THE BIODIVERSITY MIRAGE: THE RESPONSE OF GROUND-DWELLING FOREST BIRDS, TENRECS AND LEMURS TO HABITAT DEGRADATION AND EXOTIC PREDATORS IN NORTHEASTERN MADAGASCAR

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ABSTRACT

Madagascar is one of the world's top conservation priorities due to the intense anthropogenic pressures on its diverse and endemic wildlife. There have been very few studies conducted in the largest protected area complex in Madagascar, the Masoala-Makira landscape (northeastern Madagascar). My goal was to examine the response of ground-dwelling forest birds, tenrecs (Lipotyphla: Tenrecidae) and lemurs to habitat degradation and the presence of exotic predators, and monitor population trends at resurveyed sites from 2008 to 2013. Using camera trap surveys and distance sampling, we observed 26 bird species (n = 4,083 observations), three spiny tenrec species (n = 244 observations) and 12 lemur species (n = 1,172 observations). Out of 13 focal species (seven bird, three tenrec and three lemur species), seven had higher point estimates of occupancy or density at intact forests when compared to intermediately degraded or degraded forest sites. Common tenrecs (*Tenrec ecaudatus*) and cathemeral lemurs changed their activity patterns, becoming more nocturnal in degraded forests. Feral cat (*Felis sp.*) trap success was negatively related to the detection of three bird species (red-breasted coua, *Coua serriana*; scaly ground-roller, *Geobiastes squamiger*; and Madagascar crested ibis, *Lophotibis cristata*). At two resurveyed sites (S02 and S05), out of 19 and 17 species, only four and eight species did not show consistent declines in occupancy or encounter rates, respectively, over a six-year period. This research highlights the urgent need for immediate conservation action in the Masoala-Makira protected area complex in order to protect one of the world's biodiversity hotspots.

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

Chapter Two:

Coalmine Canaries: Landscape And Dynamic Occupancy Trends Of Ground-Dwelling Forest Birds In The Masoala-Makira Protected Area Complex, Northeastern Madagascar

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Chapter Three:

An Unstable Prey Base: Landscape And Cross-Year Occupancy Trends Of Three Spiny Tenrec (Lipotyphla: Tenrecidae: Tenrecinae) Species In Northeastern Madagascar

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Chapter Four:

Flagships In Peril: Habitat Degradation and Trends In Lemur Population Dynamics In Northeastern Madagascar

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Chapter 3:
An unstable prey base: landscape and cross-year occupancy trends of three spiny tenrec (Lipotyphla: Tenrecidae: Tenrecinae) species in northeastern Madagascar.

Appendix C.1. Representative camera trap photographs of the three spiny tenrec species analyzed: A) common tenrec (*Tenrec ecaudatus*), B) lowland streaked tenrec (*Hemicentetes semispinosus*) and C) greater hedgehog tenrec (*Setifer setosus*). Photographs have been cropped and edited for better viewing.

Appendix C.2. Station-level[1] and landscape-level habitat[2] features (SE) for the seven sites in the Masoala-Makira protected area complex, northeastern Madagascar. Sites are coded from least degraded (S01) to most degraded (S07). Table modified and used with permission from Farris (2014).

Appendix C.3. Comparison of spiny tenrec trap success rates (TS; [number of individual captures/total survey trap nights]*100) in the eastern rainforests between studies conducted with different methods: invasive baited live/pitfall trapping and noninvasive unbaited camera trapping. Included is the region and forest type that the study was conducted in, the method of capture, total trap nights and which species (lowland streaked, greater hedgehog and common tenrec) were captured.

Chapter 4:
Flagships in peril: habitat degradation and trends in lemur population dynamics in northeastern Madagascar.

Appendix D.1. Survey details for the 420 lemur surveys conducted at six sites across the Masoala-Makira protected area complex (2010-2013). Included range of elevations that lemurs were observed, number of diurnal and nocturnal surveys conducted, total distance surveyed (km), number of species and individuals observed. Sites are ranked from least degraded (S01) to most degraded (S06) based on metrics in Appendix D.2 and as described in Farris (2014).

Appendix D.2. Station-level[1] and landscape-level[2] habitat features (SE) for the six forest sites in the Masoala-Makira landscape, northeastern Madagascar. Sites are organized from least degraded (S01) to most (S06). Table modified and used with permission from Farris (2014).

Chapter 1

THE BIODIVERSITY MIRAGE: THE RESPONSE OF GROUND-DWELLING FOREST BIRDS, TENRECS AND LEMURS TO HABITAT DEGRADATION AND EXOTIC PREDATORS IN NORTHEASTERN MADAGASCAR

Introduction

Madagascar, as a biodiversity hotspot, is of high international conservation concern (Myers *et al.* 2000, Brooks *et al.* 2002, Brooks *et al.* 2006, Mittermeier *et al.* 2010). Fifty-two percent of its native birds, all of its native mammals and over 88% of its native amphibians and reptiles are found nowhere else in the world (Irwin *et al.* 2010). Of the species that are assessed by the International Union for the Conservation of Nature (IUCN), 38% of amphibians/reptiles, 14.5% of birds and 56% of mammals are listed as Vulnerable, Endangered or Critically Endangered (IUCN 2014).The main threats to Madagascar's biodiversity are habitat loss and habitat degradation, unsustainable hunting, and the presence of exotic species (Golden 2009, Goodman 2012, Allnutt *et al.* 2013). Habitat loss reduces the amount of habitat available, while habitat degradation reduces the quality of the habitat left available, thus increasing its vulnerability to further anthropogenic pressures (Brooks *et al.* 2002, Fahrig 2003). Hunting and the presence of exotic predators can act synergistically with habitat degradation, increasing the potential for negative effects on native species (Peres 2001, Laurance & Useche 2009, Farris *et al.* 2014).

Despite being important as seed dispersers (Ganzhorn *et al.* 1999, Razafindratsima *et al.* 2014), pollinators (Kress *et al.* 1994) and prey to native Malagasy predators (Karpanty 2006, Goodman 2012), lemurs are still relatively understudied. One area where lemur research is lacking is the area of robust and precise density estimates, which are vital to planning efficient and effective conservation strategies (Araldi *et al.* 2014). Line transect surveys are often used to estimate lemur density, but very rarely do studies employ conventional distance sampling (CDS) although its use is facilitated by the available and free software Program DISTANCE (Buckland *et al.* 2001, Thomas *et al.* 2010).

In addition to ecological gaps, there are geographic gaps in the published lemur literature. Few in-depth studies on lemurs have occurred in northeastern Madagascar, despite the fact that the northeastern rainforests have the highest lemur species diversity and highest lemur extinction risk (Rasolofoson *et al.* 2007, Schwitzer *et al.* 2014). There are also very few published studies on Madagascar's ground-dwelling birds and tenrecs (Lipotyphla: Tenrecidae). Ground-dwelling birds and tenrecs are important prey resources for native predators (Morris & Hawkins 1998, Karpanty & Goodman 1999, Soarimalala & Goodman 2011, Goodman 2012), and ground-dwelling birds provide various important ecosystem services such as seed dispersal and pest regulation (Sekercioglu 2006). Unfortunately, habitat loss and degradation (Scott *et al.* 2006, Herrera *et al.* 2011), intensive hunting throughout Madagascar (Golden 2009, Gardner & Davies 2014) and the presence of exotic predators (Goodman 2012, Farris 2014) threatens all three groups.

Goal and Objectives

My goal was to aid conservation and management efforts in Madagascar by increasing the knowledge of how lemurs, ground-dwelling birds and tenrecs respond to habitat degradation and the presence of exotic predators. I also wanted to provide the first large-scale study on these three groups and monitor their population trends over time at resurveyed sites in the Masoala-Makira protected area complex (hereafter, Masoala-Makira landscape). Virginia Tech, in collaboration with the Wildlife Conservation Society (WCS), has worked in the Masoala-Makira landscape surveying wildlife since 2008 using camera traps and line transects. Over seven sites, 13 surveys, and six years, we've collected over 9,000 observations of six native and three exotic carnivore, 28 ground-dwelling forest bird, three tenrec, and 12 lemur species (Tables 1 and 2). With this dataset, my detailed objectives—found within the following three chapters of my thesis—were to:

II. Coalmine canaries: landscape and dynamic occupancy trends of ground-dwelling forest birds in the Masoala-Makira protected area complex, northeastern Madagascar.

a. Estimate landscape occupancy and detection probability for ground-dwelling forest birds,

b. Determine the relationships between ground-dwelling forest bird occupancy/detection and habitat degradation and the presence of exotic species presence, and

c. Examine trends over time in ground-dwelling forest bird occupancy, detection, local colonization, and local extirpation at three resurveyed forest sites.

III. An unstable prey base: landscape and cross-year occupancy trends of three spiny tenrec (Lipotyphla: Tenrecidae: Tenrecinae) species in northeastern Madagascar.

a. Estimate spiny tenrec landscape trap success, occupancy and detection probability,

b. Determine the relationships between spiny tenrec occupancy/detection and habitat degradation and the presence of exotic carnivores,

c. Investigate changes in daily activity patterns of spiny tenrecs across intact, intermediately-degraded (hereafter, intermediate) and degraded forest sites, and

d. Examine spiny tenrec occupancy and detection trends at two resurveyed forest sites.

IV. Flagships in peril: habitat degradation and trends in lemur population dynamics in northeastern Madagascar.

a. Estimate lemur encounter rates and density using CDS in Program DISTANCE,

b. Examine the relationships between the encounter rates and/or density estimates of multiple lemur species and habitat degradation,

c. Investigate how the activity patterns of cathemeral lemurs change over intact, intermediate and degraded forests, and

d. Monitor lemur encounter rates through the years at two resurveyed forest sites.

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Table 1. Summary information of camera trap and lemur surveys at seven sites in the Masoala-Makira landscape, northeastern Madagascar (2008-2013), not including data from S03 collected by our collaborators in 2013.

Study Site (Survey Dates; Season[1])	Camera Stations	Tot. TNs[2]	NC[3] (TS)	EC[4] (TS)	B[5] (TS)	T[6] (TS)	Diur. Lemur Surveys	Noct. Lemur Surveys	Dist. Surveyed (km)	L[7] (n)
S01 (Mar – May 2009; HW)	20	989	4 (2.22)	2 (0.51)	12 (15.1)	2 (4.25)	15	15	60	9 (263)
S02 (Sept – Nov 2008; CW)	20	1,315	6 (26.1)	2 (2.13)	12 (64.9)	3 (3.19)	--	--	--	--
S02 (Sept – Nov 2010; HD)	25	1,230	6 (20.6)	2 (0.98)	10 (40.5)	3 (2.36)	17	17	68	7 (126)
S02 (Aug – Oct 2011; CW)	24	1,383	6 (16.6)	3 (1.52)	9 (30.4)	2 (0.65)	17	16	66	4 (57)
S02 (Jul – Oct 2012; CW)	24	1,536	6 (6.84)	3 (3.06)	8 (10.6)	1 (0.65)	24	23	94	4 (59)
S02 (Sept – Oct 2013; CW)	24	1,198	6 (9.77)	2 (1.34)	10 (10.0)	1 (0.17)	30	19	85	7 (87)
S03 (Aug – Oct 2009; CW)	19	1,067	3 (1.50)	3 (6.09)	9 (9.56)	2 (2.44)	15	15	60	4 (31)
S04 (Jun – Aug 2011; CW)	23	1,462	4 (4.93)	2 (17.2)	8 (24.1)	1 (0.14)	18	18	72	3 (108)
S05 (Mar – May 2011; HW)	24	1,509	5 (16.3)	3 (27.4)	9 (23.5)	2 (0.86)	18	18	72	6 (114)
S05 (Jun – July 2012; CW)	24	1,015	5 (10.7)	2 (13.9)	10 (10.8)	--	14	15	58	5 (39)
S05 (Nov 2013 – Jan 2014; HD)	24	1,188	5 (15.3)	2 (39.7)	9 (9.43)	2 (0.67)	41	25	128	8 (241)
S06 (Nov 2009 – Jan 2010; HD)	18	881	5 (4.20)	3 (2.38)	8 (25.9)	2 (3.52)	--	--	--	--
S07 (Dec 2010 – Feb 2011; HD)	24	1,570	6 (6.12)	2 (20.7)	12 (31.1)	3 (1.91)	15	15	60	4 (47)
TOTAL		**16,343**	**6 (11.2)**	**3 (11.1)**	**26 (24.2)**	**3 (1.49)**	**224**	**196**	**823**	**12 (1,172)**

[1] Season that the site was surveyed: HW (Hot-Wet; February-May), HD (Hot-Dry; October-January) and CW (Cold-Wet; June-September)
[2] TN: trap nights or the number of 24-hour periods that a camera station was active (with at least one camera functioning properly)
[3] NC (TS): # of native carnivore species detected and native carnivore trap success rate ([# of native carnivore individuals observed/TN]*100)
[4] EC (TS): # of exotic carnivore species detected and exotic carnivore trap success rate ([# of exotic carnivore individuals observed/TN]*100)

[5] B (TS): # of bird species detected and bird trap success rate ([# of bird individuals observed/TN]*100)
[6] T (TS): # of tenrec species detected and tenrec trap success rate ([# of tenrec individuals observed/TN]*100)
[7] L (n): # of lemur species observed and # of lemur individuals observed

Table 2. Species observed in the Masoala-Makira landscape, northeastern Madagascar. IUCN status is provided, along with whether the species is known to be hunted or not. Species in light gray will be the subjects of future analyses[1].

Taxa	Common Name	Scientific Name	IUCN Status	Hunted
Native Carnivore	Fosa	*Cryptoprocta ferox*	Vulnerable	Y
	Falanouc	*Eupleres goudotii*	Near Threatened	Y
	Malagasy civet	*Fossa fossana*	Near Threatened	Y
	Ring-tailed vontsira	*Galidia elegans*	Least Concern	Y
	Broad-striped vontsira	*Galidictis fasciata*	Near Threatened	--
	Brown-tailed vontisra	*Salanoia concolor*	Vulnerable	--
Exotic Carnivore	Domestic dog	*Canis familiaris*	--	--
	Feral cat	*Felis sp.*	--	Y
	Small Indian civet	*Viverricula indica*	Least Concern	Y
Lemur	Hairy-eared dwarf lemur[2]	*Allocebus trichotis*	Vulnerable	Y
	Eastern woolly lemur	*Avahi laniger*	Vulnerable	Y
	Furry-eared dwarf lemur[3]	*Cheirogaleus crossleyi*	Data Deficient	--
	Geoffroy's dwarf lemur[3]	*Cheirogaleus major*	Data Deficient	--
	Aye-aye	*Daubentonia madagascariensis*	Endangered	Y
	White-fronted brown lemur	*Eulemur albifrons*	Endangered	Y
	Red-bellied lemur	*Eulemur rubriventer*	Vulnerable	Y
	Western lesser bamboo lemur	*Hapalemur occidentalis*	Vulnerable	Y
	Indri	*Indri indri*	Critically Endangered	Y
	Seal's sportive lemur	*Lepilemur seali*	Vulnerable	Y
	MacArthur's mouse lemur[2]	*Microcebus macarthurii*	Endangered	Y
	Mittermeier's mouse lemur[2]	*Microceubs mittermeieri*	Endangered	Y
	Unnamed mouse lemur[2]	*Microcebus sp. nova*	--	Y
	Silky sifaka	*Propithecus candidus*	Critically Endangered	Y
	Red ruffed lemur	*Varecia rubra*	Critically Endangered	Y
	Black-and-white ruffed lemur	*Varecia variegata subcinta*	Critically Endangered	Y
Forest Bird	Frances's sparrowhawk	*Accipiter francesiae*	Least Concern	--
	Madagascar sparrowhawk	*Accipiter madagascariensis*	Near Threatened	--
	Rufous-headed ground-roller	*Atelornis crossleyi*	Near Threatened	Y

Table 2 continued from previous page.

Taxa	Common Name	Scientific Name	IUCN Status	Hunted
Forest Bird	Pitta-like ground-roller	*Atelornis pittoides*	Least Concern	Y
	Madagascar buzzard	*Buteo brachypterus*	Least Concern	--
	Madagascar coucal	*Centropus toulou*	Least Concern	--
	Madagascar magpie-robin	*Copsychus albospecularis*	Least Concern	--
	Ashy cuckooshrike	*Coracina cinerea*	Least Concern	--
	Blue coua	*Coua caerulea*	Least Concern	--
	Red-fronted coua	*Coua reynaudii*	Least Concern	Y
	Red-breasted coua	*Coua serriana*	Least Concern	Y
	Madagascar yellowbrow	*Crossleyia xanthophrys*	Near Threatened	--
	White-throated rail	*Dryolimnas cuvieri*	Least Concern	--
	Helmet vanga	*Euryceros prevostii*	Vulnerable	--
	Madagascar serpent-eagle	*Eutriorchis astur*	Endangered	--
	Domestic chicken	*Gallus gallus domesticus*	Least Concern	--
	Scaly ground-roller	*Geobiastes squamiger*	Vulnerable	--
	Madagascar crested ibis	*Lophotibis cristata*	Near Threatened	Y
	Madagascar wood-rail	*Mentocrex kioloides*	Least Concern	--
	Brown mesite	*Mesitornis unicolor*	Vulnerable	--
	Crossley's babbler	*Mystacornis crossleyi*	Least Concern	--
	Madagascar turtle-dove	*Nesoenas picturatus*	Least Concern	Y
	Helmeted guineafowl	*Numida meleagris*	Least Concern	--
	Bernier's vanga	*Oriolia bernieri*	Vulnerable	--
	Madagascar scops-owl	*Otus rutilus*	Least Concern	--
	White-throated oxylabes	*Oxylabes madagascariensis*	Least Concern	--
	Madagascar harrier-hawk	*Polyboroides radiatus*	Least Concern	--
	Madagascar paradise-flycatcher	*Terpsiphone mutata*	Least Concern	--
Tenrec	Lowland streaked tenrec	*Hemicentetes semispinosus*	Least Concern	Y
	Short-tailed shrew tenrec	*Microgale brevicaudata*	Least Concern	--
	Cowan's shrew tenrec	*Microgale cowani*	Least Concern	--
	Dobson's shrew tenrec	*Microgale dobsoni*	Least Concern	--
	Douhard's shrew tenrec	*Microgale drouhardi*	Least Concern	--

Table 2 continued from previous page.

Taxa	Common Name	Scientific Name	IUCN Status	Hunted
Tenrec	Dryad shrew tenrec	*Microgale dryas*	Vulnerable	--
	Pale-footed shrew tenrec	*Microgale fotsifotsy*	Least Concern	--
	Gracile shrew tenrec	*Microgale gracilis*	Least Concern	--
	Naked-nosed shrew tenrec	*Microgale gymnorhyncha*	Least Concern	--
	Major's long-tailed tenrec	*Microgale majori*	Least Concern	--
	Montane shrew tenrec	*Microgale monticola*	Vulnerable	--
	Pygmy shrew tenrec	*Microgale parvula*	Least Concern	--
	Greater long-tailed shrew tenrec	*Microgale principula*	Least Concern	--
	Shrew tenrec	*Microgale soricoides*	Least Concern	--
	Talzac's shrew tenrec	*Microgale talazaci*	Least Concern	--
	Tavia shrew tenrec	*Microgale tavia*	Least Concern	--
	Greater hedgehog tenrec	*Setifer setosus*	Least Concern	Y
	Common tenrec	*Tenrec ecaudatus*	Least Concern	Y
Rodents	Ellerman's tufted-tailed rat	*Eliurus ellermani*	Data Deficient	--
	Grandidier's tufted-tailed rat	*Eliurus grandidieri*	Least Concern	--
	Major's tufted-tailed rat	*Eliurus majori*	Least Concern	--
	Lesser tufted-tailed rat	*Eliurus minor*	Least Concern	--
	Dormouse tufted-tailed rat	*Eliurus myoxinus*	Least Concern	--
	Tanala tufted-tailed rat	*Eliurus tanala*	Least Concern	--
	Webb's tufted-tailed rat	*Eliurus webbi*	Least Concern	--
	Lowland red forest rat	*Nesomys audeberti*	Least Concern	--
	Eastern red forest rat	*Nesomys rufus*	Least Concern	--

[1] Shrew tenrecs (*Microgale spp.*) and rodents (*Eliurus spp.* and *Nesomys spp.*) have been identified to species by Dr. Steven Goodman (Field Museum of Natural History, Chicago, IL) and have yet to be entered into a database. Thus, the species in light gray are species present in Masoala-Makira, based on IUCN (2014) range maps, and were potentially detected by our camera trap surveys.
[2] *Allocebus trichotis* and the three species of *Microcebus spp.* present in the Masoala-Makira landscape are difficult to distinguish non-invasively.
[3] It is difficult to distinguish between *Cheirogaleus major* and *C. crossleyi* under normal field conditions.

Chapter 2

COALMINE CANARIES: LANDSCAPE AND DYNAMIC OCCUPANCY TRENDS OF GROUND-DWELLING FOREST BIRDS IN THE MASOALA-MAKIRA PROTECTED AREA COMPLEX, NORTHEASTERN MADAGASCAR

Abstract

Madagascar's ground-dwelling forest birds are threatened by habitat degradation and the increasing presence of exotic predators. From 2008 to 2013, we used photographic surveys to examine the population dynamics of terrestrial wildlife at seven sites across the Masoala-Makira protected area complex in northeastern Madagascar. Photographic captures of forest birds were modeled in Program PRESENCE to estimate landscape occupancy and monitor occupancy trends at three resurveyed sites for seven species. In 18,056 trap nights, we obtained 4,083 photographic captures of 28 bird species. Landscape occupancy probabilities ranged from 0.75 (SE 0.09; Madagascar magpie-robin *Copsychus albospecularis*) to 0.25 (SE 0.06; Scaly ground-roller *Geobiastes squamiger*). Four species had higher point estimates of occupancy at intact sites and three species were detected less often at sites with high feral cat trap success. There were strong declines in occupancy for at least three species at each resurveyed site, with Madagascar magpie-robin occupancy declining by more than 90 percent at one site. These declines could have ecosystem-wide consequences as bird species provide necessary ecosystem services such as seed dispersal and pest regulation. We demonstrate the value of camera trap data on non-target species by providing the first landscape-scale study to simultaneously examine the relationships between ground-dwelling forest bird species' occupancy/detection and habitat degradation and the presence of exotic species in Madagascar. Our results are consistent with

other studies showing the strong negative relationship between feral cat presence and native wildlife presence. We suggest immediate conservation measures be implemented to protect native ground-dwelling forest birds and other threatened taxa across this landscape.

Introduction

Unprecedented rates of biodiversity loss are currently occurring globally, with the majority of the loss occurring in tropical ecosystems (Bradshaw *et al.* 2009, Gardner *et al.* 2009). Perhaps the main factor causing tropical extinctions is habitat loss and degradation, which reduces the amount and quality of habitat, increases patch vulnerability to further anthropogenic pressures, and impedes dispersal and gene flow, increasing the probability of local extirpation (Peres 2001, Brooks *et al.* 2002, Fahrig 2003, Cox *et al.* 2004, Sodhi *et al.* 2004). The presence of exotic species can act synergistically with habitat loss and degradation, negatively affecting native species (Laurance & Useche 2009). Exotic species such as the domestic dog (*Canis familiaris*) and feral cat (*Felis sp.*), through competition, disease transmission, and/or predation, have had many documented negative effects on wildlife worldwide (Lacerda *et al.* 2009, Vanak & Gompper 2009, Bonnaud *et al.* 2011, Medina *et al.* 2011, Farris *et al.* 2014).

