity and occupancy in degraded sites compared to non-degraded sites (capture rates were too low to provide estimates for non-degraded forest).

The low number of captures prevented us from conducting multi-season occupancy analyses; however, over a six year period at one site trap success changed from 1.37 in 2008 to 0.35 in 2013. Further, at an additional repeat survey site I found trap success was relatively consistent from 3.78 in 2011 to 3.62 in 2013.

In both Ranomafana and Makira/Masoala, Ring-tailed Vontsira presence was strongly negatively correlated with feral/wild cat occupancy, which is highest near villages (Gerber et al. 2014, Farris and Kelly 2011; Farris, Chapter 2).

Habitat and Ecology:

Ring-tail vontsira was more active and had a higher probability of occupancy in degraded forest sites; however, its occupancy was positively associated with bird activity and negatively influenced by distance to village. This negative association with villages may be a reflection of the intense hunting pressure for this carnivore (Farris and Kelly 2011; Farris et al. 2012; Farris, Chapter 2).

Ring-tail vontsira were primarily captured in pairs. My temporal activity analyses revealed ring-tail vontsira were primarily diurnal; however, ring-tail vontsira did exhibit some crepuscular and limited nocturnal activity which may be related to seasonal changes (Farris, Chapter 3).

Threats:

Deforestation and forest disturbance across the range of the Ring-tailed Vontsira has increased significantly since 2009. R. Rajaonson (pers comm) estimates that deforestation in eastern forest increased from 0.5% per annum between 2005-2010 to 0.94% per annum in 2010- 2013. Allnut et al. (2009) estimate that in Masoala NP, annual rates of deforestation in the study area increased to 1.27% per annum in 2011. High levels of illegal settlement in protected areas, especially around the Bay of Antongil, are linked to artisanal mining (for quartz) and logging of rosewood, and hunting for food using dogs has increased greatly in these areas as a result. Some villages have seen increases in populations of between 200 and 300% (C.Golden pers. comm.).

Hunting and/or bushmeat consumption presents a serious concern for ring-tailed vontsira across the eastern rainforest. Golden et al (in review) report 21 Ring-tailed Vontsira hunted in one year at Betampona SNR. In the Masoala-Makira landscape a total of 169 ring-tail were consumed within four villages (n = 144 households) from 2005 to 2011 near the Makira Natural Park. Hunting rates were positively associated with ring-tail vontsira occupancy, meaning hunters appear to be focusing their efforts in non-degraded forest where this carnivore most abundant. In addition, the ring-tail vontsira consistently was the most purchased and most trapped across the landscape, which is likely a reflection of their overall apparent abundance and higher level of activity in and around anthropogenic areas (Farris, Chapter 2).

Ring-tail vontsira had very strong temporal activity overlap with dogs and moderate overlap with feral/wild cats, revealing the potential for increased interactions and competition (Farris, Chapter 3).

My co-occurrence models demonstrate strong negative interactions between ring-tail vontsira and exotic Indian civets. In particular, ring-tail vontsira do not co-occur with the exotic Indian civet, meaning ring-tail vontsira do not occur at sites where Indian civet activity is very high. Further, ring-tail vontsira probability of occupancy is greatly decreased in the presence of Indian civets (Farris, Chapter 4).

Appendix E. Summary of findings on broad-stripe vontsira *Galidictis fasciata* from my dissertation research across the Masoala-Makira landscape in NE Madagascar. Prepared for recent updates by the IUCN specialist group for red list classifications.

Galidictis fasciata (Broad-stripe Vontsira)

Current classification: Near threatened

Geographic range:

Now known from Marojejy National Park (Hawkins 2012[b]), around 100 km north of previously recognized range.

Also confirmed in Makira Natural Park and between Masoala and Makira (Farris et al. 2012).

Population:

Camera-trap surveys revealed a low probability of occupancy (0.28 SE ± 0.07) across the Masoala-Makira landscape for broad-striped Vontsira, including a much higher probability of occupancy in non-degraded (0.49 SE ± 0.15) compared to degraded (0.36 SE ± 0.11) forest sites (Farris, Chapter 2). Broad-striped Vontsira occupancy had a strong positive association with small mammal trap success; however, dog (*C. familiaris*) occupancy had an inverse relationship revealing a strong possibility of killing or competitive exclusion of broad-striped vontsira by dogs particularly in degraded forest (Farris and Kelly 2011; Farris, Chapter 2).

My photographic surveys over a six year period (2008-2013) and resulting multi-season occupancy analyses at one contiguous forest site shows occupancy of this species decreased significantly from 0.77 (2008) to 0.18 (2013) (trap success decreased from

2.59 in 2008 to 0.25 in 2013) which resulted in a high probability of local extirpation of 0.60 (0.12). This dramatic decrease in occupancy and high probability of local extirpation, which were correlated with distance to forest edge, for this native carnivore in a contiguous, non-degraded forest site presents a serious conservation/management issue (Farris et al. 2014). Further, at an additional repeat survey site over a three year period I found trap success increased from 0.20 in 2011 to 1.68 in 2013; however, these remain low capture rates for this poorly known carnivore.

Habitat and Ecology:

Broad-striped vontsira probability of occupancy was positively associated with small mammal activity, but negatively influenced by distance to village. Broad-stripe vontsira were observed more often and had a higher probability of occupancy in non-degraded, contiguous forest sites (Farris and Kelly 2011; Farris et al. 2012; Farris, chapter 2). Broad-striped vontsira had an extremely low activity and resulting probability of occupancy in highly fragmented and degraded sites with only a single capture in fragmented forests > 5 km from contiguous forest.