Tropical forest birds disperse seeds and aid in the regeneration of degraded habitat, regulate pest species, create burrows and cavities that other species use, provide protein sources for local people in the form of bushmeat, and attract the economic benefits of ecotourism to local communities (Sekercioglu 2002, Sekercioglu 2006, Caves *et al.* 2013, Gardner & Davies 2014). Species that are rare, habitat specialists, or unable to use and/or disperse across matrix habitat tend to be the most sensitive to habitat loss and degradation (Sodhi & Smith 2007, Irwin *et al.* 2010, Chang *et al.* 2013). Species persistence in fragmented and degraded habitat can be influenced by factors such as body size or diet, with insectivorous ground-dwelling birds being especially sensitive to habitat loss (Thiollay 1999, Lambert & Collar 2002, Sekercioglu *et al.* 2002, Sodhi & Smith 2007, Korfanta *et al.* 2012).

Madagascar is a biodiversity hotspot and is home to numerous endemic species, many of which are threatened due to continuing habitat loss and a rapidly growing human population (Myers *et al.* 2000, Brooks *et al.* 2002, Brooks *et al.* 2006). Fifty-one percent of Madagascar's birds are endemic and only 15 percent of Madagascar's endemic ground-dwelling birds can live in open habitats (Hawkins & Goodman 2004). Watson *et al.* (2004a) found that 80 percent of Madagascar's insectivorous ground-dwelling and large-bodied birds were sensitive to forest patch size, while Scott *et al.* (2006) found that forest-dependent birds were either entirely absent or had a lower relative abundance in cleared habitat. In addition to steady rates of habitat loss and degradation, exotic species have invaded Madagascar's forests. The few studies examining the impact of domestic dogs and feral cats on Madagascar's native species have focused on sympatric lemurs and carnivores (Brockman *et al.* 2008, Farris *et al.* 2012, Gerber *et al.* 2012, Farris *et al.* 2014, Farris *et al.* 2015, Farris *et al.* in press). The relationships between Madagascar's forest birds and the presence of exotic species on Madagascar's forest birds are unknown, although feral cats pose a serious threat to birds worldwide (Bonnaud *et al.* 2011, Medina *et al.* 2011, Ferreira *et al.* 2014).

We obtained information on ground-dwelling forest birds from camera trap surveys originally set up for surveying carnivores and tenrecs (Lipotyphla: Tenrecidae) at seven sites in Madagascar's largest contiguous area of protected forest, the Masoala-Makira area complex. Our study takes advantage of abundant ancillary data from camera traps to (1) examine the response of Madagascar's little-studied ground-dwelling forest birds to habitat degradation and exotic species presence and (2) examine trends over time in ground-dwelling forest bird occupancy, detection, local colonization, and local extirpation at three sites.

Methods

Study Area

From 2008 to 2013 we conducted 15 camera trap surveys at seven sites across the Masoala-Makira landscape to monitor native carnivore and tenrec populations (Fig. 1 and Appendix B.1). Located in northeastern Madagascar, the Masoala-Makira protected area complex (6,124 km^2, excluding community-managed buffer; hereafter, Masoala-Makira landscape) is the largest contiguous area of protected forest in Madagascar and is home to six native and three exotic carnivores (dogs, feral cats and the small Indian civet *Viverricula indica*), 22 lemurs, and 85 bird species (Thorsrom & Watson 1997, Kremen 2004, Garbutt 2007, Holmes 2007, Mittermeier *et al.* 2010, Goodman 2012). Masoala-Makira's biodiversity faces increasing pressure from hunting (Golden 2009, 2011, Golden *et al.* 2011, Golden *et al.* 2014), habitat loss and degradation (Kremen *et al.* 1999, Farris *et al.* 2012, Allnutt *et al.* 2013, Farris 2014) and exotic species (Farris *et al.* 2014, Farris *et al.* 2015, Farris *et al.* in press).

Camera Trap Surveys

Our 15 camera trap surveys consisted of grids with 18 to 30 unbaited camera stations. Each camera station had two camera traps operating 24 h/d, which were positioned 20-30 cm above the ground on opposite sides of wildlife (0.0-0.5 m) or human-made trails (> 0.5 m). Cameras were checked every five to ten days for maintenance purposes. We used four different camera trap brands: one film (DeerCam DC300) and three digital (Reconyx PC85 and HC500; Moultrie D50 and D55; Cuddeback IR). We set up camera stations with two different camera trap brands at each station to avoid detection biases based on camera trap brand. Camera stations for 13 surveys were spaced 400-600 m apart; this design was based on the home range size of one native carnivore, the spotted fanaloka, *Fossa fossana* (Kerridge *et al.* 2004). The remaining two surveys of one site (S03 in 2013) were spaced 200-300 m apart to monitor tenrecs.

We define a 'photographic event' as an animal, by movement and body heat, triggering a camera, which results in one to many pictures of the animal. By convention, a 'photographic capture' is the number of distinctly different individuals of a species within a 30-min period regardless of the number of photographs (Di Bitetti *et al.* 2006). We calculated trap success (TS) as the number of photographic captures of a species divided by the total number of trap nights for that survey and multiplied by 100. Trap nights (TN) are the number of 24-h periods that a camera station had at least one camera trap functional. We combined the trap success rates of three small carnivores—the ring-tailed vontsira (*Galidia elegans*), the broad-striped vontsira (*Galidictis fasciata*), and the brown-tailed vontsira (*Salanoia concolor*) —to create one 'small carnivore' trap success rate due to their sympatry, similar size and likelihood of preying upon birds (Goodman 2012, Farris *et al.* 2015).

Landscape-level and Station-Level Habitat Sampling

Landscape-level habitat characteristics such as distance to forest edge, distance to the nearest village, percentage of rainforest cover, and the number of habitat patches on the landscape (landscape patchiness or heterogeneity), were estimated using Landsat satellite imagery (2006 and 2009) provided by the Wildlife Conservation Society, Madagascar program, and ERDAS Imagine (Intergraph Corporation) and FRAGSTATS (McGarigal *et al.* 2012). For all of our resurveyed sites, we re-measured distance to edge and village for each survey due to annual forest clearing by local villagers. To measure station-level habitat characteristics, we walked three 50-m habitat transects (0°, 120° and 240°) from each camera station. We measured canopy height and percent canopy cover every 10 m. At 25 m and 50 m, we used the point-quarter method to measure tree density and basal area for any stem/tree that was greater than 5 cm diameter at breast height (DBH; Cottam & Curtis 1956). At 20 m and 40 m, we ran 20-m understory cover transects that were perpendicular to the established 50-m transect. Understory cover was measured at three levels (0.0-0.5 m, 0.5-1.0 m and 1.0-2.0 m) by using a 2-m pole held perpendicular to the ground at 1-m intervals, recording the presence (1) or absence (0) of vegetation touching the pole (Davis *et al.* 2011). Due to insufficient resources we were unable to measure station-level habitat characteristics for one of our seven sites (S06).

We ranked our sites from least to most degraded using a maximum likelihood estimated (MLE) principal components analysis (PCA) of the landscape-level and station-level habitat data, resulting in the classification of two intact (S01 and S02), three intermediately degraded (hereafter, intermediate; S03, S04 and S05) and two degraded sites (S06 and S07; see Farris 2014 and Appendix B.2). We labeled sites based on their level of degradation (01 = least degraded; 07 = most degraded) to protect the identities of local villages near our sites, due to the sensitivity of hunting data used in other, related publications.

Landscape and Multi-Season Occupancy Analyses

We examined the relationship between habitat degradation and exotic species trap success rates and the landscape occupancy and detection of ground-dwelling forest birds across Masoala-Makira using single-season occupancy analysis in Program PRESENCE (v 6.4; MacKenzie *et al.* 2005, Hines 2006). The final capture history, consisting of 1's (species detected) and 0's (species not detected), for each species included seven surveys representative of our seven sites. From our resurveyed sites, we included the survey with the most captures of the species of interest. Model covariates included landscape-level and station-level habitat characteristics, native/exotic species and human trap success, and climatological season that the survey was conducted (Farris 2014). We ran a Pearson's correlation on covariates (habitat and sympatric species trap success rates) and removed one covariate from each pair of covariates if they were highly correlated ($|r| > 0.70$). All covariates were then normalized within PRESENCE (Hines 2006). We ran goodness of fit (GOF) tests on our most parameterized models and corrected for overdispersion ($\hat{c} \geq 3.0$; Lebreton *et al.* 1992).

We conducted repeated surveys of one intact (S02) and two intermediate (S03 and S05) sites. S02 was surveyed annually between 2008 and 2013, with the exception of 2010 due to political unrest in Madagascar. S05 was surveyed annually from 2011-2013 (Appendix B.1). Camera station locations were similar or identical for repeated surveys at S02 and S05. We examined trends in occupancy, detection, local colonization, and local extirpation at S02 and S05 using multi-season occupancy analysis in Program PRESENCE. Local colonization is the probability that, at year *t*, a species colonizes a site where it was absent from in the previous year (*t*-1; MacKenzie *et al.* 2005). Local extirpation is the probability that, at year *t*, a species is extirpated from a site where it was present in the previous year (*t*-1; MacKenzie *et al.* 2005). Due to low sample sizes through the years, we did not include covariates in multi-season occupancy models for S02 and S05.

At S03 the placement and number of camera stations was not identical between 2009 (24 stations; 400-600 m spacing) and 2013 (25-30 stations; 200-300 m spacing). Because the majority of the station locations for the 2009 and the two 2013 surveys of S03 did not overlap, we estimated bird occupancy and detection for both years using a single-season occupancy analysis. We included covariates in the models, ran a GOF test and estimated ĉ. Although camera trap grids at S03 were not in the same location, they overlapped geographically and covered similar habitat types, validating our above methodology.

Overall, single-season and multi-season occupancy models were considered competing if they had a ΔAIC or a ΔQAIC ≤ 2.0 and parameter/beta estimates were model-averaged unless the top model was strongly supported (model weight ≥ 80%; Akaike 1973). For species with an estimated ĉ ≥ 3.0 in the single-season occupancy analyses, and species whose multi-season occupancy models did not converge, we estimated naïve occupancy—the number of camera stations a species was detected at divided by total number of camera stations surveyed.

Results

From 2008 to 2013, we accumulated 18,056 TNs and obtained 4,083 captures of 26 identifiable native bird species and two exotic species (chickens *Gallus gallus domesticus* and helmeted guineafowl *Numida meleagris*; Table 1). Although 84 percent of our captures were of ground-dwelling forest birds, we captured a variety of species including arboreal raptors (e.g., Madagascar serpent-eagle *Eutriorchis astur*). Total bird trap success across the landscape, including birds we were unable to identify to species, was 22.61 birds/100 TN. The highest number of species detected at one site was 16 (S02) and the lowest was seven (S04). Seven species had a sufficient number of captures for analyses: the Red-breasted coua (*Coua serriana*; 7.36/100 TN), Madagascar wood-rail (*Mentocrex kioloides*; 3.41/100 TN), Madagascar turtle-dove (*Nesoenas picturatus*; 2.82/100 TN), Scaly ground-roller (*Geobiastes squamiger*; 2.70/100 TN), Madagascar magpie-robin (*Copsychus albospecularis*; 2.43/100 TN), Madagascar crested ibis (*Lophotibis cristata*; 1.90/100 TN) and Red-fronted coua (*C. reynaudii*; 0.69/100 TN; Table

1; Appendix B.3). With the exception of the Madagascar magpie-robin, all analyzed species were ground-dwelling forest birds.

Landscape Occupancy and Detection

The Madagascar magpie-robin had the highest probability of occupancy across the landscape ($\psi = 0.75 \pm$ SE 0.09) and the Scaly ground-roller had the lowest ($\psi = 0.25 \pm$ SE 0.06; Fig. 2 and Appendix B.4A). The Madagascar magpie-robin, Scaly ground-roller, and Madagascar crested ibis were estimated to have higher point estimates of occupancy at intact sites, while Red-breasted couas and Madagascar wood-rails had similar occupancy probabilities at intact, intermediate, and degraded sites (Fig. 3). Only the Madagascar turtle-dove had a higher point estimate of occupancy at degraded sites. Madagascar magpie-robin occupancy was higher, and Red-breasted coua occupancy was lower, at sites with a higher percentage of rainforest cover ($\beta = 0.93 \pm$ SE 0.26 and $\beta = -0.67 \pm$ SE 0.24, respectively; see Table 2). Madagascar crested ibises and Madagascar wood-rails had higher occupancy probabilities at sites with higher levels of landscape habitat patchiness ($\beta = 1.03 \pm$ SE 0.45 and $\beta = 1.38 \pm$ SE 0.28, respectively). Madagascar magpie-robin occupancy was positively related to small carnivore trap success ($\beta = 1.15 \pm$ SE 0.57). Red-fronted coua models were overdispersed ($\hat{c} > 3.0$); therefore, their naïve landscape occupancy was $\psi = 0.30$ and was higher at intact sites (Fig. 2 and 3).

Red-breasted couas had the highest probability of detection across the landscape ($p = 0.51 \pm$ SE 0.06) and Madagascar crested ibises had the lowest ($p = 0.11 \pm$ SE 0.03; Fig. 2). Three bird species were detected more often at camera stations with high native carnivore trap success. Red-breasted coua detection was positively related to falanouc (*Eupleres goudotii*) trap success ($\beta = 0.32 \pm$ SE 0.08; Table 2), Madagascar crested ibis detection was positively related to spotted fanaloka (*Fossa fossana*) trap success (β = 0.23 ± SE 0.1), and Madagascar turtle-dove detection was positively related to falanouc and small carnivore trap success (β = 0.15 ± SE 0.06 and β = 0.18 ± SE 0.08, respectively). Scaly ground-roller, Red-breasted coua and Madagascar crested ibis detection was negatively related to feral cat trap success (β = -0.50 ± SE 0.25, β = -0.29 ± SE 0.1 and β = -37.15 ± SE 7.24, respectively). Madagascar magpie-robins were detected more often on human-made trails (β = 0.49 +/- SE 0.11) and less often at camera stations with higher zebu (domestic livestock; *Bos primigenius*) trap success (β = -0.66 +/- SE 0.21; Table 2 and Appendix B.4A).

Multi-Year Trends

Estimated and naïve occupancy probabilities declined for most ground-dwelling forest birds at S02 and S05 (Table 3 and Appendix B.4B). At the intact site S02, all seven species declined in occupancy, with Red-breasted couas declining by the greatest amount (76%). At intermediate disturbance sites, three out of five species at S03, and six out of seven species at S05, declined in occupancy with Madagascar magpie-robins declining by the greatest amounts (91% and 74% declines, respectively; Table 3 and Appendix B.4B). At S03, Red-breasted coua occupancy was higher at camera stations located in primary rainforest (β = -1.21 ± SE 0.56) and Madagascar wood-rail detection was lower at camera stations with high human trap success (β = -16.89 ± SE 8.13; Appendix B.4C). Detection probability declined at S02 for all species, while at S05 it was more variable, and detection tended to increase at S03. Madagascar magpie-robins went undetected at S02 in 2013. Average local extirpation probability for three species at S02, and all species at S05, was higher than average local colonization probability (Table 3).

Discussion

This study is the first to use ancillary data obtained from remote camera traps to examine bird population status in Madagascar. While point counts and mist nets are the most common methods used in bird studies, we show that camera traps can be useful to detect rare or elusive ground-dwelling, forest birds (Jeganathan *et al.* 2002, Dinata *et al.* 2008, Posa 2011, Kuhnen *et al.* 2013). We detected a wide variety of elusive bird species, including the endangered Madagascar serpent-eagle. We recognize that our camera traps were located close to the ground, hence our sampling was biased towards ground-dwelling birds, and only such birds (with the exception of the Madagascar magpie-robin) were detected often enough for us to use in our analyses. However, this study highlights the utility of using such ancillary data to determine forest bird distribution and occupancy trends through time, thus providing useful insight for bird conservation.

Habitat Degradation and Exotic Species

For the seven species modeled, we found that four species had higher point estimates of occupancy at intact sites (Madagascar magpie-robin, Red-fronted coua, Scaly ground-roller and Madagascar crested ibis), two had similar occupancy probabilities at all forest types (Red-breasted coua and Madagascar wood-rail), and only one had a higher point estimate of occupancy at degraded sites (Madagascar turtle-dove), providing evidence of the need for intact forest for Madagascar's ground-dwelling forest birds. The Madagascar turtle-dove is widespread across Madagascar and has been found to be highly adaptable to habitat degradation, a trend that is supported in our study (Morris & Hawkins 1998, Langrand & Sinclair 2003). The Red-breasted coua's and the Madagascar wood-rail's similar occupancy estimates at all three forest types suggest that they are able to adapt to any level of habitat degradation. Interestingly, while the Madagascar crested ibis occupancy was higher at intact sites, its occupancy was also positively related to landscape patchiness, in contrast to the finding in Watson *et al.* (2004b) of Madagascar crested ibises avoiding edge habitat. Our results suggest that some of Madagascar's ground-dwelling forest birds might tolerate slight habitat disturbance and may benefit from landscape-level habitat heterogeneity, but many still prefer areas with large amounts of intact forest habitat at the landscape and station-level habitat level. Our primary forest sites did have human disturbance, however, and we suggest that future research focus on surveying the ground-dwelling forest bird community across a broader spectrum of habitat degradation, including more primary forest sites with very little to no habitat disturbance and/or anthropogenic pressure.

Native carnivore presence was positively associated with occupancy and/or detection of four bird species—Madagascar magpie-robin, Red-breasted coua, Madagascar turtle-dove, and Madagascar crested ibis—an effect that is likely habitat-mediated. It is possible that native carnivores and birds are influenced by similar resources or avoiding exotics in similar ways. The relationship between exotic species presence and the detection of our focal birds was very clear. The Madagascar magpie-robin had a lower detection probability at camera stations with high zebu trap success, possibly due to how zebu impact understory. Red-breasted couas, Madagascar crested ibises and Scaly ground-rollers were detected less at camera stations with high feral cat trap success. Feral or domestic cats are thought to have caused at least 14 percent of global mammal, avian and reptilian extinctions, and are primary threats to eight percent of critically endangered species (Medina *et al.* 2011). Feral cat landscape occupancy in Masoala-Makira is 0.37 (SE 0.08), higher than that of three native carnivores: the brown-tailed vontsira, the broad-striped vontsira and the falanouc (Farris 2014). Feral cats trap rates did not appear to impact bird occupancy; however cats may be having an impact on ground-dwelling forest birds in Masoala-Makira that we were unable to measure and management actions may be necessary to prevent negative interactions (Farris 2014, Medina *et al.* 2014).

Dynamic Trends of Masoala-Makira's Ground-dwelling Forest Birds

Every bird species in the intact site (S02) had a 28 percent or greater decline in occupancy, and six out of seven species at one intermediate site (S05) had a 20 percent decline or greater in occupancy. During these same years, we did not observe any change in station-level habitat characteristics, nor evidence of forest loss and degradation, within and in near proximity of our camera trap grids. Thus, these are alarming trends that we are unable to explain based solely on habitat degradation. In addition, the Madagascar magpie-robin, which had the highest decline in occupancy of any bird at any site, did not colonize any new camera stations at S02 or S05. The intermediate S03 site had variable changes in occupancy. Future surveys at this site should focus on surveying in similar locations to determine occupancy trends in this bird community.

Red-breasted couas, Red-fronted couas, Madagascar crested ibises and Madagascar turtle-doves are highly prized by locals as bushmeat (Goodman & Wilmé 2004, Gardner & Davies 2014). Intense hunting pressure by humans and feral cats could account for the sharp declines in forest bird occupancy at S02 and S05. In particular, the Red-breasted coua is restricted in range to the forests of northeastern Madagascar, making it even more vulnerable to extinction due to overhunting and feral cat predation (Morris & Hawkins 1998, Langrand & Sinclair 2003).

Conservation Implications and Future Research

Across the world, habitat continues to be degraded and the remaining habitat patches are more vulnerable to the pressures of hunting and exotic species invasion (Chapin III *et al.* 2000, Corlett 2007, Bradshaw *et al.* 2009, Gardner *et al.* 2009, Newbold *et al.* 2014). It has been predicted that 13 percent of the world's birds will go extinct before 2100 and tropical biodiversity hotspots like Madagascar will become extinction hotspots (Brooks *et al.* 2002, Sodhi *et al.* 2004, Bradshaw *et al.* 2009, Gardner *et al.* 2009).

While we realize that our study represents only a small portion of the entire forest bird community in northeastern Madagascar, we highlight the successful use of ancillary data from remote cameras to garner information on non-target species. Too often data from remote camera traps on non-target species goes unused, although it possesses information highly useful for conservation of other elusive species. To improve on our initial findings, we suggest expanded surveys at sites representing a wider spectrum in habitat degradation. Additionally, estimation of consumption rates of Madagascar's native forest birds by local people is critical. In Madagascar, bushmeat hunting—which is very important to local nutrition and livelihoods—can occur at unsustainable rates (Golden 2009, Golden *et al.* 2011). Finally, we need detailed ecological studies on feral cats in the Masoala-Makira landscape, especially on diet, home range size and habitat use, to inform management practices and removal programs (Farris 2014, Medina *et al.* 2014, Recio *et al.* 2014).