Broad-striped vontsira were primarily observed in pairs and are exclusively nocturnal (Farris, Chapter 3).

Threats:

Deforestation and forest disturbance across the range of the Broad-striped vontsira has increased significantly since 2009. R. Rajaonson (pers comm) estimates that deforestation in eastern forest increased from 0.5% per annum between 2005-2010 to 0.94% per annum in 2010- 2013. High levels of illegal settlement in protected areas, especially around the Bay of Antongil, are linked to artisanal mining (for quartz) and logging of rosewood, and hunting for food using dogs has increased greatly in these areas as a result. Some villages have seen increases in populations of between 200 and 300% (C.Golden pers. comm.). Hunting and/or bushmeat consumption appear to be less of a concern for broad-stripe vontsira across the Masoala-Makira landscape. My research showed only 7 broad-stripe were consumed across four villages (n = 55 households) from 2005 to 2011 near the Makira Natural Park. However, hunting rates were still positively associated with broad-stripe vontsira occupancy demonstrating hunting efforts are highest where this carnivore is most active/abundant (Farris, Chapter 2).

Golden et al (in review) report 3 Broad-striped vontsira hunted in one year at Betampona SNR.

Broad-stripe vontsira showed strong temporal activity overlap with the exotic Indian civet, revealing the potential for interactions and competition (Farris, Chapter 3).

My co-occurrence models demonstrate strong negative interactions between broad-stripe vontsira and both exotic dogs and Indian civets. In particular, broad-stripe vontsira do not co-occur with the exotic dogs or Indian civet, meaning broad-stripe vontsira do not occur at sites where dog and/or Indian civet activity is very high. Further, broad-stripe vontsira probability of occupancy is greatly decreased in the presence of both dogs and Indian civets (Farris, Chapter 4).

Appendix F. Summary of findings on brown-tail vontsira *Salanoia concolor* from my dissertation research across the Masoala-Makira landscape in NE Madagascar. Prepared for recent updates by the IUCN specialist group for red list classifications.

Salanoia concolor (Brown-tail Vontsira)

Current classification: Vulnerable

Geographic range:

Known recently (last 20 years) only from Masoala National Park, Makira Natural Park, Betampona Strict Nature Reserve, Mananara Nord, and Zahamena (Hawkins 2012[a]), thus only in the northern portion of the eastern rainforest. Individuals at Lake Alaotra have been identified as a new taxon, Durrell's Vontsira *Salanoia durrelli* (Durbin et al. 2010).

Range Description:

My studies provided the first confirmation of this carnivore within the Makira Natural Park, including captures extending its northern most range (Farris et al. 2012).

Population:

Population:

Rarely seen even in the site with most records, Masoala (Hawkins 2012a).

Brown-tail vontsira had the lowest probability of occupancy (0.25 SE ± 0.09) for any native/endemic carnivore across the landscape, providing further support of the overall rarity of this carnivore across the Masoala-Makira landscape. Brown-tail vontsira occupancy had a strong positive association with bird trap success (Farris et al. 2012; Farris, Chapter 2). I did not detect brown-tail vontsira in forest fragments > 5 km distance from contiguous forest.

My photographic surveys over a six year period (2008-2013) and resulting multi-season occupancy analyses at one contiguous forest site shows brown-tail occupancy decreased significantly from 0.87 (2008) to 0.16 (2013) (trap success decreased from 0.99 in 2008 to 0.67 in 2013) which resulted in an extremely high probability of local extirpation of 0.49 (0.13). This represents the greatest decrease in multi-season occupancy for any carnivore. No brown-tail vontsira were captured at my additional repeat survey sites. In fact, across the landscape I only found this carnivore at two survey sites. These findings combined with the overall rarity of this poorly known carnivore represents an alarming trend which demands attention (Farris et al. 2014).

Habitat and Ecology:

Brown-tail vontsira were captured in both degraded and non-degraded forest sites. They were observed at a maximum elevation of 680 m and they did not occur at sites having high activity of dogs, cats, or ring-tail vontsira (Farris and Kelly 2011; Farris et al. 2012; Farris, Chapter 2).

Brown-tail vontsira were observed primarily in pairs, singles were very rare. My temporal activity analyses reveal brown-tail vontsira are almost exclusively diurnal with peak activity contrasting with ring-tail vontsira (Farris, Chapter 3).

Threats:

Deforestation and forest disturbance across the range of the Fosa has increased significantly since 2009. R. Rajaonson (pers comm) estimates that deforestation in eastern forest increased from 0.5% per annum between 2005-2010 to 0.94% per annum in 2010- 2013. Allnut et al. (2009) estimate that in Masoala NP, annual rates of deforestation in the study area increased to 1.27% per annum in 2011. High levels of illegal settlement in protected areas, especially around the Bay of Antongil, are linked to artisanal mining (for quartz) and logging of rosewood, and hunting for food using dogs has increased greatly in these areas as a result. Some villages have seen increases in populations of between 200 and 300% (C.Golden pers. comm.).

In the Makira-Masoala region there is little data on consumption rates of this carnivore which is likely a reflection of its overall rarity (Farris, Chapter 2). In Betampona Strict Nature Reserve, Golden et al. (in review) report 6 Brown-tailed Vontsira hunted in one year.

Brown-tail vontsira had very strong temporal activity overlap with dogs and moderate overlap with feral/wild cats, revealing the potential for increased interactions and competition. These potential interactions and competition may contribute to the absence of brown-tail vontsira at sites where dog activity is high (Farris, Chapter 3).