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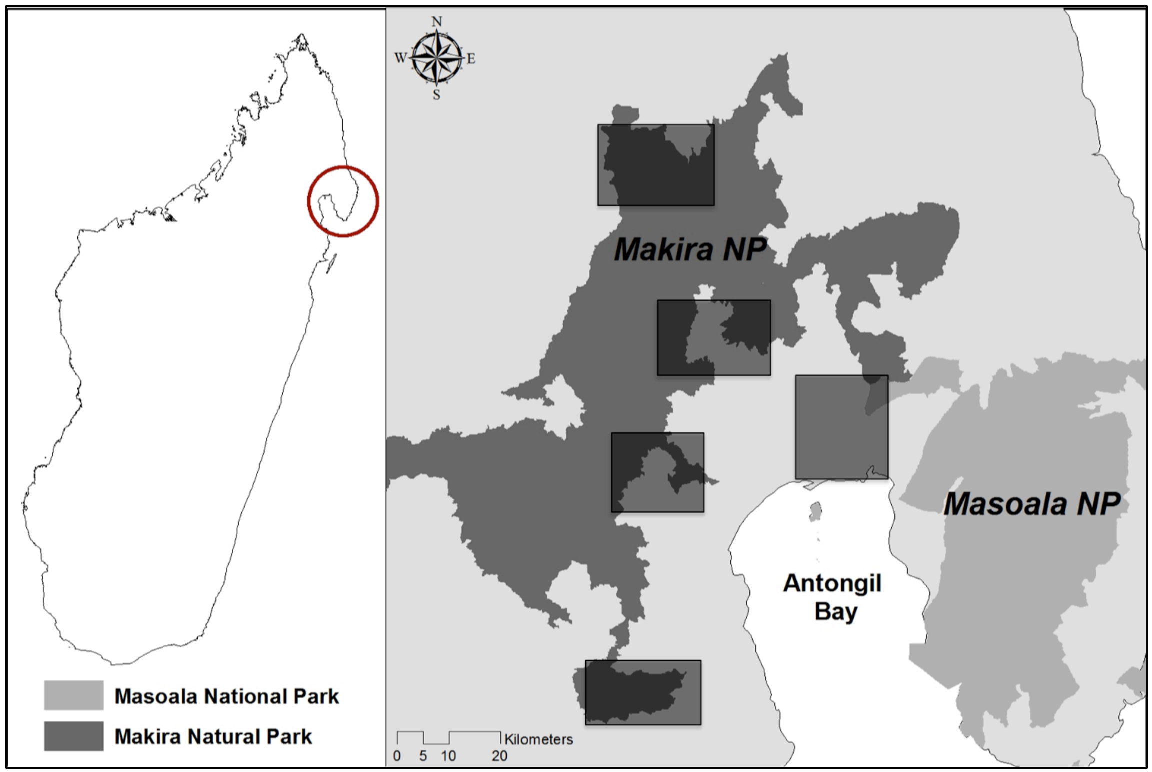

Figure 1. Makira Natural Park and Masoala National Park (Masoala-Makira protected area complex) in northeastern Madagascar. At 6,124.7 km^2, excluding community-managed buffers, the Masoala-Makira landscape is the largest area of protected contiguous forest in Madagascar. Seven sites (S01-S07) were photographically surveyed with camera traps from 2008 to 2013 in the regions outlined by the boxes.

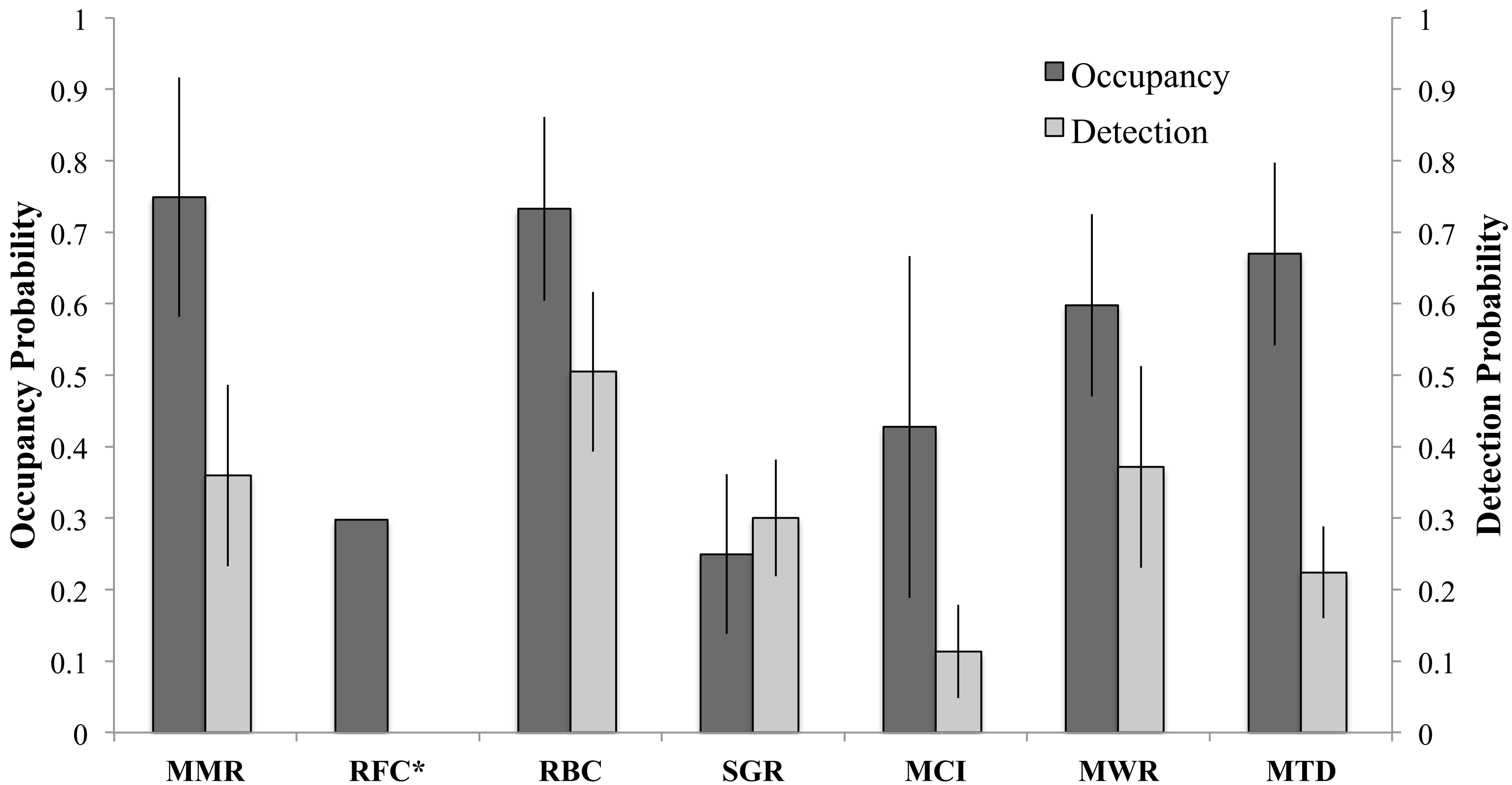

Figure 2. Landscape occupancy and detection estimates, including 95% CIs, of seven native forest birds detected in camera trap surveys in the Masoala-Makira landscape, northeastern Madagascar (2008-2013). Species abbreviations are as follows: Madagascar magpie-robin (MMR), Red-fronted coua (RFC), Red-breasted coua (RBC), Scaly ground-roller (SGR), Madagascar crested ibis (MCI), Madagascar wood-rail (MWR) and Madagascar turtle-dove (MTD). * indicates naïve landscape occupancy.

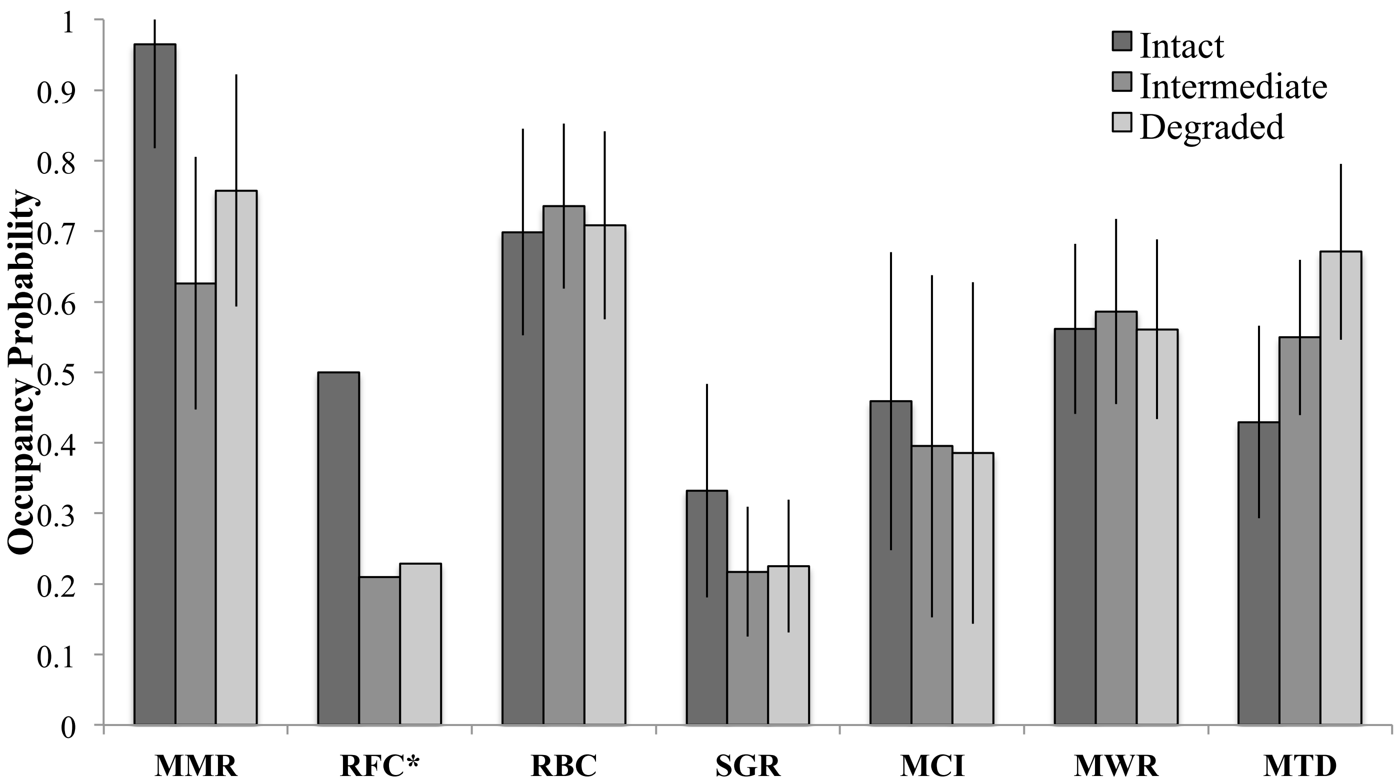

Figure 3. Occupancy estimates at intact, intermediate, and degraded sites, including 95% CIs, of seven native forest birds detected in camera trap surveys in the Masoala-Makira landscape, northeastern Madagascar (2008-2013). Species abbreviations are as follows: Madagascar magpie-robin (MMR), Red-fronted coua (RFC), Red-breasted coua (RBC), Scaly ground-roller (SGR), Madagascar crested ibis (MCI), Madagascar wood-rail (MWR) and Madagascar turtle-dove (MTD). * indicates naïve landscape occupancy.

Table 1. Total captures, trap success, sites detected, and IUCN status for all forest bird species captured during photographic surveys at the seven sites (denoted S01 to S07) in the Masoala-Makira landscape, northeastern Madagascar (2008-2013).

Common Name	Scientific Name	Total # of Captures	Overall TS[1]	Sites Detected	IUCN Status[2]
Red-breasted coua	*Coua serriana*	1,329	7.36	S01-S07	LC
Madagascar wood-rail	*Mentocrex kioloides*	616	3.41	S01-S07	LC
Madagascar turtle-dove	*Nesoenas picturatus*	510	2.82	S01-S07	LC
Scaly ground-roller	*Geobiastes squamiger*	487	2.70	S01-S03, S05-S07	VU
Madagascar magpie-robin	*Copsychus albospecularis*	439	2.43	S01-S07	LC
Madagascar crested ibis	*Lophotibis cristata*	343	1.90	S01-S05, S07	NT
Red-fronted coua	*Coua reynaudii*	125	0.69	S01-S07	LC
Pitta-like ground-roller	*Atelornis pittoides*	25	0.14	S02-S03	LC
White-throated fail	*Dryolimnas cuvieri*	13	0.07	S01, S05	LC
Crossley's babbler	*Mystacornis crossleyi*	11	0.06	S01-S02, S06	LC
Domestic chicken	*Gallus gallus domesticus*	8	0.04	S05	LC
Helmeted guineafowl	*Numida meleagris*	8	0.04	S02, S04, S07	LC
Madagascar scops-owl	*Otus rutilus*	8	0.04	S02-S03, S06	LC
Blue coua	*Coua caerulea*	7	0.04	S02, S05, S07	LC
Helmet vanga	*Euryceros prevostii*	7	0.04	S05	VU
Madagascar coucal	*Centropus toulou*	5	0.03	S02, S04-S05	LC
Madagascar sparrowhawk	*Accipiter madagascariensis*	4	0.02	S03	NT
Frances's sparrowhawk	*Accipiter francesiae*	3	0.02	S02, S07	LC
Brown mesite	*Mesitornis unicolor*	2	0.01	S02	VU
Rufous-headed ground-roller	*Atelornis crossleyi*	1	0.01	S01	NT
Madagascar buzzard	*Buteo brachypterus*	1	0.01	S07	LC
Ashy cuckooshrike	*Coracina cinerea*	1	0.01	S02	LC
Madagascar yellowbrow	*Crossleyia xanthophrys*	1	0.01	S01	NT
Madagascar serpent-eagle	*Eutriorchis astur*	1	0.01	S02	EN
Bernier's vanga	*Oriolia bernieri*	1	0.01	S07	VU

Table 1 continued from previous page.

Common Name	Scientific Name	Total # of Captures	Overall TS[1]	Sites Detected	IUCN Status[2]
White-throated oxylabes	*Oxylabes madagascariensis*	1	0.01	S05	LC
Madagascar harrier-hawk	*Polyboroides radiatus*	1	0.01	S03	LC
Madagascar paradise-flycatcher	*Terpsiphone mutata*	1	0.01	S01	LC
Unidentified		124	0.69		
OVERALL		**4,083**	**22.61**		

[1] Overall TS (trapping success) estimated by dividing total number of independent photographic capture events of the species by the total number of trap nights from 2008-2013 and then multiplying by 100.
[2] IUCN status: LC = least concern; NT = near threatened; VU = vulnerable; EN = endangered (IUCN 2014).

Table 2. Summary of covariates with strongly supported relationships—confidence intervals on normalized beta values do not overlap zero—from landscape and S03's single-season analyses and their relationships to bird occupancy (ψ) and/or detection (p) for six species of native ground-dwelling forest bird in the Masoala-Makira landscape, northeastern Madagascar. Positive (+) and negative (-) relationships are noted. Red-fronted coua not shown due to estimated overdispersion (ĉ > 3.0).

	Madagascar magpie-robin	Red-breasted coua	Scaly ground-roller	Madagascar crested ibis	Madagascar wood-rail	Madagascar turtle-dove
Percent Rainforest Cover	ψ(+)	ψ(-)				
Total # of Habitat Patches				ψ(+)	ψ(+)	
Season					p(-)	
Station-level Habitat Characterization (S03-only)		ψ(+)				
Trail Type	p(+)					
Malagasy Civet TS				p(+)		
Falanouc TS		p(+)				p(+)
Small Carnivore TS	ψ(+)					p(+)
Feral Cat TS		p(-)	p(-)	p(-)		
Zebu TS	p(-)					

Table 3. Averaged local colonization (the probability that a species colonizes a site it was absent from in the previous year) and extirpation (the probability that a species is extirpated from a site it was present from in the previous year) probability estimates (SE), and % change in occupancy, for seven forest bird species at S02 (2008-2013), S05 (2011-2013) and S03 (2009 and 2013), in the Masoala-Makira landscape, northeastern Madagascar.

				Occupancy		
Site	Species	Avg. Local Colonization	Avg. Local Extirpation	Initial Year[1]	Final Year	% Change[2]
S02	Madagascar magpie-robin	0	0.12 (0.08)	0.95 (0.08)	0.68 (0.39)	-39
	Red-fronted coua	--	--	0.70	0.08	-88
	Red-breasted coua	0.66 (0.18)	0.32 (0.11)	0.87 (0.11)	0.65 (0.18)	-76
	Scaly ground-roller	0.32 (0.12)	0.46 (0.13)	0.58 (0.14)	0.44 (0.18)	-28
	Madagascar crested ibis	0.18 (0.15)	0.25 (0.09)	0.89 (0.12)	0.40 (0.11)	-51
	Madagascar wood-rail	0.25 (0.08)	0.40 (0.11)	0.80 (0.09)	0.39 (0.31)	-52
	Madagascar turtle-dove	--	--	0.65	0.25	-62
S05	Madagascar magpie-robin	0	0.68(0.28)	0.66 (0.19)	0.06 (0.07)	-91
	Red-fronted coua	--	--	0.04	0.17	+300
	Red-breasted coua	0.34(0.13)	0.48(0.11)	0.75 (0.09)	0.44 (0.09)	-41
	Scaly ground-roller	0.27(0.20)	1	0.36 (0.10)	0.23 (0.14)	-35
	Madagascar crested ibis	--	--	0.21	0.17	-20
	Madagascar wood-rail	--	--	0.42	0.17	-60
	Madagascar turtle-dove	0.35(0.16)	0.47(0.18)	0.55 (0.13)	0.44 (0.12)	-21
S03	Madagascar magpie-robin	--	--	0.26	0.07	-74
	Red-breasted coua	--	--	0.72 (0.12)	0.52 (0.13)	-29
	Scaly ground-roller	--	--	0.58 (0.17)	0.59 (0.17)	+3
	Madagascar wood-rail	--	--	0.14 (0.07)	0.20 (0.10)	+42
	Madagascar turtle-dove	--	--	0.37	0.14	-61

[1] Initial year/final year surveyed for sites: S02 (2008/2013), S05 (2011/2013) and S03 (2009/2013).
[2] Change in occupancy estimated by subtracting final year's occupancy and detection estimate from the initial year's estimate, dividing by the initial year's estimate and multiplying by 100. For species whose $\hat{c} \geq 3.0$ or whose models had suspect parameter estimates, we present change in naïve occupancy through time.

Chapter 3

AN UNSTABLE PREY BASE: LANDSCAPE AND CROSS-YEAR OCCUPANCY TRENDS OF THREE SPINY TENREC (LIPOTYPHLA: TENRECIDAE: TENRECINAE) SPECIES IN NORTHEASTERN MADAGASCAR

Abstract

Understanding habitat preferences and effects of anthropogenic pressures on species, particularly via long-term monitoring, is important for prioritizing biodiversity conservation actions. The spiny tenrecs (Lipotyphla: Tenrecidae: Tenrecinae) of Madagascar are little studied, yet they are important prey for native predators and are a protein resource in many of Madagascar's local bushmeat markets. From 2008 to 2013, we photographically surveyed terrestrial wildlife at seven forest sites across the Masoala-Makira protected are complex in northeastern Madagascar. Using single-season and multi-season occupancy modeling in Program PRESENCE, we examined the relationships between habitat degradation and the presence of exotic species on the occupancy and detection probabilities of the common tenrec (*Tenrec ecaudatus*), greater hedgehog tenrec (*Setifer setosus*), and lowland streaked tenrec (*Hemicentetes semispinosus*). Landscape trap success rate of all three spiny tenrecs combined was 1.49/100 TN. Lowland streaked tenrec occupancy was higher at intact sites ($\psi = 0.16 \pm$ SE 0.13) than at degraded sites ($\psi = 0.06 \pm$ SE 0.06), while common and greater hedgehog tenrec occupancy was lower at intact sites ($\psi = 0.70 \pm$ SE 0.19 and 0.44 ± SE 0.11, respectively) than at degraded sites ($\psi = 0.77 \pm$ SE 0.20 and 0.48 ± SE 0.09, respectively). Despite the higher occupancy at degraded sites, the common tenrec showed behavioral changes by shifting its activity from diurnal at intact sites to nocturnal at intermediate and degraded sites. Tenrec occupancy declined noticeably at one site from 2008 to

2013, and two species (the common and the lowland streaked tenrec) went undetected at that site in the final one to two years of the study. We suggest that significant effort be devoted to continued long-term monitoring of spiny tenrec populations with the goal of providing in-depth information on their ecology and role as an important prey resource in native ecological communities.

Introduction

Madagascar is one of the world's top biodiversity hotspots and is home to numerous endemic species, many of which are threatened due to continuing habitat loss and a rapidly growing human population (Myers *et al.* 2000, Brooks *et al.* 2002, Brooks *et al.* 2006). Although 47% of Madagascar's small mammals are listed as Vulnerable, Endangered, or Data Deficient (IUCN 2014), and despite the pressures they face from ongoing habitat loss (Ganzhorn *et al.* 1990, Goodman & Rakotondravony 2000, Andrianjakarivelo *et al.* 2005, Garbutt 2007), bushmeat hunting and consumption (Golden 2009, 2011, Golden *et al.* 2011, Jenkins *et al.* 2011, Gardner & Davies 2014), and exotic species (Goodman *et al.* 2004, Soarimalala & Goodman 2011, Farris 2014), they remain relatively little studied. Tenrecinae (Lipotyphla: Tenrecidae) is one of Madagascar's endemic mammalian subfamilies, with five species of primarily terrestrial and solitary 'spiny' tenrecs (Goodman *et al.* 2004, Olson & Goodman 2004, Garbutt 2007, Soarimalala & Goodman 2011). The majority of studies examining the effects of habitat degradation on spiny tenrecs have occurred in the western deciduous forests (Ganzhorn *et al.* 1990, Goodman & Rakotondravony 2000, Scott *et al.* 2006). Spiny tenrecs seem to adapt to habitat disturbance, being commonly found in villages and gardens; however, the landscape-level and microhabitat preferences for many spiny tenrec species are still unknown (Ganzhorn *et al.* 1990, Soarimalala & Goodman 2011).

Pressures exerted by exotic species like the domestic dog (*Canis familiaris*) and feral cat (*Felis sp.*) can act synergistically with habitat loss and degradation, compounding negative effects and increasing local extirpation probabilities (Lacerda *et al.* 2009, Laurance & Useche 2009, Vanak & Gompper 2009, Bonnaud *et al.* 2011, Medina *et al.* 2011, Ferreira *et al.* 2014).

The few studies examining interactions between Madagascar's native and exotic species have focused on lemurs and carnivores (Brockman *et al.* 2008, Farris *et al.* 2012, Gerber *et al.* 2012, Farris 2014, Farris *et al.* 2014, Farris *et al.* 2015, Farris *et al.* in press). How exotic carnivores interact with spiny tenrecs is essentially unknown, although it is highly likely that feral cats and dogs prey upon tenrecs (Soarimalala & Goodman 2011, Goodman 2012, Levesque *et al.* 2012). Understanding the effects of exotic carnivores on native tenrecs is vital as spiny tenrecs are important as prey to many native predators and any negative interactions between exotic predators and tenrecs might indirectly impact native predator populations (Karpanty & Goodman 1999, Karpanty & Wright 2007, Goodman 2012).

Through large-scale photographic sampling of terrestrial wildlife over a six-year period (2008-2013) in Madagascar's largest contiguous area of protect forest—the Masoala-Makira area complex (northeastern Madagascar; hereafter, Masoala-Makira landscape)— we obtained data on three species of spiny tenrec: the common tenrec (*Tenrec ecaudatus*), the greater hedgehog tenrec (*Setifer setosus*), and the lowland streaked tenrec (*Hemicentetes semispinosus*; Appendix C.1). Our objectives were to a) estimate spiny tenrec encounter rate (trap success), occupancy, and detection across the Masoala-Makira landscape and examine the relationships between habitat degradation and exotic carnivore presence and spiny tenrec occupancy/detection, b) investigate daily activity patterns based on time of photographic capture for each spiny tenrec species across multiple forest types and c) examine spiny tenrec occupancy and detection trends at two sites that were surveyed a minimum of three times over the six-year period (2008-2013).

Methods

Study Area

From 2008 to 2013 we conducted 13 camera trap surveys at seven forest sites across the Masoala-Makira landscape to monitor terrestrial wildlife (Figure 1 and Table 1). Located in northeastern Madagascar, the Masoala-Makira landscape (6,124 km^2, excluding community-managed buffer) is the largest contiguous area of protected forest in Madagascar and is home to at least six native carnivore species, three exotic carnivore species (domestic dog, feral cat and small Indian civet *Viverricula indica*), over 15 lemur species and 30 native small mammal species (Kremen 2004, Andrianjakarivelo *et al.* 2005, Holmes 2007, Soarimalala & Goodman 2011). Despite the expansiveness of the protected area, the species present in the Masoala-Makira landscape face increasing pressure from hunting (Golden 2009, 2011, Golden *et al.* 2011), habitat loss/degradation (Kremen *et al.* 1999, Farris *et al.* 2012, Allnutt *et al.* 2013, Farris 2014), and exotic carnivores (Farris *et al.* 2012, Farris 2014, Farris *et al.* 2014, Farris *et al.* 2015, Farris *et al.* in press).

Camera Trap Surveys

Our 13 camera trap surveys consisted of grids with 18 to 25 unbaited camera stations. Each camera station had two camera traps operating 24 hours/day, which were positioned 20-30 cm off the ground on opposite sides of wildlife (0.0-0.5 m) or human (> 0.5 m) trails. Cameras were checked every five to ten days for maintenance purposes. We used four different camera trap brands: one film (DeerCam DC300) and three digital (Reconyx PC85 and HC500; Moultrie D50 and D55; Cuddeback IR). We set up camera stations with two different camera trap brands at each station to avoid detection biases based on camera trap brand. Camera station spacing

(400-600 m apart) was based on the home range size of one native carnivore (spotted fanaloka, *Fossa fossana*; Kerridge *et al.* 2004).

We define a ‘photographic event’ as an animal—by movement and body heat—triggering a camera, which results in one to many pictures of the animal. By convention, a ‘photographic capture’ is the number of distinctly different individuals of a species within a 30-minute period regardless of the number of photographs (Di Bitetti *et al.* 2006).We estimated species-specific trap success rates of the three spiny tenrecs and sympatric native/exotic carnivores and humans (non-researchers). We also estimated a combined ‘spiny tenrec’ trap success rate to examine broad trends in spiny tenrec encounter rates across the landscape. We calculated trap success (TS) as the number of photographic captures of a species divided by the total number of trap nights for that survey and multiplied by 100. Trap nights (TN) are the number of 24-hour periods that a camera station had at least one camera functional. We combined the trap success rates of three small carnivores—the ring-tailed vontsira (*Galidia elegans*), the broad-striped vontsira (*Galidictis fasciata*), and the brown-tailed vontsira (*Salanoia concolor*) —to create one ‘small carnivore’ trap success rate due to their similar size and likelihood of preying upon spiny tenrecs (Goodman 2012, Farris 2014).

Landscape-level and Station-level Habitat Sampling

Landscape-level habitat characteristics such as distance to forest edge, distance to the nearest village, percentage of rainforest cover, and the number of habitat patches on the landscape (landscape patchiness or heterogeneity), were estimated using Landsat satellite imagery (2006 and 2009) provided by the Wildlife Conservation Society, Madagascar program, and ERDAS Imagine (Intergraph Corporation) and FRAGSTATS (McGarigal *et al.* 2012). For all of our long-term sites, we re-measured distance to edge and village for each survey due to annual forest clearing by local villagers. To measure station-level habitat characteristics, we walked three 50-m habitat transects (0°, 120°, and 240°) from each camera station. We measured canopy height and percent canopy cover every 10 m. At 25 m and 50 m, we used the point-quarter method to measure tree density and basal area for any stem/tree that was greater than 5 cm diameter at breast height (DBH; Cottam & Curtis 1956). At 20 m and 40 m, we ran 20-m understory cover transects that were perpendicular to the established 50-m transect. Understory cover was measured at three levels (0.0-0.5 m, 0.5-1.0 m and 1.0-2.0 m) by using a 2-m pole held perpendicular to the ground at 1-m intervals, recording the presence (1) or absence (0) of vegetation touching the pole (Davis *et al.* 2011). Due to insufficient resources we were unable to measure station-level habitat characteristics for one of our seven sites (S06).

We ranked our sites from least to most degraded using a maximum likelihood estimated (MLE) principle components analysis (PCA) of the landscape-level and station-level habitat data, resulting in two intact (S01 and S02), three intermediate disturbance (hereafter, intermediate; S03, S04 and S05) and two degraded sites (S06 and S07; see Farris 2014 and Appendix S2). We labeled sites based on their level of degradation (01 = least degraded; 07 = most degraded) to protect the identities of local villages near our sites, due to the sensitivity of hunting data used in other, related publications.

The Response of Spiny Tenrec Occupancy and Detection to Habitat Degradation and Exotic Carnivore Presence

We examined the response of spiny tenrec landscape occupancy and detection to habitat degradation and exotic carnivore trap success rates across the Masoala-Makira landscape using single-season occupancy analysis in Program PRESENCE (v 6.4; MacKenzie *et al.* 2005, Hines 2006). The final capture history, consisting of 1's (species detected) and 0's (species not detected), for each species included seven surveys representative of our seven sites. From our resurveyed sites, we included the survey with the most captures of the species of interest. We also combined the captures of all three species into one 'combined' spiny tenrec capture history so that we could examine how spiny tenrec occupancy responded to habitat degradation and exotic carnivore presence, regardless of species. Model covariates included landscape-level and station-level habitat characteristics, native/exotic carnivores and human trap success, and climatological season that the survey was conducted (Farris 2014). We ran a Pearson's correlation on all covariates and removed one covariate from each pair of covariates if they were highly correlated ($|r| > 0.70$); the final covariates were then normalized within PRESENCE. We ran goodness of fit (GOF) tests on our most parameterized models and corrected for over dispersion ($\hat{c} \geq 3.0$; Lebreton *et al.* 1992).

Tenrec Daily Activity Patterns

We examined patterns in the photographic captures of all three spiny tenrec species over a 24-hour period. We obtained historical daily time-of-sunrise and time-of-sunset data for all surveys we conducted. We determined the earliest and latest sunrise/sunset time recorded for each survey and then estimated an 'average' sunrise/sunset time (Farris *et al.* 2015). We used these average sunrise/sunset times to determine the hours that comprised dawn and dusk, a two-hour period defined here as one hour before and after sunrise and sunset, respectively. 'Day' is the time period between dawn and dusk, and 'night' is the time period between dusk and dawn (Gerber *et al.* 2012).

We determined the hours available in these time periods for each survey, with dawn and dusk comprised of two hours, and day and night comprised of approximately 10 hours. For each species, we found the proportion of captures in each time period (the number of captures in the time period divided by the total number of captures for that survey). To determine selection or avoidance of each time period, we used Ivlev's resource selection index (Ivlev 1961), adapted by Jacobs (1974), calculated as:

$$D = (r - p) / [(r + p) - 2rp]$$

Where r is the proportion of captures in the time period, p is the proportion of time available in that time period out of 24 hours and D is the selection index value (Blanco-Garrido *et al.* 2008). We estimated the resource selection index value (D) for all four time-periods in each survey for each species; $D < 0$ indicating avoidance of the time period, $D > 0$ indicating selection and $D = 0$ means no preference either way (Blanco-Garrido *et al.* 2008, Monterroso *et al.* 2009). To obtain an overall daily activity pattern for all surveys, we averaged D values over all surveys for each time period for each species, discarding surveys where the species was absent. To examine the difference between daily activity patterns were in the different forest types, we averaged D values for each species for all surveys separated by the three forest types (intact, intermediate and degraded).

Multi-Season Tenrec Occupancy and Detection Trends

We conducted repeated surveys of one intact (S02) and one intermediate (S05) site. S02 was surveyed annually between 2008 and 2013, with the exception of 2010 due to political unrest in Madagascar. S05 was surveyed annually from 2011-2013. We examined trends in occupancy, detection, local colonization, and local extirpation at S02 and S05 using multi-season occupancy analysis in Program PRESENCE. Local colonization is the probability that, at year *t*, a species colonizes a site where it was absent from in the previous year (*t*-1; MacKenzie *et al.* 2005). Local extirpation is the probability that, at year *t*, a species is extirpated from a site where it was present in the previous year (*t*-1; MacKenzie *et al.* 2005). Due to low sample sizes through the years, we did not include covariates in multi-season occupancy models for S02 and S05.

Overall, single-season and multi-season occupancy models were considered competing if they had a ΔAIC or ΔQAIC ≤ 2.0. Parameter/beta estimates were model-averaged unless the top model was strongly supported (model weight ≥ 80%; Akaike 1973). For species with an estimated ĉ ≥ 3.0 in the single-season occupancy analyses, and species whose multi-season occupancy models did not converge, we estimated naïve occupancy—the number of camera stations a species was detected at divided by total number of camera stations surveyed.

Results

From 2008 to 2013, we accumulated 16,431 TNs and obtained 244 photographic captures of spiny tenrecs. Total spiny tenrec trap success across the landscape was 1.49/100 TN. The majority of spiny tenrec captures were of the greater hedgehog tenrec (n = 159; 0.97/100 TN), while the common tenrec (n = 71; 0.43/100 TN) and the lowland streaked tenrec (n = 14; 0.09/100 TN) were detected less often. All three species were detected at two sites (S02 and S07), while only the greater hedgehog tenrec was detected at S04.

The Response of Spiny Tenrec Occupancy and Detection to Habitat Degradation and Exotic Carnivore Presence

Spiny tenrecs combined had a landscape occupancy probability of ψ = 0.53 (SE 0.09; Table 2). Common tenrecs had the highest species-specific probability of occupancy across the landscape ($\psi = 0.64 \pm$ SE 0.19) and lowland streaked tenrecs had the lowest ($\psi = 0.10 \pm$ SE 0.10). Greater hedgehog tenrecs were found to have a lower probability of occupancy at camera stations with taller canopy height ($\beta = -0.52 \pm$ SE 0.25), while spiny tenrecs combined had higher occupancy probabilities at sites with more rainforest cover ($\beta = 4.27 \pm$ SE 1.95).

Overall, spiny tenrecs had a detection probability (p) of 0.24 (SE 0.06), with spiny tenrecs being detected more often on narrow wildlife trails ($\beta = -4.97 \pm$ SE 1.31; Table 2). Greater hedgehog tenrecs had the highest species-specific probability of detection across the landscape ($p = 0.23 \pm$ SE 0.08), and they were also detected more often on narrow wildlife trails ($\beta = -1.75 \pm$ SE 0.45), while lowland streaked tenrecs had the lowest detection probability ($p = 0.13 \pm$ SE 0.10). Common tenrecs, with a landscape detection probability of 0.10 (SE 0.06), were detected more often during the hot-wet season (February-May; $\beta = 2.26 \pm$ SE 0.55) than the hot-dry and cold-wet season.

Lowland streaked tenrecs and spiny tenrecs combined had higher occupancy probabilities at intact sites, while common and greater hedgehog tenrecs had higher occupancy probabilities at degraded sites, although these differences are not significant (95% CIs overlap; Figure 2). Although the occupancy of spiny tenrecs combined was found to be negatively related to feral cat TS ($\beta = -0.27 \pm$ SE 0.27) and the detection of the lowland streaked tenrec was found to be positively related to dog TS ($\beta = 0.01 \pm$ SE 0.06), these relationships are not strongly supported (i.e., 95% CIs on normalized β values overlap zero; Table 2).

Tenrec Daily Activity Patterns

All species were captured at least once during daytime hours. Overall, all three species showed avoidance of the dawn and dusk periods across all forest types (Figure 3). Common and greater hedgehog tenrecs demonstrated mainly nocturnal activity, although this finding is only strongly supported for greater hedgehog tenrecs. In contrast, the lowland streaked tenrec showed a clear preference for diurnal activity. Activity patterns shifted noticeably for common and lowland streaked tenrecs across forest types. Common tenrecs were diurnal at intact sites, but strongly nocturnal at intermediate and degraded sites. Lowland streaked tenrecs shifted their use of the dawn and dusk periods, being more active at dawn at degraded sites and more active at dusk at intermediate sites.

Multi-Season Tenrec Occupancy and Detection Trends

We were only able to analyze the long-term data (six-year period) from one site (S02) for the greater hedgehog tenrec and combined spiny tenrec capture histories in Program PRESENCE (Table 3). Due to small sample sizes, for the common tenrec and lowland streaked tenrec, and all species at S05, we estimated naïve occupancy. At S02, estimated and naïve occupancy probabilities declined for all species (Figure 4). Common and lowland streaked tenrecs showed the highest decline in naïve occupancy, with 2011 and 2012 being the last year we detected common and lowland streaked tenrecs at S02, respectively. Spiny tenrec occupancy in general declined from $\psi = 0.64$ (SE 0.13) in 2008 to $\psi = 0.06$ (SE 0.06) in 2013. Average local extirpation probability ($\varepsilon = 0.47 \pm$ SE 0.27) for spiny tenrecs was higher than average local colonization probability ($\gamma = 0.18 \pm$ SE 0.15).

We did not detect the lowland streaked tenrec at S05. Greater hedgehog tenrecs showed a slight decline in naïve occupancy, from an estimate of 0.13 in 2011 to 0.08 in 2013; common tenrecs showed a slight increase in naïve occupancy from an estimate of 0.13 in 2011 to 0.17 in

2013. Spiny tenrec naïve occupancy in general did not change between 2011 and 2013 at S05 (ψ = 0.21 in 2011 and 2013). All species, however, went undetected in 2012.

Discussion

This study is the first to use ancillary, by-catch camera trap data to study tenrec ecology. It is also the first to estimate tenrec occupancy and detection, examine multi-year tenrec occupancy trends, and evaluate the response of tenrec occupancy, detection, and time use to anthropogenic disturbance (e.g. habitat degradation and exotic carnivores). Small mammals in Madagascar are usually studied by using live traps and pitfall traps (Ganzhorn *et al.* 1990, Stephenson 1993, 1994a, b, 1995, Goodman & Rakotondravony 2000, Andrianjakarivelo *et al.* 2005, Soarimalala & Goodman 2011). However, spiny tenrec trap success rates using such techniques is low in the eastern rainforests (Soarimalala & Goodman 2011) with the highest published trap success rate for the eastern rainforests being 0.81/100 TN (Stephenson 1995, Appendix C.3). Although the data we used for this study were from unbaited noninvasive camera trap surveys with a focus on carnivore populations, we had higher trap success than other invasive studies and were able to 'catch' 1.49 spiny tenrecs every 100 TNs. We suggest that camera traps can be highly useful when attempting to estimate the occupancy and examine the species diversity or habitat use of the larger, terrestrial members of Tenrecidae.

Tenrec Population Responses to Habitat Degradation and Exotic Carnivore Presence

Although tenrec species richness is positively related to forest fragment patch size (Goodman & Rakotondravony 2000), spiny tenrecs have been found to be highly adaptable to habitat degradation, often inhabiting villages and gardens (Soarimalala & Goodman 2011). We observed only one greater hedgehog tenrec and only one lowland streaked tenrec near human habitations, with the lowland streaked tenrec seen near a garden in a large town (Murphy, personal observation). However, it is likely that there are regional differences in habitat preferences of spiny tenrecs. While Stephenson (1995) only captured the lowland streaked tenrec in degraded forest, Andrianjakarivelo *et al.* (2005) found that lowland streaked tenrecs were restricted to intact forests. Although we had a low sample size for the lowland streaked tenrec, our results suggest that the species prefers intact forest. However, Andrianjakarivelo *et al.* (2005) found that the majority of their greater hedgehog captures occurred in undisturbed forest, while we found greater hedgehog tenrec occupancy to be higher at degraded sites. Even though these studies overlapped geographically, the difference between our results and those from Andrianjakarivelo *et al.* (2005) could be due to differences in habitat classification, or regional/local differences in the effects of habitat degradation on these three species. Spiny tenrecs in general had a higher occupancy probability at intact sites and at sites with more rainforest cover, suggesting that although they may adapt to habitat disturbance, the presence of intact forests is important for spiny tenrec populations.

Although we found a negative relationship between combined spiny tenrec occupancy and feral cat TS, and a positive relationship between lowland streaked tenrec detection and dog TS, these relationships were not strongly supported. Dogs are used to hunt the two larger spiny tenrec species—common and greater hedgehog—in the Masoala-Makira landscape (Golden 2009, Soarimalala & Goodman 2011). Lowland streaked tenrec detection was positively related to dog trap success, a relationship that is either habitat-mediated or related to the higher rates of hunting in intact forests (Farris 2014). Combined spiny tenrec occupancy was negatively related to the trap success of feral cat, which had a higher landscape occupancy probability in the

Masoala-Makira landscape than that of three native carnivores ($\psi = 0.37 \pm$ SE 0.08; Farris 2014). Feral cats are known to have caused 14% of mammal extinctions across the world (Medina *et al.* 2011), and it is possible that they are negatively impacting tenrecs. More research is needed to determine the nature of the interactions between exotic carnivores and spiny tenrecs.

Tenrec Daily Activity Patterns

Habitat degradation and the resulting changes in the local habitat, ecological community and hunter presence can affect spiny tenrec behavior. We were not able to formally examine the relationship between spiny tenrec activity patterns and the presence of exotic carnivores and local hunters, but it is possible that the presence of exotic carnivores and/or local hunters could be influencing spiny tenrec activity. Farris *et al.* (2015) found that feral cats were crepuscular (selecting for dawn and dusk periods) and that dogs were highly diurnal. Local hunters actively hunt during the day (Golden 2011). Lowland streaked tenrecs—the smallest of the three focal species—was also the only species that showed a preference for diurnal activity, although they avoided activity at dusk in degraded forest sites and avoided activity at dawn in intermediately degraded forests. It is possible that the lowland streaked tenrec is spatially avoiding dogs, feral cats and local hunters. It is also possible that it is not preferred prey of the two exotic carnivores or hunters due to its small size. Future research should go into examining any potential spatial interactions between tenrecs and exotic carnivores and humans, as well as determining the consumption rates of lowland streaked tenrecs by locals.

In contrast, the common tenrec—the largest speices and one of the most intensively hunted—shifted its activity from diurnal in intact forest to nocturnal in intermediate and degraded forests. This might have been a way to avoid being active at the same time as dogs, feral cats (Farris *et al.* 2015) and hunters. The greater hedgehog tenrec, another intensively hunted species, showed exclusive preference for nocturnal activity, a time period dogs and feral cats did not select for and when locals do not actively hunt. The greater hedgehog tenrec also had the highest landscape detection probability out of all three species. Its avoidance of the time periods when two exotic carnivores and local hunters were most active might be why greater hedgehog tenrecs were detected most often.

Although we had low sample sizes for our analysis of time use for these three tenrec species, and our results should be cautiously interpreted, it is still highly likely that the presence of exotic carnivores and intensive hunting pressure by the locals are having impacts on spiny tenrecs that we were unable to measure. In light of the possible negative relationships between feral cats and spiny tenrec occupancy, the potential temporal overlap of exotic carnivores with spiny tenrecs, and the known unsustainable hunting and consumption rates of tenrecs in the Masoala-Makira landscape (Golden 2009), we suggest that plans for the management of exotic carnivores and bushmeat hunting must be made and implemented immediately (Medina *et al.* 2011, Farris 2014).

Spiny Tenrec Dynamic Trends in the Masoala-Makira Landscape

The occupancy of all three species declined at S02. The greater hedgehog tenrec was the only spiny tenrec detected at S02 in 2013; however, it was detected at very few camera stations and at very low rates. The common tenrec was last detected at S02 in 2011, while the last detections of lowland streaked tenrecs were in 2012. In contrast, spiny tenrec naïve occupancies at S05 were similar between 2011 and 2013. No tenrecs were detected at S05 in 2012, but this is likely a seasonal effect. S05's 2012 survey occurred during the austral winter, when spiny tenrecs hibernate (Soarimalala & Goodman 2011, Levesque *et al.* 2012), while the 2011 and 2013 surveys occurred during the austral fall and spring, respectively. Overall, at S05, there was no change in spiny tenrec naïve occupancy. This might be due to the remoteness of the site, as S05 is further from villages than S02, or this might be an artifact of camera trap placement. Future surveys at this site should provide insight into the continued status of the spiny tenrecs.

The dramatic declines at S02 might be due to hunting. (Farris 2014) found that local hunters tend to focus most of their hunting effort on intact forests with high carnivore occupancy; this pattern may hold true for tenrec hunting, as well. The common tenrec and greater hedgehog tenrec are hunted intensively across Madagascar (Golden 2009, Jenkins *et al.* 2011, Soarimalala & Goodman 2011, Gardner & Davies 2014). Ninety-one percent of households in Makira hunt tenrecs, with the bushmeat trade contributing a substantial amount to locals' annual revenues (Golden 2011). Although spiny tenrecs can be incredibly fecund and seem to be able to handle intense hunting pressure by humans in other areas of Madagascar, the addition of exotic carnivores may make it harder for spiny tenrec populations to rebound (Soarimalala & Goodman 2011, Levesque *et al.* 2013). Declines in spiny tenrec populations might have unknown effects on native ecological communities, especially since they are an abundant prey resource to many native species (Soarimalala & Goodman 2011, Goodman 2012, Levesque *et al.* 2013).

Implications and Future Research

With this study, we highlight the need for in-depth studies on spiny tenrec ecology and the effects of exotic carnivores on spiny tenrecs in the Masoala-Makira landscape to inform management practices and exotic carnivore removal programs which are urgently needed (Farris

2014, Medina *et al.* 2014, Recio *et al.* 2014). It is vital that we determine how important spiny tenrecs are as a prey base to native predators in northeastern Madagascar, to predict the potential for declines in native predator populations due to decreases in spiny tenrec abundance. Our results reveal alarming trends in tenrec occupancy. We suggest urgent conservation actions such as enforcement of hunting regulations and exotic carnivore removal are needed in order to halt these declines and preserve endemic biodiversity in Madagascar.

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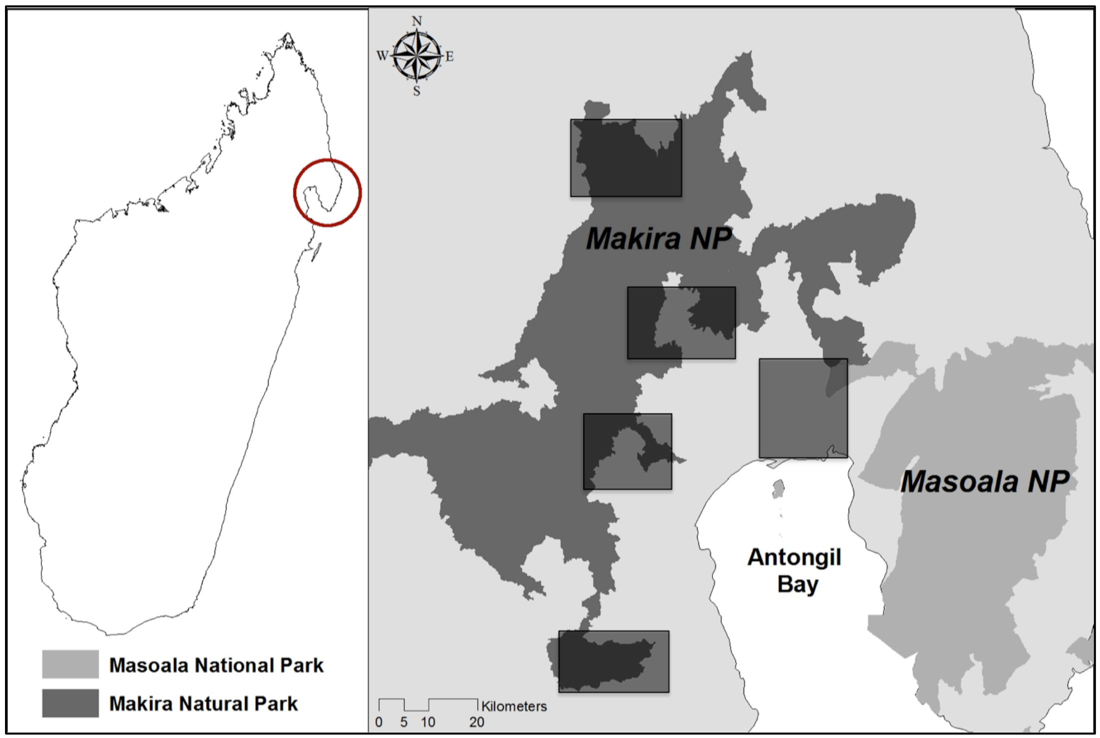


Figure 1. Makira Natural Park and Masoala National Park (Masoala-Makira protected area complex) in northeastern Madagascar. At 6,124.7 km^2, excluding community-managed buffers, the Masoala-Makira landscape is the largest area of protected contiguous forest in Madagascar. Seven sites (S01-S07) were photographically surveyed with camera traps from 2008 to 2013 in the regions outlined by the boxes.

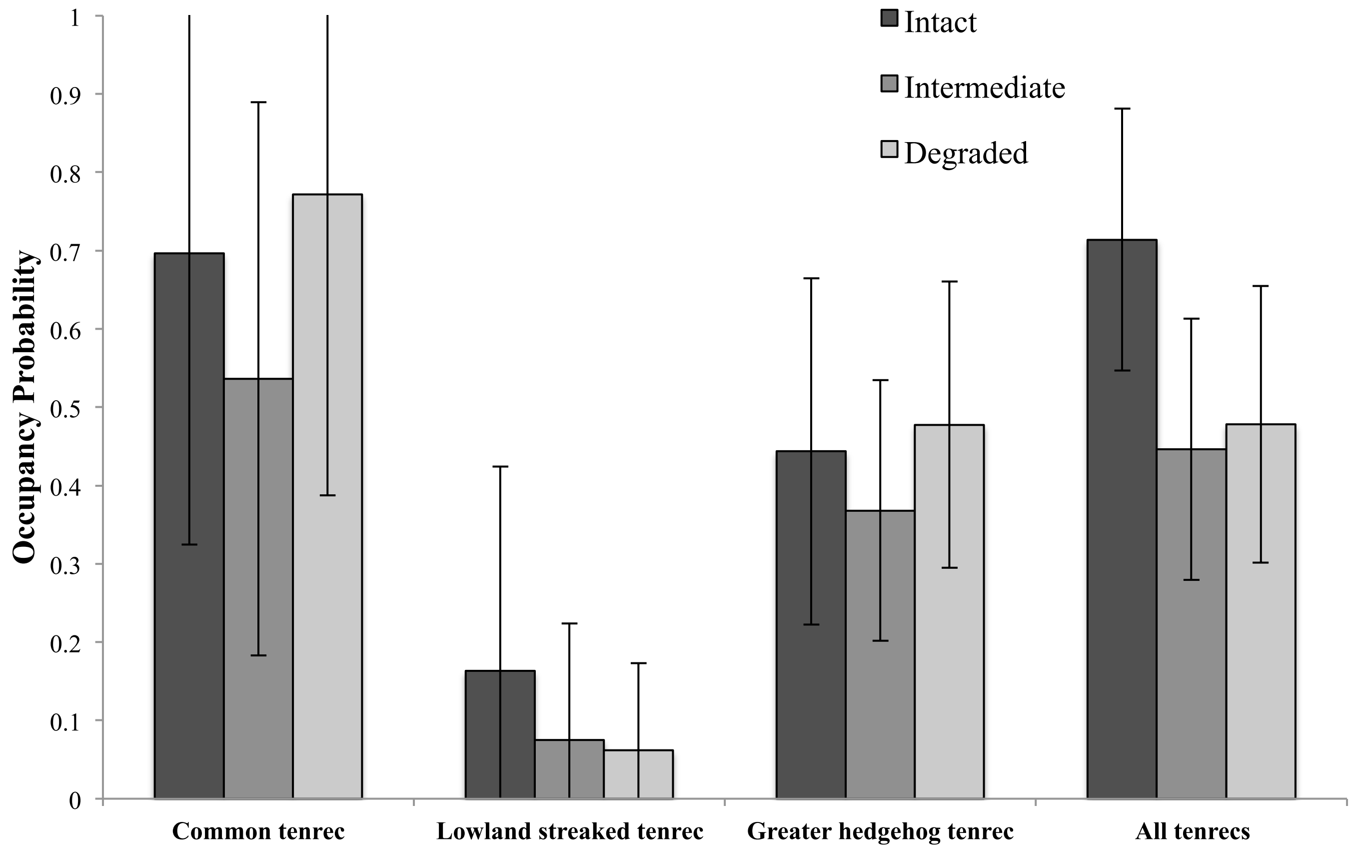


Figure 2. Occupancy probabilities of three spiny tenrec species (and all spiny tenrecs) at intact, intermediate and degraded sites in the Masoala-Makira landscape, northeastern Madagascar (2008-2013). Error bars are 95% CIs.

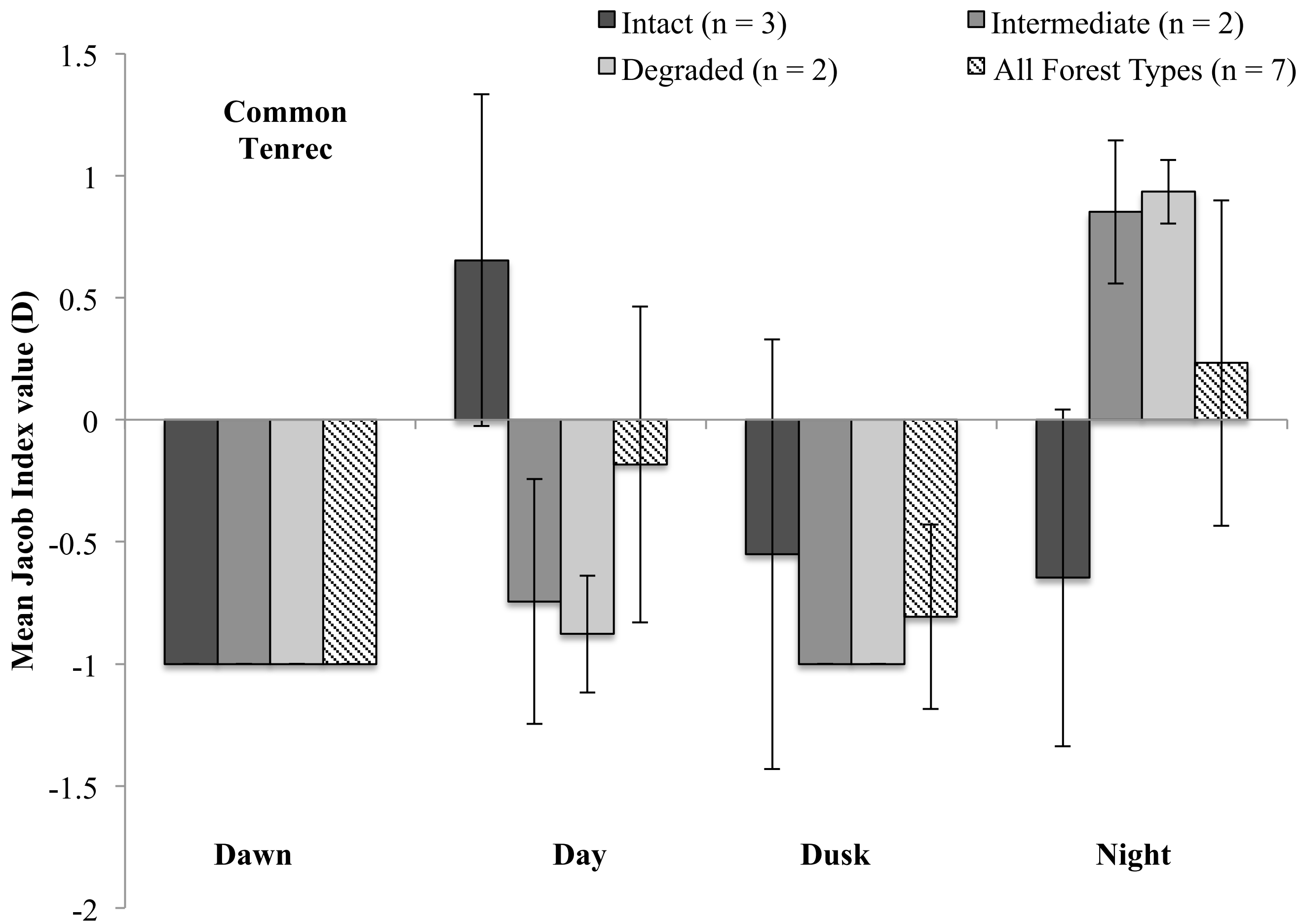
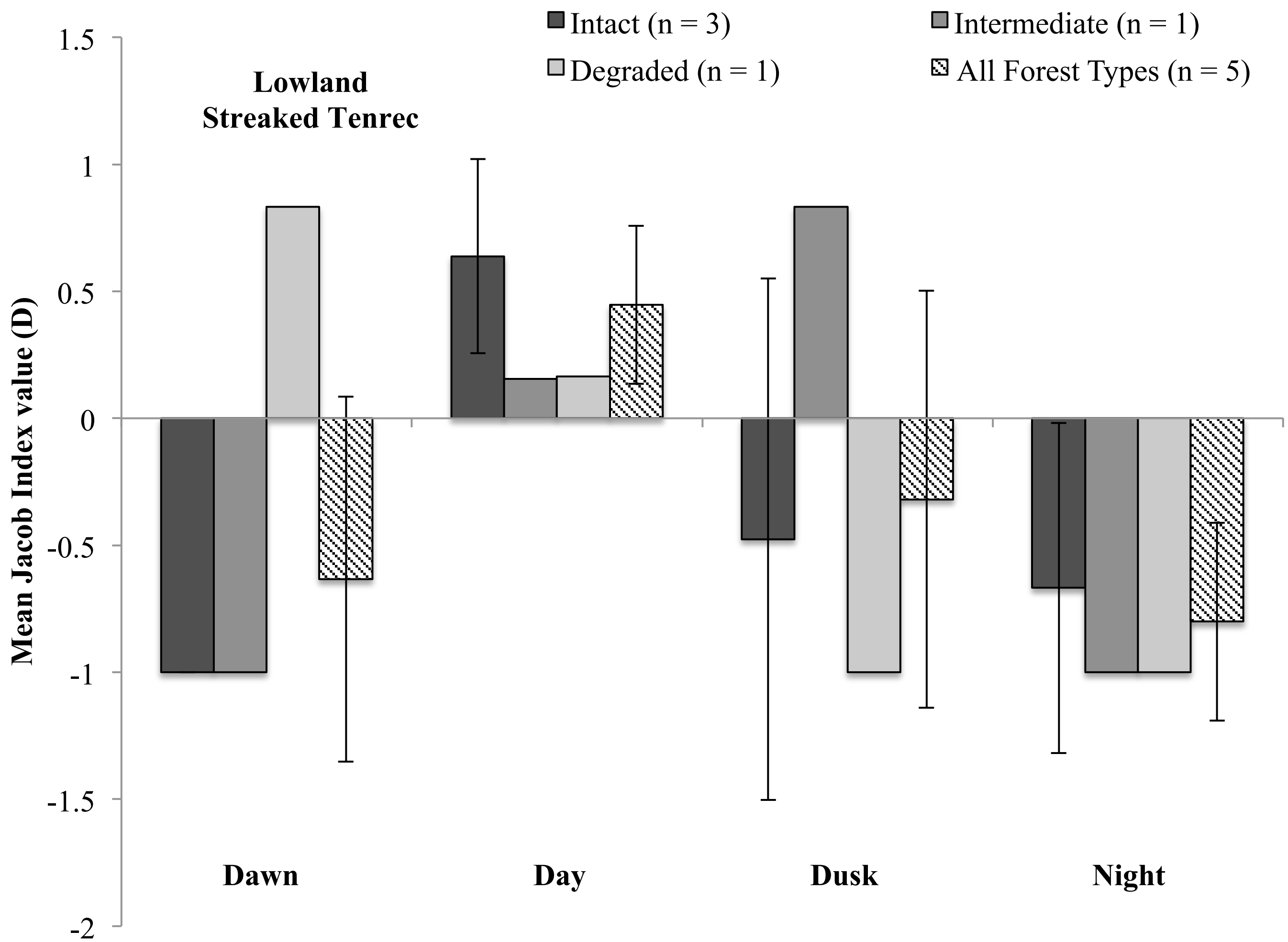


Figure 3. Daily activity patterns and 95% confidence intervals of the common tenrec, lowland streaked tenrec and greater hedgehog tenrec at the three forest types (intact, intermediate and degraded) and at all forest types in the Masoala-Makira landscape, northeastern Madagascar. N indicates how many surveys were used to estimate D. D < 0 means avoidance of that time period, D > 0 means selection for that time period and D = 0 means no preference.



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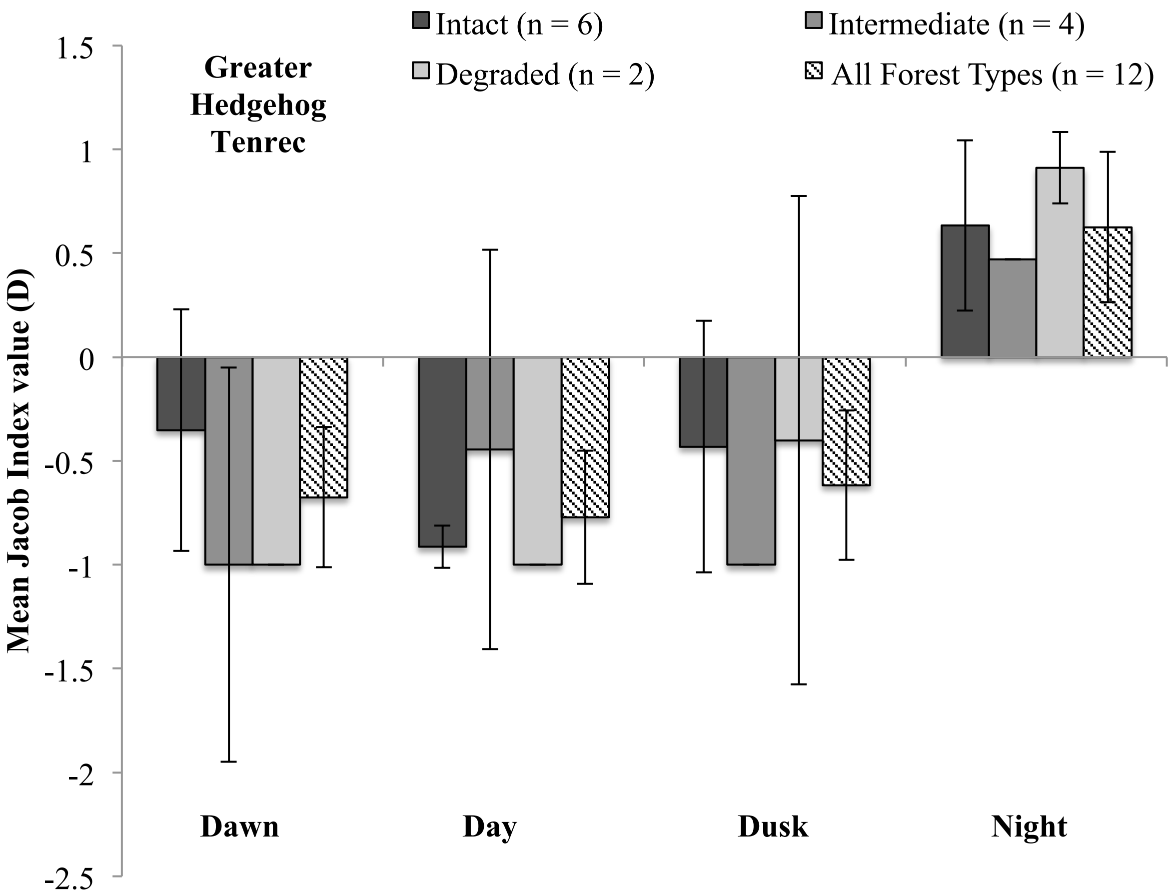

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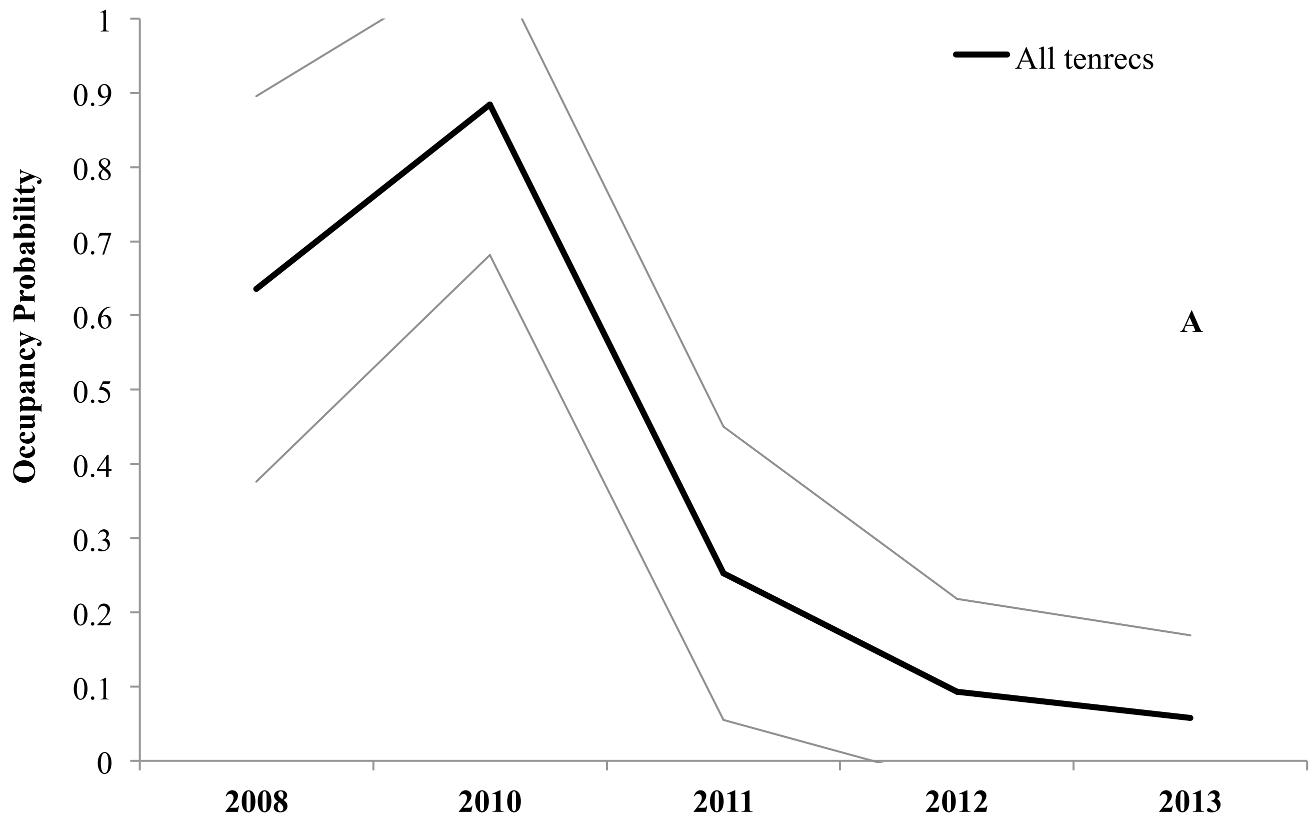

Figure 4. Trends at S02 for A) combined estimated spiny tenrec occupancy (95% confidence intervals in gray) and B) common, lowland streaked and greater hedgehog tenrecs naïve occupancy from 2008 to 2013. Naïve occupancy presented due to low sample sizes.

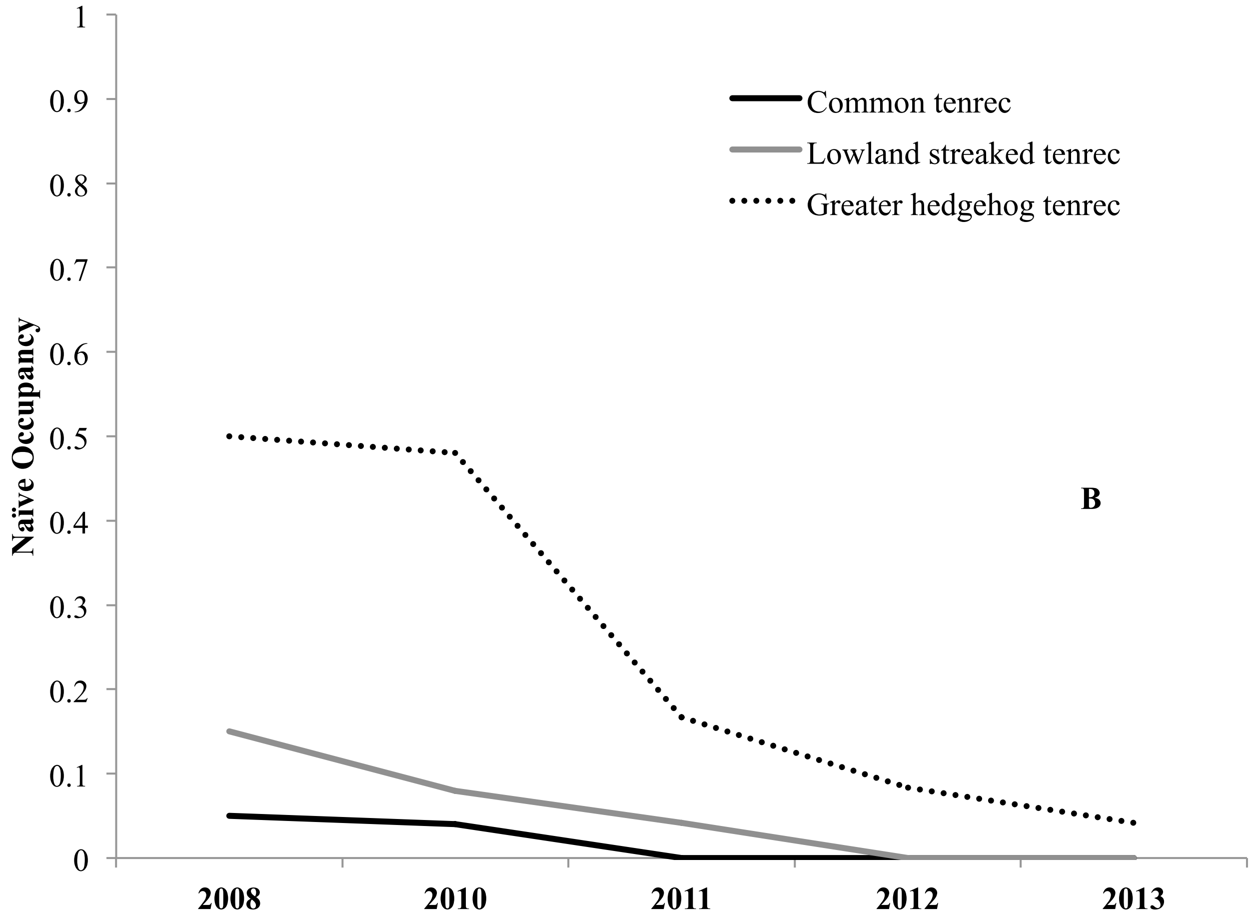

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Table 1. Survey details for the 13 photographic surveys across seven sites (camera trapping grids), including repeated surveys of two sites, ranked from least degraded (S01) to most degraded (S07) and trap success rates (TS) for lowland streaked, greater hedgehog, and common tenrecs. Photographic surveys occurred from 2008 to 2013 across the Masoala-Makira landscape, northeastern Madagascar.

Study Site (Survey Dates)[1]	# of Camera Stations	Total # of Trap Nights	Elevation (m)	Lowland Streaked Tenrec TS[2]	Greater Hedgehog Tenrec TS	Common Tenrec TS
S01 (Mar – May 2009; HW)	20	989	1000-1400	--	0.38	3.62
S02 (Sept – Nov 2008; CW)	20	1315	350-706	0.38	2.74	0.08
S02 (Sept – Nov 2010; HD)	25	1230		0.32	1.91	0.08
S02 (Aug – Oct 2011; CW)	24	1383		0.07	0.58	--
S02 (Jul – Oct 2012; CW)	24	1536		--	0.65	--
S02 (Sept – Oct 2013; CW)	24	1198		--	0.17	--
S03 (Aug – Oct 2009; CW)	19	1067	380-550	0.19	2.25	--
S04 (Jun – Aug 2011; CW)	23	1462	21-385	--	0.14	--
S05 (Mar – May 2011; HW)	24	1509	308-796	--	0.20	0.66
S05 (Jun – July 2012; CW)	24	1015		--	--	--
S05 (Nov 2013 – Jan 2014; HD)	24	1188		--	0.25	0.42
S06 (Nov 2009 – Jan 2010; HD)	18	881	580-820	--	2.95	0.57
S07 (Dec 2010 – Feb 2011; HD)	24	1570	93-507	0.13	1.08	0.70

[1] Season that the site was surveyed: HW (Hot-Wet; February-May), HD (Hot-Dry; October-January) and CW (Cold-Wet; June-September)
[2] TS: Trap success rate of tenrec species (# of photographic captures/total # trap nights for that site)*100.

Table 2. Competing (ΔQAIC $\leq$ 2.0) landscape occupancy models from single-season occupancy analyses for the common tenrec, lowland streaked tenrec, and greater hedgehog tenrec, and spiny tenrecs combined, across the Masoala-Makira landscape, northeastern Madagascar (2008-2013). Included are landscape occupancy (ψ) and detection (p) estimates, model weight (w_i) and likelihood, number of model parameters (k), and the estimated over dispersion value ($\hat{c}$) from the goodness of fit (GOF) test implemented in program PRESENCE. Covariates with a strongly supported relationship with occupancy and/or detection are denoted positive $^{(+)}$ /negative $^{(-)}$; if the relationship of the covariate is not denoted as previously stated, then beta estimates overlapped zero and the strength and direction of the relationship could not be determined.

Species	Model[1]	ΔQAIC	w_i	Likelihood	k	Deviance	$\hat{c}$	ψ (SE)	p (SE)
Common tenrec	ψ(treedens), p(survey + season$^{(+)}$)	0.00	0.57	1.00	11	199.6	0.60	0.64 (0.19)	0.10 (0.06)
	ψ(treedens + %rf), p(survey + season$^{(+)}$)	1.91	0.22	0.39	12	199.5			
Lowland streaked tenrec	ψ(ffTS), p(season + ffTS)	0.00	0.30	1.00	5	74.4	0.92	0.10 (0.09)	0.13 (0.10)
	ψ(ffTS), p(season)	1.48	0.14	0.48	4	77.9			
	ψ(ffTS + totpatches), p(season + ffTS)	2.00	0.11	0.37	6	74.4			
Greater hedgehog tenrec	ψ(canht$^{(-)}$ + ffTS), p(survey + trailwidth$^{(-)}$)	0.00	0.52	1.00	12	441.0	1.11	0.42 (0.10)	0.23 (0.08)
	ψ(canht$^{(-)}$ + %rf + ffTS), p(survey + trailwidth$^{(-)}$)	1.41	0.26	0.49	13	440.3			
All tenrecs	ψ(ffTS + %rf$^{(+)}$ + catTS), p(survey + trailwidth$^{(-)}$)	0.00	0.38	1.00	13	566.1	1.68	0.53 (0.09)	0.24 (0.06)
	ψ(ffTS + %rf$^{(+)}$), p(survey + trailwidth$^{(-)}$)	0.43	0.31	0.81	12	570.2			

[1] Description of covariates included in models: treedens = average tree density at camera station; canht = average canopy height at camera station; %rf = percent of landscape consisting of rainforest; totpatches = total number of rainforest, degraded and matrix habitat patches within the camera trap grid buffer; catTS = trap success rate of the exotic feral cat; ffTS = trap success rate of an endemic, medium-sized carnivore, the spotted fanaloka (*Fossa fossana*); trailwidth = width of trail camera station is focused on; season = season camera trap survey occurred in (cold-wet = 1, hot-dry = 2, hot-wet = 3); survey = detection varies by survey occasion.

Table 3. Competing (ΔAIC $\leq$ 2.0) multi-season occupancy models from multi-season occupancy analyses for spiny tenrecs combined at S02 (2008-2013). Included is model weight (w_i) and likelihood and number of parameters included in the model (k). Estimated parameters include occupancy (ψ), local colonization (γ; probability that a species is detected at a site that it wasn't detected at the year before), local extirpation (ε; the probability that a species isn't detected at a site that it was detected at the year before) and detection (p).

Model	ΔAIC	w_i	Likelihood	k	Deviance
ψ, γ(2010/2012 = 0)), ε(2008 = 0), p(.)[1]	0.00	0.95	1.00	10	328.4

[1] Local colonization probability (γ) is fixed to '0' for the years of 2010 and 2012; local extirpation probability (ε) is fixed to 0 for the year of 2008.

Chapter 4

FLAGSHIPS IN PERIL: HABITAT DEGRADATION AND TRENDS IN LEMUR POPULATION DYNAMICS IN NORTHEASTERN MADAGASCAR

Abstract

The Masoala-Makira protected area complex (hereafter, Masoala-Makira landscape) in northeastern Madagascar is home to at least 15 highly threatened and little-studied lemur species. In an effort to understand the response of lemur populations to habitat degradation in the Masoala-Makira landscape, we conducted a total of 420 nocturnal and diurnal lemur transect surveys at six forest sites varying in habitat disturbance over a four-year period (2010-2013), collecting 1,172 lemur observations of 12 species, including the critically endangered silky sifaka (*Propithecus candidus*), the red ruffed lemur (*Varecia rubra*), and the black-and-white ruffed lemur (*Varecia vareigata subcinta*). Lemur species richness was higher at intact forest sites (n =12) when compared to intermediately degraded (n =8) and degraded (n =4) sites. We estimated landscape densities of the white-fronted brown lemur (*Eulemur albifrons*), the eastern woolly lemur (*Avahi laniger*) and a category combining the hairy-eared dwarf lemur (*Allocebus trichotis*) and mouse lemur (*Microcebus spp.*) using Program DISTANCE. We found that white-fronted brown and eastern woolly lemur densities were lower in intermediately degraded forests than in intact forests. Cathemeral lemurs were observed more often at night at our degraded site, suggesting that lemurs might exhibit behavioral changes in an effort to adapt to a changing environment. At two sites that were resurveyed annually, we found that lemur encounter rates either declined over the years or were affected by season. Our results demonstrate the sensitivity of many of the lemurs in the Masoala-Makira landscape to habitat degradation and reveal a

decline in lemur encounter rates through time at a resurveyed site. We urge that immediate conservation action such as regulating bushmeat hunting be implemented.

Introduction

Madagascar is one of the world's top conservation priorities based on its diverse, endemic taxa, which include numerous lemur species (Myers *et al.* 2000, Brooks *et al.* 2006, Mittermeier *et al.* 2010). However, Madagascar's lemurs are threatened by habitat loss and habitat degradation (Brooks *et al.* 2002, Dunham *et al.* 2008, Herrera *et al.* 2011, Gerber *et al.* 2012a) unsustainable hunting rates (Dunham *et al.* 2008, Barrett & Ratsimbazafy 2009, Jenkins *et al.* 2011, Razafimanahaka *et al.* 2012, Borgerson 2015) and the presence of exotic species such as domestic dogs (*Canis familiaris*) and feral cats (*Felis sp.*) (Goodman 2004, Brockman *et al.* 2008, Moresco *et al.* 2012, Farris *et al.* 2014). Although conservation efforts have been made to protect lemurs due to their importance as seed dispersers (Ganzhorn *et al.* 1999, Razafindratsima *et al.* 2014), pollinators (Kress *et al.* 1994) and prey to many endemic predators (Karpanty 2006, Goodman 2012), seventy percent of extant lemur species remain listed by the IUCN as Endangered or Critically Endangered (IUCN 2014).

Reliable density estimates are vital when it comes to prioritizing conservation actions for threatened and endangered primates (Araldi *et al.* 2014, Kun-Rodrigues *et al.* 2014). Line transect surveys and distance sampling methods are often used to estimate lemur density, requiring information such as number of animals seen, length of the transect surveyed, and the effective strip width (ESW; Buckland 1985, Lehman 2006, Quemere *et al.* 2010, Meyler *et al.* 2012, Kun-Rodrigues *et al.* 2014). However, only the conventional distance sampling (CDS) method, as implemented in Program DISTANCE, explicitly models the decreasing probability of detecting an animal as its distance from the transect increases (Buckland *et al.* 2001). Despite this, lemur density is often estimated using less reliable methods (Rakotondratsima & Kremen

2001, Lehman 2006, Banks *et al.* 2007, Rasolofoson *et al.* 2007, Erhart & Overdorff 2008), which can lead to density estimates being inaccurate (Meyler *et al.* 2012). The use of CDS can be facilitated by widely available and free tools such as Program DISTANCE (Thomas *et al.* 2010) and should be more commonly implemented to provide more statistically defensible density estimates and promote better lemur conservation plans (Kun-Rodrigues *et al.* 2014).

Lemur species diversity and extinction risk is high in northeastern Madagascar, with the Masoala-Makira landscape home to more than 15 species of threatened lemurs, including indri (*Indri indri*), silky sifaka (*Propithecus candidus*), white-fronted brown lemur (*Eulemur albifrons*), two species of ruffed lemurs (*Varecia rubra* and *V. variegata subcinta*), and three species of recently discovered mouse lemurs (*Microcebus spp.*) (Table 1; Rasolofoson *et al.* 2007, Radespiel *et al.* 2008, Mittermeier *et al.* 2010, Schwitzer *et al.* 2014). Lemurs in the Masoala-Makira landscape are threatened by unregulated exploitation, and a sizeable portion of the remaining habitat is no longer suitable for many species (Golden 2009, Rasolofoson *et al.* 2014). Despite the intense pressure on these threatened lemur species, there have been very few studies conducted in the Masoala-Makira landscape that have attempted to quantify the response of lemur populations to habitat degradation (Farris *et al.* 2014, Rasolofoson *et al.* 2014) and no study has yet attempted to estimate lemur density using CDS in Program DISTANCE.

We conducted diurnal and nocturnal lemur surveys at six sites in the Masoala-Makira landscape (2010-2013). Our objectives were to a) estimate lemur encounter rates and density using Program DISTANCE, b) examine how encounter rates and/or densities of multiple lemur species respond to habitat degradation, c) investigate how time use of cathemeral lemurs respond to habitat degradation, and d) monitor lemur encounter rates through time at two resurveyed sites.

Methods

Study Area

From 2010 to 2013 we conducted diurnal and nocturnal lemur surveys at six sites across the Masoala-Makira landscape, concurrent with camera trap surveys to monitor terrestrial wildlife populations (Figure 1 and Appendix D.1; Farris *et al.* 2015, Farris *et al.* in press). Located in northeastern Madagascar, the Masoala-Makira landscape (6,124 km^2, excluding community-managed buffer) is the largest contiguous area of protected forest in Madagascar and is home to six native carnivore species, three exotic carnivore species (domestic dogs, feral cats, and small Indian civet *Viverricula indica*) and at least 15 lemur species (Kremen 2004, Holmes 2007, Rasolofoson *et al.* 2007, Goodman 2012, Farris 2014). Despite the expansiveness of the protected area, the lemurs present in the Masoala-Makira landscape face increasing pressure from hunting (Rakotondratsimba *et al.* 2008, Golden 2009, Golden *et al.* 2011), habitat loss/degradation (Kremen *et al.* 1999, Allnutt *et al.* 2013), and exotic species (Farris *et al.* 2014).

Lemur Surveys

From 2010 to 2013, we conducted lemur surveys at six sites; each site was surveyed at least once, with two sites surveyed annually over three to four years (see Appendix D.1 for details). We marked out three to four line transects at each of our sites. The majority of these line transects measured 2 km in length, with only two line transects measuring less (1.75 km and 1 km, respectively). To avoid further disturbance of forest sites and in compliance with the requests of Madagascar's National Association for the Management of Protected Areas

(ANGAP) and the Wildlife Conservation Society (WCS), line transects were placed on existing trails. Although it is argued that the use of trails in distance sampling may be undesirable due to the lack of randomness in placement (Buckland *et al.* 2001), few studies have actually found the use of trails to be detrimental to accurate density estimation (Johnson & Overdorff 1999), and the trails we selected covered a variety of habitats.

We conducted diurnal (6:30 to 12:00) and nocturnal (17:30 to 22:00) lemur surveys on each transect. The mean number of diurnal and nocturnal surveys per transect was 6.4 and 5.6 surveys, respectively (Appendix D.1). Surveys for each site were spread out over approximately two months to avoid temporal dependence among observations. Each survey was conducted by at least two observers who walked slowly (< 1km/h) along each transect. Observers changed transects and teams between each lemur survey to reduce observational biases (Buckland *et al.* 2001).

When a lemur was observed, we noted observation date and time, species, group size, sighting distance from observer to group center (m) and compass bearing from observer to lemur(s) to compute perpendicular distances and the method of detection (sight/sound). Due to the ruggedness of the terrain and the thickness of the vegetation, we estimated sighting distance visually. Before beginning surveys at each site, observers were trained and refreshed in visual distance estimation against measured distances to ensure accuracy of measurements. For species detected mainly by sound (i.e., indri and ruffed lemurs), we determined the compass bearing to the call, minimum distance from observer to the call, and the minimum number of individuals believed to be present. For nocturnal surveys, lemurs were located and then identified using headlamps. We did not begin lemur surveys when there was heavy rainfall.

Landscape-level and Station-level Habitat Sampling

We ranked our sites from least to most degraded using a maximum likelihood estimated (MLE) principle components analysis (PCA) of landscape-level and camera station-level habitat data collected during concurrent camera trap surveys; see Appendix D.2 and detailed results in Farris (2014). Landscape-level habitat characteristics (i.e., distance to village or forest edge), were estimated using Landsat satellite imagery (2006 and 2009) provided by the Wildlife Conservation Society, Madagascar program, and ERDAS Imagine (Intergraph Corporation) and FRAGSTATS (McGarigal *et al.* 2012).

We measured camera station-level habitat characteristics by walking three 50-m habitat transects (0°, 120°, and 240°) arrayed around individual camera stations that were spaced systematically at 500-m intervals across the study site (n = 18-25 stations per site). We measured canopy height and percent canopy cover every 10 m. At 25 m and 50 m, we used the point-quarter method to measure tree density and basal area for any stem/tree that was greater than 5 cm diameter at breast height (DBH; Cottam & Curtis 1956). At 20 m and 40 m, we ran 20-m understory cover transects that were perpendicular to the established 50-m transect. Understory cover was measured at three levels (0.0-0.5 m, 0.5-1.0 m and 1.0-2.0 m) by using a 2-m pole held perpendicular to the ground at 1-m intervals, recording the presence (1) or absence (0) of vegetation touching the pole (Davis *et al.* 2011). The station-level and landscape-level habitat features were analyzed in the MLE-PCA to classify different forest types. The MLE-PCA resulted in two intact (S01 and S02), three intermediately degraded (hereafter, intermediate; S03, S04, and S05) and one degraded sites (S06; see Farris 2014 and Appendix D.2). We labeled sites based on their level of degradation (01 = least degraded; 06 = most degraded) to protect the identities of local villages near our sites, due to the sensitivity of hunting data used in other, related publications.

Landscape Lemur Encounter Rates and Density Estimation

We removed lemur observations from the same transect and date that were < 500 m apart for mobile/fast-moving species (e.g., white-fronted brown and ruffed lemurs) to avoid any potential of double-counting. For lemur encounter rates, we included observations where we did not collect sighting distance and compass bearing. When the true number of individuals was unknown for an observation, we marked the number of individuals observed as ‘1’. We took the minimum number of individuals observed for observations where a species was detected and the number of individuals was estimated as a range (e.g., 4 individuals observed for a range of 4-5 potential individuals).

To avoid under- or overestimation of total nocturnal, diurnal and cathemeral lemur encounter rates, we divided the total number of individuals observed by the distance surveyed during surveys where we had the highest chance of seeing them. For example, total nocturnal lemur encounter rate equals total number of individuals from strictly nocturnal species observed divided by the total distance surveyed during nocturnal surveys. The encounter rates of species that were detected during both diurnal and nocturnal surveys (hereafter, cathemeral) were estimated using the total distance surveyed. We defined a species as cathemeral when we had multiple observations of that species during both diurnal and nocturnal surveys. Based on this definition, we found red ruffed, black-and-white ruffed, red-bellied (*Eulemur rubriventer*) and white-fronted brown lemurs to be cathemeral. We then added nocturnal, cathemeral and lemur encounter rates to get a total lemur encounter rate across the landscape. Species-specific landscape encounter rates were estimated by dividing the number of individuals of a species observed by the total distance surveyed, dependent on that species' activity patterns.

Three species of mouse lemur (*Microcebus macarthurii*, *Microcebus mittermeieri* and *Microcebus sp. nova*) are present in the Masoala-Makira landscape, along with the hairy-eared dwarf lemur (*Allocebus trichotis*). Due to the difficulty of noninvasively distinguishing these four species from each other, we lumped all potential *Microcebus* and *Allocebus* observations into one *Allocebus/Microcebus* category and estimated encounter rates for this category. In 2013, observers did not include indri, red ruffed, and black-and-white ruffed lemur observations that were detected by sound in their data collection, meaning that estimated encounter rates and annual trends may underestimate true indri and ruffed lemur encounter rates.

We estimated lemur density in Program DISTANCE (version 6.2), which explicitly models detection based on the distance of an animal from the transect and uses Akaike's information criterion (AIC) to select between various models (Akaike 1973, Buckland *et al.* 2001, Thomas *et al.* 2010). We decided to use the half-normal key function to model detection because it is able to provide more reliable estimates despite data 'spikiness' (Buckland *et al.* 2001). For lemur density estimation, we removed all lemur observations that had no recorded sighting distances or compass bearings. Observations where we did not have observed group size were entered as '-1', which would indicate to the program to use that observation while determining the detection function and estimating encounter rate, but ignore it when estimating expected cluster (group) size.

We pooled all observations from each survey for each species and then right-truncated at least 5% of the data. We then binned the observations into discrete distance classes based on suggestions from the model to improve detection function fit. Models that did not pass the goodness-of-fit (GOF) tests ($p \leq 0.05$) were discarded. We selected the best models based on ΔAIC values, coefficients of variation (CVs) and if the model passed the GOF test. We did not use results from models that did not pass the GOF tests. When more than one model was competing (ΔAIC ≤ 2.0), we chose the model with better precision (i.e., the lower CV). Because we included annual resurveys of S02 (2010-2013) and S05 (2011-2013), we gave each transect a unique code to ensure that area surveyed was not underestimated and lemur density was not overestimated. We multiplied the number of surveys conducted on a transect by the transect length to estimate total transect length per survey. For strictly diurnal and nocturnal species, we multiplied the number of diurnal or nocturnal surveys, respectively, by the transect length to estimate total transect length. This was to ensure we did not underestimate density by including surveys where we had little chance of detecting a species due to the time the survey was conducted. We included the observed weather at the start and end of each survey (clear, cloudy, rain, foggy) and season of the survey as covariates on the detection function. Seasons were classified as cold-wet (June-September), hot-dry (October-January) and hot-wet (February-May).

Response of Lemur Encounter Rates and Density to Habitat Degradation

To examine the response of lemur encounter rates to habitat degradation, we estimated mean nocturnal, diurnal and cathemeral lemur encounter rates for each forest type. We estimated mean lemur encounter rate by determining the total nocturnal, diurnal or cathemeral lemur encounter rate for each line transect surveyed within a forest type (intact = 16, intermediate = 16, degraded = 3). We then averaged these encounter rates to get a mean nocturnal, diurnal and cathemeral lemur encounter rate per forest type. We also estimated mean species-specific encounter rates at each forest type using the same method. Strong differences between encounter rates were determined using non-overlapping 95% confidence intervals (CIs). To examine the response of lemur density to habitat degradation on lemur density, we stratified lemur observations in Program DISTANCE by forest type (intact or intermediate). We did not include data from the degraded site (S06) due to very low numbers of lemur observations. After truncating and binning, we fit global and strata-specific detection functions to the data and selected the best model based on ΔAIC values, coefficients of variation (CVs), and the results of the GOF tests. We used 95% CIs to determine whether there were different density estimates between forest types.

Cathemeral Lemur Time Use Response to Habitat Degradation

We examined the response of cathemeral lemur time use to habitat degradation by determining avoidance or selection of certain time periods for cathemeral lemurs at the different forest types. We obtained historical, daily time-of-sunrise and time-of-sunset data for all surveys and determined the earliest and latest sunrise/sunset time recorded for each survey; we then estimated an 'average' sunrise/sunset time (Farris *et al.* 2015). We used these average sunrise/sunset times to determine the hours that comprised day and night. 'Day' is the time period between sunrise and sunset, while 'night' is the time period between sunset and sunrise (Gerber *et al.* 2012b).

We determined the hours available in these time periods for each survey, with both day and night comprised of approximately 12 hours. By pooling all cathemeral lemur observations across species, including observations where we did not have a recorded sighting distance or compass bearing, we found the proportion of observations in each time period (the number of observations in the time period divided by the total number of observations) for that survey. To determine selection or avoidance of each time period, we used Ivlev's resource selection index (Ivlev 1961), adapted by Jacobs (1974), calculated as:

$$D = (r - p) / [(r + p) - 2rp]$$

We estimated the resource selection index value (*D*) for both time periods in each survey for all cathemeral lemurs; $D < 0$ indicates avoidance of the time period, $D > 0$ indicates selection of the time period and $D = 0$ indicates no preference either way. To examine how activity patterns were affected by habitat degradation, we averaged *D* values for cathemeral lemurs from all surveys for day and night for the three forest types (intact, intermediate and degraded). We used 95% CIs to determine whether there was a strong selection for a certain time period; when 95% CIs did not overlap with 0, this indicated a strong selection or avoidance of that time period.

Trends in Lemur Encounter Rates at Resurveyed Sites

We conducted repeated surveys of one intact (S02) and one intermediate (S05) site. S02 and S05 were surveyed annually between 2010 and 2013 and 2011 and 2013, respectively. Transect locations were identical throughout the years, with the addition of two new transects and increased effort at S02 and S05 in 2013. We examined trends in mean nocturnal, diurnal, cathemeral and species-specific encounter rates over the years. We estimated these mean encounter rates using the same method detailed in *Response of Lemur Encounter Rates and Density to Habitat Degradation*. We used 95% CIs to determine whether there was a strong difference in encounter rates over the years. We did not estimate lemur density through the years due to low sample sizes.

Results

From 2010 to 2013, we conducted 420 lemur surveys (224 diurnal and 196 nocturnal), surveying 823 km and obtaining 1,168 lemur observations of 12 species and 4 of unidentifiable nocturnal species for a total of 1,172 lemur observations. Total nocturnal, diurnal and cathemeral lemur encounter rate across the landscape were 1.38, 0.18 and 0.68 lemurs/km, respectively. Total lemur encounter rate across the landscape was 2.24 lemurs/km. The majority of lemur observations were of white-fronted brown lemurs (n = 480), eastern woolly lemurs (*Avahi laniger*; n = 328) and *Allocebus/Microcebus* (n = 151). We also detected dwarf lemurs (*Cheirogaleus spp.*), aye-aye (*Daubentonia madagascariensis*), western lesser bamboo lemurs (*Hapalemur occidentalis*), sportive lemurs (*Lepilemur spp.*) and silky sifaka (Table 2). *Allocebus/Microcebus* and eastern woolly lemurs were observed at all six sites, while aye-aye and red ruffed lemurs were only observed at one site (S02). Based on observation times, we observed six species were strictly nocturnal (*Allocebus/Microcebus*, eastern woolly lemur, dwarf lemur, aye-aye, western lesser bamboo lemur and sportive lemur), two were strictly diurnal (indri and silky sifaka) and four were cathemeral (white-fronted brown lemur, red-bellied lemur, red ruffed lemur and black-and-white ruffed lemur).

Landscape Lemur Encounter Rates and Densities

The species with the highest encounter rate across the landscape was the eastern woolly lemur (0.85 lemurs/km), while the aye-aye and western lesser bamboo lemur had the lowest encounter rates (0.005 lemurs/km; Table 1). We only had enough observations (>30) to estimate the densities of three species: white-fronted brown lemur, eastern woolly lemur and *Allocebus/Microcebus*. White-fronted brown lemur landscape density was estimated as 46 individuals/km^2, eastern woolly lemur was 58 individuals/km^2 and *Allocebus/Microcebus* was 28 individuals/km^2 (Table 3 and Figure 2). The weather at the end of a survey having an effect on the scale of detection was included in the top model for *Allocebus/Microcebus*, but this effect was not strongly supported (Table 3).

Response of Lemur Encounter Rates and Density to Habitat Degradation

We detected 12 lemur species at our intact forest sites (S01-S02), eight lemur species at our intermediate forest sites (S03-S05) and only four lemur species at our degraded site (S06; Table 2). Mean nocturnal lemur encounter rates were similar at intact, intermediate and degraded forest sites. Mean diurnal lemur encounter rates were similar at intact and intermediate forest sites; however, no strictly diurnal lemur species were observed at our degraded site. Mean cathemeral lemur encounter rates at intact forest sites was significantly higher than mean cathemeral lemur encounter rates at degraded forest sites (Figure 3). For species observed at every forest type, only the white-fronted brown lemur showed a significant difference between intact mean encounter rate (0.79 ± SE 0.23) and degraded mean encounter rate (0.16 ± SE 0.06; Table 2).

White-fronted brown lemur and eastern woolly lemur density estimates were higher at intact forest sites, while *Allocebus/Microcebus* density estimates were higher at intermediate forest sites, although 95% CIs overlapped (Table 3 and Figure 3). Season of survey and weather at the end of a survey were part of the top models for eastern woolly lemurs and *Allocebus/Microcebus*, respectively, but these effects on the scale of detection was not strongly supported (Table 3).

Cathemeral Lemur Time Use Response to Habitat Degradation

We had more observations of the cathemeral white-fronted brown lemurs, red-bellied lemurs, red ruffed lemurs, and black-and-white ruffed lemurs during our diurnal surveys (n = 309, 12, 3 and 31 observations, respectively) than during our nocturnal surveys (n = 153, 10, 2 and 22 observations, respectively). Cathemeral lemurs showed no selection or avoidance of day or night at intact forest sites, whereas they did select day and avoided night at intermediate forest sites. In contrast to intact and intermediate forest sites, at our one degraded site (S06), cathemeral lemurs selected night and avoided day (Figure 4).

Trends in Lemur Encounter Rates at Resurveyed Sites

Mean lemur encounter rate at S02 (2010-2013) declined from 2010 to 2012, and then increased in 2013, although these differences were not significant (Table 4). Out of the nine species observed at S02 throughout the years, five species had lower point estimates of encounter rates, and four species had higher, in 2013 when compared to 2010. *Allocebus/Microcebus* and white-fronted brown lemur encounter rates were significantly lower in 2013 when compared to 2010, while eastern woolly lemur encounter rates were not significantly different between the initial and final years of the surveys. In contrast, at S05 (2011-2013), mean lemur encounter rate, excluding the lemur observations unidentifiable to species (n = 2), dropped from 2011 to 2012, and then increased in 2013, although these differences were not significant (Table 4). Out of the eight species observed at S05 throughout the years sampled, seven species had higher point estimates of encounter rates in 2013 when compared to 2011. Only indri had a lower encounter rate in 2013 when compared to 2010; however, due to not including indri observations detected by sound during this year, this is likely an underestimate of indri encounter rate during this year

(Table 4). *Allocebus/Microcebus*, white-fronted brown and eastern woolly lemur encounter rates were not significantly different between the initial and final years of the surveys.

Discussion

Despite the widespread use of Program DISTANCE for density estimation for other species, this study is the first to use Program DISTANCE to estimate lemur density in the Masoala-Makira landscape on a large geographic scale. It is also one of the few studies that monitored lemur populations in northeastern Madagascar over multiple years (Rakotondratsima & Kremen 2001, Rasolofoson *et al.* 2007, Rasolofoson *et al.* 2014). We also provide the first density estimates for white-fronted brown lemurs, eastern woolly lemurs and *Allocebus/Microcebus* in northeastern Madagascar obtained through Program DISTANCE. Finally, we are the first to examine the response of cathemeral lemur time use to habitat degradation in northeastern Madagascar.

Landscape Lemur Encounter Rates and Densities

Eastern woolly lemurs had the highest landscape encounter rates of any lemur species (0.85 individuals/km), while aye-aye and western lesser bamboo lemurs had the lowest (0.005 individuals/km). We only included direct observations (sight or sound) of lemurs in our data, whereas a majority of field studies on aye-aye include indirect evidence of aye-aye presence, such as their teeth marks on seeds (Mittermeier *et al.* 2010, Farris *et al.* 2011, Andriaholinirina *et al.* 2014). The exclusion of indirect evidence of aye-aye presence likely led to underestimates of true aye-aye encounter rates in the Masoala-Makira landscape. The densities of the western lesser bamboo have been estimated to be up to 71 individuals/km^2 in the western deciduous dry forests of Manongarivo Special Reserve (Rakotoarinivo *et al.* 2011). It is likely that western lesser bamboo lemurs have much lower densities in the Masoala-Makira landscape, as suggested by our low encounter rate for bamboo lemurs compared to encounter rates in other studies (Sterling & Rakotoarison 1998).

Another species of interest with a low landscape encounter rate (0.006 individuals/km), was the red ruffed lemur, which was only detected at one site (S02). The range of red ruffed lemurs includes the Masoala peninsula and the forests immediately north of Antongil Bay, with its northwestern geographic range limited by the Antainambalana and Sahantaha rivers (Hekkala *et al.* 2007). We are able to provide further evidence that red ruffed lemurs occur in the forests north of Antongil Bay, with five individuals detected by sight and sound at S02 from 2010-2012 (Rasolofoson *et al.* 2007, Patel & Andrianandrasana 2008). The lack of red ruffed lemur observations in 2013, despite high survey effort (n = 85 km surveyed) and their ease of detection due to loud vocalizations, highlights the likelihood of this critically endangered species being extirpated from the forests north of Antongil Bay (Hekkala *et al.* 2007).

Our estimates of white-fronted brown lemur, eastern woolly lemur and *Allocebus/Microcebus* landscape density were similar to density estimates in Makira (Rasolofoson *et al.* 2007), while our estimates of white-fronted brown lemur density were much higher than density estimates from Masoala (Rakotondratsima & Kremen 2001). However, Rakotondratsima and Kremen (2001) and Rasolofoson *et al.* (2007) used less reliable methods to estimate lemur density. Future research should focus on estimating lemur density on local scales using Program DISTANCE in an effort to understand the effects of local conditions on lemur density and to reliably determine the numbers of individuals of these species are present in the Masoala-Makira landscape.

Response of Lemur Encounter Rates and Density to Habitat Degradation

All 12 species were present at intact sites, whereas only four species were present at our degraded site. While mean nocturnal lemur encounter rates were similar throughout forest types, we did not detect silky sifaka or indri at our degraded site. Both species are strictly diurnal and large-bodied (> 5kg; Table 1); their selection for day, their large size or both characteristics might cause them to be more sensitive to lowered habitat quality and the anthropogenic pressures present at degraded sites (Table 1; Lehman *et al.* 2006c, Irwin *et al.* 2010). Mean cathemeral lemur encounter rates at intact forest sites ere significantly higher than mean cathemeral lemur encounter rates at our degraded forest site, suggesting that cathemeral lemurs are present in degraded forests in lower numbers than they are in intact forests. Out of the four cathemeral species (white-fronted brown, red-bellied, red ruffed and black-and-white ruffed lemur), only the white-fronted brown lemur was present at the degraded site. While the two ruffed lemurs are known to be sensitive to habitat disturbance, due to their frugivory, large body size and high consumption rates by locals (Golden 2009, Herrera *et al.* 2011, Jenkins *et al.* 2011, Borgerson 2015), the responses of red-bellied lemurs to habitat disturbance appears to vary due to its flexibility in diet and activity patterns (Durham 2003, Lehman *et al.* 2006b, Herrera *et al.* 2011).

White-fronted brown lemur and eastern woolly lemur density estimates were higher at intact forest sites. Rakotondratsima and Kremen (2001) found white-fronted brown lemur densities to be higher at disturbed sites than at intact sites; while brown lemurs (*Eulemur spp.*) have been found to be adaptable to habitat disturbance (Campera *et al.* 2014, Borgerson 2015). Our contrary findings might be due to differences in habitat classification. Eastern woolly lemurs are thought to not be particularly sensitive to habitat disturbance (Lehman *et al.* 2006a), but there is some evidence that they prefer intact sites over degraded sites (Herrera *et al.* 2011). Meanwhile, *Allocebus/Microcebus* density estimates were higher at intermediate forest sites. There have been very few studies on the hairy-eared dwarf lemur (Biebouw 2009, Mittermeier *et al.* 2010), but it seems that hairy-eared dwarf lemurs and mouse lemurs (*Microcebus spp.*) are able to tolerate some habitat disturbance (Schütz & Goodman 1998), possibly due to their small size and foliovorous/insectivorous nature (Lehman *et al.* 2006a, Herrera *et al.* 2011). Future research should examine the synergistic effects of hunting and habitat degradation on lemur population dynamics, as white-fronted brown, eastern woolly, and mouse lemurs are all hunted at highly unsustainable rates in the Masoala-Makira landscape (Golden 2009, Borgerson 2015).

Cathemeral Lemur Time Use Response to Habitat Degradation

The changes in the local habitat and ecological community resulting from habitat degradation can affect lemur behavior (Gerber *et al.* 2012a, Crowley *et al.* 2013, Seiler *et al.* 2013) and cathemeral lemurs often change their activity patterns as a way to adapt to changing conditions (Overdorff 1988, Donati *et al.* 2009, LaFleur *et al.* 2014). Overdorff (1988) and LaFleur *et al.* (2014) suggested that predator avoidance might be one reason why lemurs change their activity patterns; LaFleur *et al.* (2014) and Donati *et al.* (2009) also found that diet, particularly diet quality, might have an effect on lemur time use. We found that in intact and intermediate forests, cathemeral lemurs selected for day and avoided night, while at our degraded forest site, they avoided day and selected for nighttime activity. Multiple lemur species are hunted at unsustainable rates in the Masoala-Makira landscape (Golden 2009) and Farris (2014) found that local hunters tend to target intact forests. Because locals only hunt actively during the day, it might be cathemeral lemurs in degraded forests are exhibiting learned behavior from when they were part of a population that was targeted by locals (Chamaille-Jammes *et al.* 2014, Dooley & Judge 2015). Further research should be conducted to determine the causes of changes in cathemeral lemur activity patterns between intact and degraded forests in the Masoala-Makira landscape.

Trends in Lemur Encounter Rates at Resurveyed Sites

The trends in mean and species-specific encounter rates at our resurveyed intact (S02) and intermediate (S05) forest sites varied throughout the years. Lemur encounter rates at S05 (2011-2013) were high in 2011, declined in 2012 and increased again in 2013. S05 was surveyed annually at different times of the year, with 2012 being surveyed during the cold-wet season (June-September). The decline in lemur encounter rates during that year can be attributed to lowered activity rates (Mittermeier *et al.* 2010). Meanwhile, S02 was surveyed at the same time of the year from 2010-2013, and showed a general decline in encounter rates from 2010 to 2012, with some increases in 2013. *Allocebus/Microcebus* and white-fronted brown lemur encounter rates were lower in 2013 when compared to 2010, while eastern woolly lemur encounter rates were not different between the initial and final years of the surveys. While the decline in white-fronted brown lemur encounter rates might be attributed to the high hunting rates at S02, the decline in *Allocebus/Microcebus* encounter rates could be due to the increase in feral cat occupancy over the years (Farris 2014). Farris *et al.* (2014) found that mouse lemurs "avoided" areas with high feral cat occupancy. Continued monitoring of lemur populations at both sites will allow us to further examine and determine the causes of future lemur population dynamics.

Implications and Future Research

Despite the Masoala-Makira landscape being the largest protected area complex in Madagascar, the lemur community appears to be threatened by habitat degradation, overexploitation, and the presence of exotic species. Our research has shown that many species are show responses to habitat degradation and that lemur species richness declines as forests become more degraded. Importantly, even intact forests might not be strongholds for lemurs if exotic predators and hunters are present, as shown by declining lemur encounter rates over time at S02. Based on our results, we urge immediate conservation action in the forests of the Masoala-Makira landscape. Halting deforestation, enforcing the protected status of Masoala-Makira's core forest and establishing anti-poaching patrols are needed to mitigate the dangers to Masoala-Makira's highly threatened lemur community.

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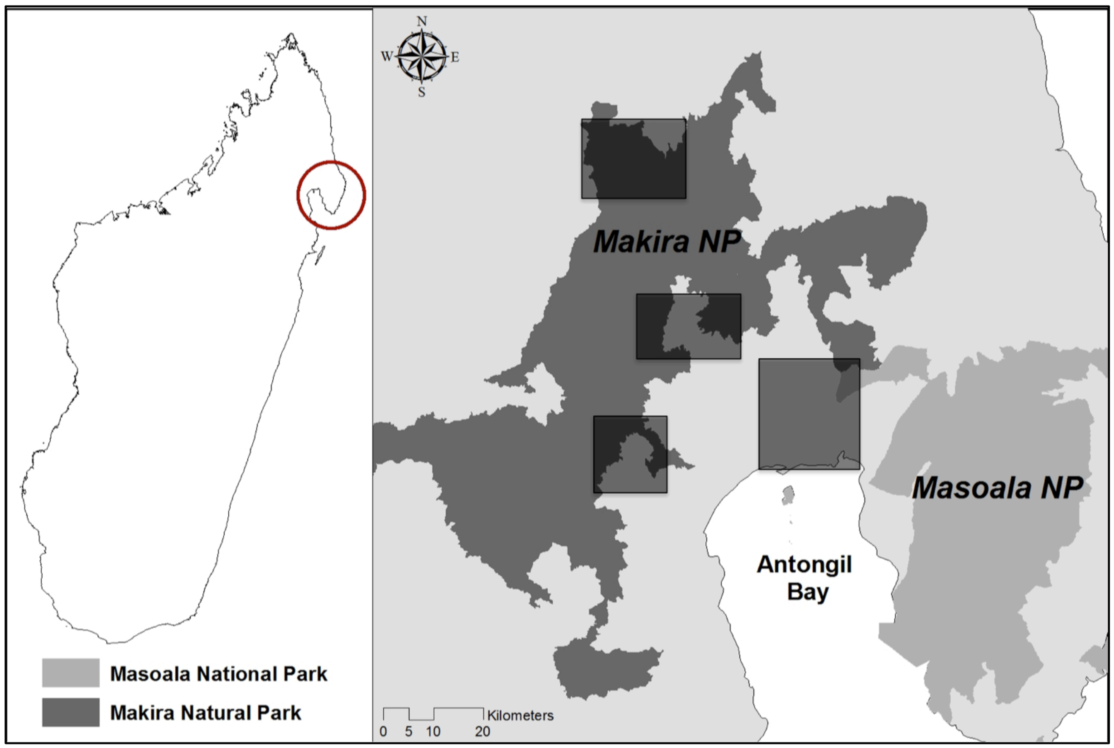

Figure 1. Makira Natural Park and Masoala National Park (Masoala-Makira protected area complex) in northeastern Madagascar. At 6,124.7 km^2, excluding community-managed buffers, the Masoala-Makira landscape is the largest area of protected contiguous forest in Madagascar. Six sites (S01-S06) in the regions highlighted were surveyed for lemurs using line transects from 2010 to 2013.

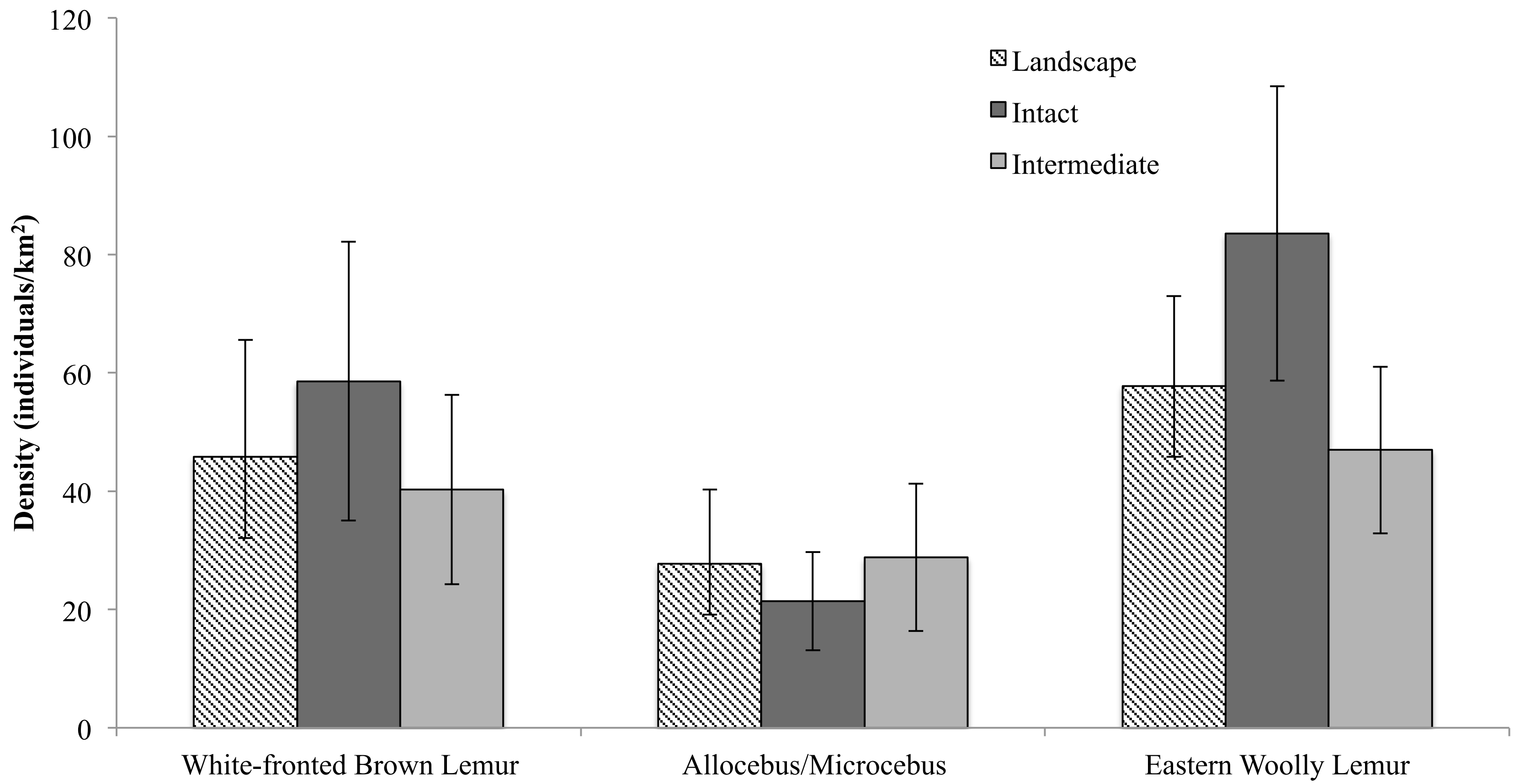

Figure 2. Density estimates for white-fronted brown lemurs, *Allocebus/Microcebus* and eastern woolly lemurs across the landscape, and at intact and intermediate forests. Error bars are confidence intervals provided by Program DISTANCE.

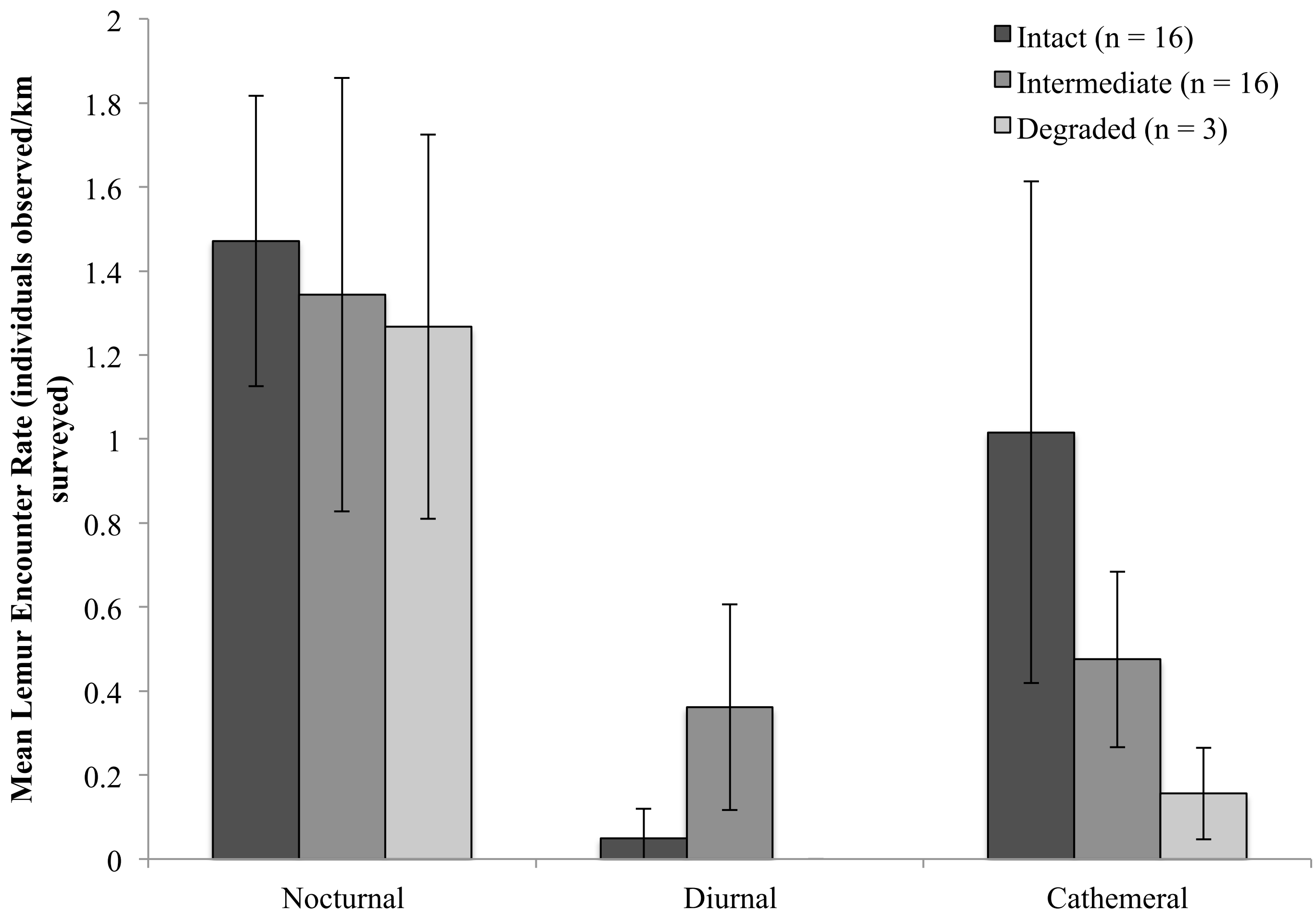

Figure 3. Mean encounter rates for nocturnal, diurnal and cathemeral lemurs in intact, intermediate and degraded forest sites. Error bars are 95% CIs. N indicates the number of line transects used in the encounter rate estimation.

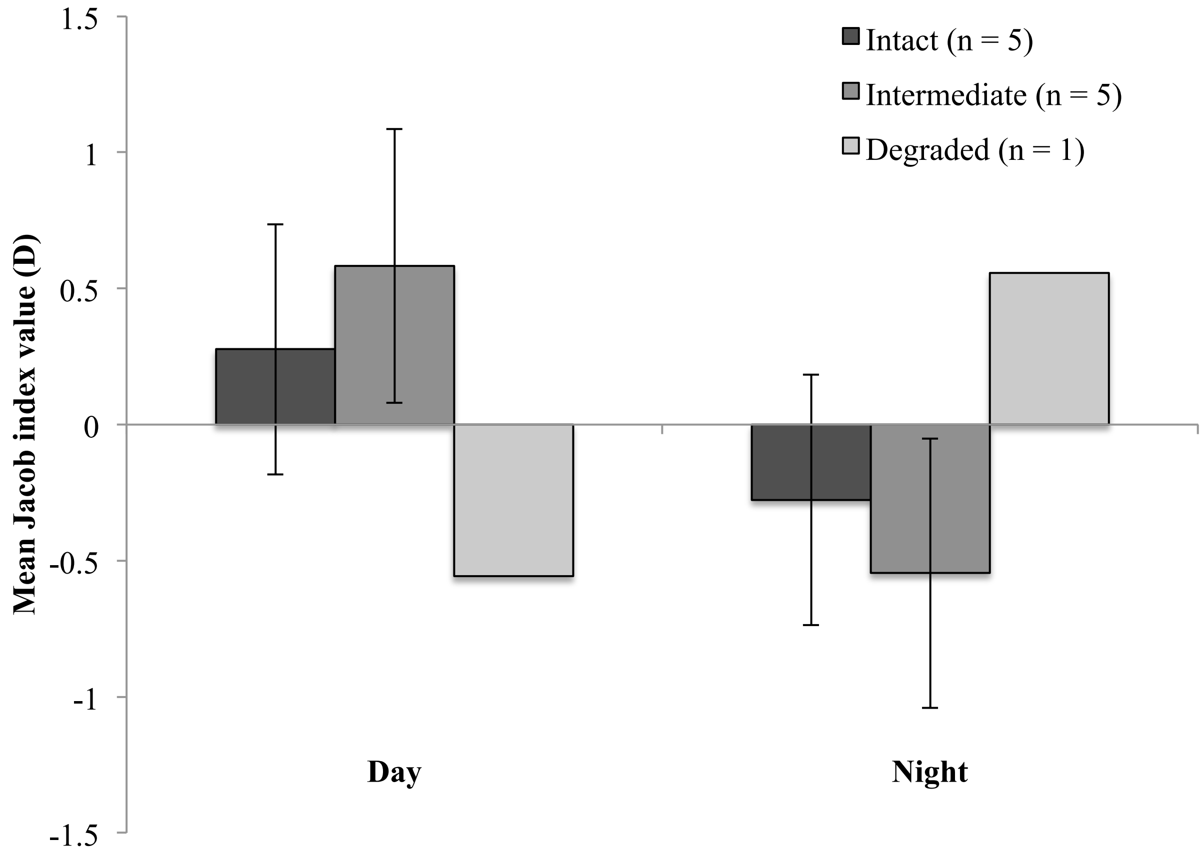

Figure 4. Activity patterns and 95% confidence intervals of cathemeral lemurs (white-fronted brown, red-bellied, red ruffed and black-and-white ruffed lemur) at the three forest types (intact, intermediate and degraded) in the Masoala-Makira landscape, northeastern Madagascar. N indicates the number of surveys used to estimate D. D < 0 means avoidance of that time period, D > 0 means selection for that time period and D = 0 (or overlapping 95% CIs) means no preference.

Table 1. Lemur species that are or might be present in the Masoala-Makira landscape (northeastern Madagascar), based largely on range maps from IUCN (2014) and Mittermeier *et al.* (2010). Included is the IUCN status, maximum published body size (kg), activity pattern, diet (components ranked in order of importance) and whether that species is hunted.

Common name	Scientific name	IUCN Status	Max. Body Size (kg)	Activity[1]	Diet[2]	Hunted[3]
Hairy-eared dwarf lemur	*Allocebus trichotis*	Vulnerable	0.09	N	I-Fo-Fru	Y
Eastern woolly lemur	*Avahi laniger*	Vulnerable	1.40	N	Fo-Fru	Y
Moore's woolly lemur	*Avahi mooreorum*	Endangered	0.92	N	Fo-Fru	Y
Furry-eared dwarf lemur	*Cheirogaleus crossleyi*	Data Deficient	--	N	Fo-Fru-I	--
Geoffroy's dwarf lemur[4]	*Cheirogaleus major*	Data Deficient	0.50	N	Fo-Fru-I	--
Aye-aye	*Daubentonia madagascariensis*	Endangered	2.60	N	Fo-I-Fru	Y
White-fronted brown lemur	*Eulemur albifrons*	Endangered	2.00	C	Fo-Fru	Y
Red-bellied lemur	*Eulemur rubriventer*	Vulnerable	2.40	C	Fru-Fo	Y
Western lesser bamboo lemur	*Hapalemur occidentalis*	Vulnerable	1.19	C	Fo-Fru	Y
Indri	*Indri indri*	Critically Endangered	9.50	D	Fo-Fru	Y
Scott's sportive lemur	*Lepilemur scottorum*	Endangered	0.95	N	Fo	Y
Seal's sportive lemur	*Lepilemur seali*	Vulnerable	0.88	N	Fo	Y
MacArthur's mouse lemur	*Microcebus macarthurii*	Endangered	0.05	N	I-Fo-Fru	Y
Mittermeier's mouse lemur	*Microceubs mittermeieri*	Endangered	0.04	N	I-Fo-Fru	Y
Unnamed mouse lemur[5]	*Microcebus sp. nova*	--	--	N	I-Fo-Fru	Y
Masoala fork-marked lemur	*Phaner furcifer*	Vulnerable	--	N	Fo	--
Greater bamboo lemur[4]	*Prolemur simus*	Critically Endangered	2.50	C	Fo	Y
Silky sifaka	*Propithecus candidus*	Critically Endangered	6.00	D	Fo-Fru	Y
Red ruffed lemur	*Varecia rubra*	Critically Endangered	3.60	D (C)	Fru-Fo	Y
Black-and-white ruffed lemur	*Varecia variegata subcinta*	Critically Endangered	3.60	D (C)	Fru-Fo	Y

[1]N—nocturnal; D—diurnal; C—cathemeral.
[2]Fru—fruit; Fo—leaves, buds, flowers, seeds, gum, nectar; I—insects.
[3]Whether species is hunted or not determined from species accounts in IUCN (2014) and Mittermeier et al. (2010)
[4]Northern limits of geographic range yet to be determined; for greater bamboo lemur, see Dolch *et al.* (2010) and Ravaloharimanitra *et al.* (2011).

[5]See Radespiel *et al.* (2008).

Table 2. The 12 species of lemur observed during our surveys at six sites across the Masoala-Makira landscape (2010-2013), separated by activity pattern. Included is: total number of individuals observed, total landscape encounter rate (ER) and ER by forest type: intact (A), intermediate (B), and degraded (C).

					Mean ER (SE)[2] by Forest Type		
Activity	Common name	Scientific name	Individuals Observed	Total ER[1]	A	B	C
Nocturnal	*Allocebus/Microcebus*[3]	*Allocebus trichotis/ Microcebus spp.*	151	0.39	0.36 (0.10)	0.40 (0.10)	0.47 (0.32)
	Eastern woolly lemur	*Avahi laniger*	328	0.85	1.00 (0.15)	0.77 (0.16)	0.73 (0.38)
	Dwarf lemurs[4]	*Cheirogaleus spp.*	33	0.09	0.08 (0.04)	0.10 (0.04)	0.07 (0.07)
	Aye-aye	*Daubentonia madagascariensis*	2	0.005	0.03 (0.03)	-	-
	Western lesser bamboo lemur	*Hapalemur occidentalis*	2	0.005	0.006 (0.006)	0.006 (0.006)	-
	Sportive lemur[5]	*Lepilemur spp.*	11	0.03	0.006 (0.006)	0.05 (0.03)	-
	Unknown[6]		4	0.01	-	0.02 (0.02)	-
		Total	**531**	**1.38**			
Diurnal	Indri[7]	*Indri indri*	71	0.16	0.006 (0.006)	0.36 (0.13)	-
	Silky sifaka	*Propithecus candidus*	7	0.02	0.04 (0.03)	-	-
		Total	**78**	**0.18**			
Cathemeral	White-fronted brown lemur	*Eulemur albifrons*	480	0.58	0.79 (0.23)	0.44 (0.10)	0.16 (0.06)
	Red-bellied lemur	*Eulemur rubriventer*	24	0.03	0.09 (0.05)	-	-
	Red ruffed lemur[7]	*Varecia rubra*	5	0.006	0.012 (0.007)	-	-
	Black-and-white ruffed lemur[7]	*Varecia variegata*	54	0.07	0.13 (0.10)	0.04 (0.01)	-
		Total	**563**	**0.68**			
	TOTAL		**1,172**	**2.24**			

[1] Total encounter rate (ER) is estimated as the total number of individuals of that species observed divided by the total distance surveyed, dependent on that species activity pattern (i.e., nocturnal species are divided by the total distance surveyed during nocturnal surveys).
[2] Mean species-specific encounter rate by forest type was estimated as the average encounter rate over all line transects surveyed in intact (n = 16), intermediate (n = 16) and degraded (n = 3) forest for that species.
[3] Due to the difficulty of noninvasively identifying hairy-eared dwarf lemur (*Allocebus trichotis*) and the three species of mouse lemur present in Masoala-Makira (*Microcebus macarthurii, M. mitttermeieri* and *M. sp. nova*), we combined all observations into an *Allocebus/Microcebus* category.

[4] There are potentially two species of dwarf lemur present in the Masoala-Makira landscape: Geoffroy's dwarf lemur (*Cheriogaleus major*) and furry-eared dwarf lemur (*C. crossleyi*).
[5] There are two species of sportive lemur present in the Masoala-Makira landscape: Scott's sportive lemur (*Lepilemur scottorum*) and Seal's sportive lemur (*L. seali*).
[6] Lemur observations that we were unable to identify to species occurred during nocturnal surveys. It is believed that they were either *Allocebus*/*Microcebus* or a dwarf lemur (*Cheirogaleus spp.*).
[7] Encounter rates for indri and red and black-and-white ruffed lemurs are underestimates due to a change in methods such that sound detections were not included in 2013.

Table 3. Competing (ΔAIC ≤ 2.0) landscape and strata-specific density models from Program Distance for the white-fronted brown lemur, eastern woolly lemur and *Allocebus/Microcebus* across the Masoala-Makira landscape, northeastern Madagascar (2010-2013). Included are landscape and strata-specific density estimates (intact [A] and intermediate [B] forests), lower and upper density confidence intervals (LCL and UCL, respectively), and the estimated coefficient of variation (CV). Models in bold were chosen based on **Δ**AIC values, CVs and the results of goodness-of-fit (GOF) tests. Covariates that strongly influenced the scale of the detection function are denoted positive $^{(+)}$ /negative $^{(-)}$; if the relationship of the covariate is not denoted as previously stated, then beta estimates overlapped zero and the strength and direction of the relationship could not be determined.

Analysis	Species	Model[1]	k	**Δ**AIC	CV	Density (SE)	LCL	UCL
Landscape	White-fronted brown lemur	hncos (sea)	3	0.00	0.17	48.8 (8.5)	34.6	68.9
		hncos	**1**	**1.31**	**0.18**	**45.9 (8.3)**	**32.1**	**65.6**
	Eastern woolly lemur	**hncos**	**1**	**0.00**	**0.12**	**57.8 (6.8)**	**45.8**	**73.0**
		hncos (sea)	3	1.63	0.12	57.7 (6.8)	45.7	73.0
	Allocebus/Microcebus	**hncos (ew)**	**4**	**0.00**	**0.19**	**27.8 (5.2)**	**19.1**	**40.3**
Strata-Specific	White-fronted brown lemur	**glo hncos**	**1**	**0.00**	**0.19**	**A: 58.6 (15.0) B: 40.2 (10.1)**	**A: 35.0; B: 24.2**	**A: 98.0; B: 66.8**
		ssp hncos	2	1.93	0.19	A: 59.9 (16.0) B: 39.2 (10.5)	A: 35.2; B: 23.0	A: 102.1; B: 66.9
	Eastern woolly lemur	**ssp hncos (sea)**	**6**	**0.00**	**0.13**	**A: 83.6 (14.5) B: 47.0 (8.3)**	**A: 58.7; B: 32.8**	**A: 119.0; B: 67.1**
		ssp hncos	2	1.33	0.13	A: 78.5 (13.5) B: 46.0 (8.1)	A: 55.4; B: 32.2	A: 111.4; B: 65.7
	Allocebus/Microcebus	**glo hncos (ew)**	**4**	**0.00**	**0.20**	**A: 21.4 (5.1) B: 28.8 (7.9)**	**A: 13.1; B: 16.3**	**A: 34.9; B: 50.8**

[1] Description of model name—hncos: half-normal cosine detection function; sea: season that survey was conducted (cold-wet, hot-dry and hot-wet); ew: weather recorded after individual surveys (clear, cloudy, rain and foggy) were concluded; ssp: strata-specific detection function, fit to observations from each strata (i.e., intact or intermediate forest) individually; glo: global detection function, fit to all observations, regardless of what strata they belong.

Table 4. Mean species-specific[1] and mean lemur encounter rates based on activity pattern[2] from an intact (S02) and an intermediate (S05) forest site that were surveyed annually from 2010 to 2013.

Site	Activity	Species	2010	2011	2012	2013
S02	Nocturnal	*Allocebus/Microcebus*[3]	0.46 (0.37)	0.35 (0.15)	0.23 (0.11)	0.19 (0.09)
		Eastern woolly lemur	1.15 (0.08)	0.82 (0.04)	0.44 (0.04)	1.33 (0.47)
		Dwarf lemurs[4]	0.32 (0.15)	-	-	0.05 (0.05)
		Aye-aye	-	-	-	0.10 (0.10)
		Sportive lemurs[5]	-	-	-	0.03 (0.03)
		Mean (SE)	**1.93 (0.44)**	**1.17 (0.13)**	**0.67 (0.07)**	**1.69 (0.42)**
	Diurnal	Silky sifaka	0.10 (0.10)	-	-	-
		Mean (SE)	**0.10 (0.10)**			
	Cathemeral	White-fronted brown lemur	0.82 (0.12)	0.32 (0.28)	0.28 (0.10)	0.27 (0.13)
		Red-bellied lemur	0.03 (0.03)	-	-	0.12 (0.12)
		Red ruffed lemur[6]	0.03 (0.03)	0.03 (0.03)	0.01 (0.01)	-
		Mean (SE)	**0.88 (0.15)**	**0.35 (0.27)**	**0.29 (0.11)**	**0.38 (0.10)**
S05	Nocturnal	*Allocebus/Microcebus*[3]	-	0.19 (0.16)	0.20 (0.06)	0.51 (0.08)
		Eastern woolly lemur	-	0.58 (0.05)	0.50 (0.31)	0.94 (0.17)
		Dwarf lemurs[4]	-	0.11 (0.07)	-	0.30 (0.03)
		Western lesser bamboo lemur	-	-	-	0.02 (0.02)
		Sportive lemurs[5]	-	-	0.03 (0.03)	0.19 (0.06)
		Mean (SE)		**0.89 (0.07)**	**0.73 (0.39)**	**2.00 (0.29)**
	Diurnal	Indri[6]	-	1.19 (0.36)	0.23 (0.08)	0.16 (0.05)
		Mean (SE)		**1.19 (0.36)**	**0.23 (0.08)**	**0.16 (0.05)**
	Cathemeral	White-fronted brown lemur	-	0.49 (0.15)	0.19 (0.16)	1.00 (0.12)
		Black-and-white ruffed lemur[6]	-	0.06 (0.04)	-	0.04 (0.04)
		Mean (SE)		**0.54 (0.17)**	**0.19 (0.16)**	**1.04 (0.15)**

[1] Mean species-specific encounter rates were estimated as the average number of individuals of that species observed over the 3-4 surveyed line transects that year, divided by the total distance surveyed, dependent on that species activity pattern (i.e., nocturnal species are divided by the total distance surveyed during nocturnal surveys).
[2] Mean nocturnal, cathemeral and diurnal lemur encounter rate was estimated by determining the encounter rates of all species at a line transect and averaging over the 3-4 line transects surveyed that year.
[3] Due to the difficulty of noninvasively identifying hairy-eared dwarf lemur (*Allocebus trichotis*) and the three species of mouse lemur present in the Masoala-Makira landscape (*Microcebus macarthurii, M. mitttermeieri* and *M. sp. nova*), we combined all observations into an *Allocebus/Microcebus* category.
[4] There are potentially two species of dwarf lemur present in the Masoala-Makira landscape: Geoffroy's dwarf lemur (*Cheriogaleus major*) and furry-eared dwarf lemur (*C. crossleyi*).
[5] There are two species of sportive lemur present in the Masoala-Makira landscape: Scott's sportive lemur (*Lepilemur scottorum*) and Seal's sportive lemur (*L. seali*).
[6] Encounter rates for indri and red and black-and-white ruffed lemurs are underestimates due to no collection of lemur observations detected by sound.

Chapter 5

PROTECTING THE OASIS: FUTURE RESEARCH AND SUGGESTED CONSERVATION ACTIONS IN THE MASOALA-MAKIRA LANDSCAPE

Introduction

In the coming century, the global human population is projected to grow to 11 billion; as such, humankind will be entering uncharted territory in regards to providing for human needs and protecting the ecosystems on which we depend (Adams *et al.* 2004, Rands *et al.* 2010). Biodiversity hotspots such as Madagascar will see the highest amounts of population growth, increasing the needs for resources and the pressures on already threatened species (Williams 2012). The Masoala-Makira protected area complex, as the largest contiguous area of protected forest left in Madagascar, can be thought of as the last stronghold for threatened species in Madagascar (Cullman 2015). Unfortunately, the ills that threaten Madagascar's biodiversity are present in full form in the Masoala-Makira landscape. Continued deforestation and degradation of intact forests (Allnutt *et al.* 2013), high rates of bushmeat hunting and consumption (Golden 2009), and the increasing presence of exotic predators (Farris 2014) threaten the high species diversity present in the northeastern rainforests. My goal was to examine the effects of habitat degradation and the presence of exotic predators on lemurs, ground-dwelling forest birds and tenrecs, as well as to monitor their populations over a few years. The dataset that I used, collected using camera trapping and line transect sampling, spanned seven forest sites and six years and resulted in over 4,000 observations of 26 identifiable native birds species, 244 observations of three spiny tenrec species and over 1,000 observations of 12 identifiable lemur species. I summarize here my major findings and provide suggestions for future research and conservation/management actions.

Major Findings

Population responses to habitat degradation: Out of the 13 species we were able to estimate either occupancy or density for, seven had higher point estimates of occupancy or density in intact forests and only three had higher point estimates of occupancy or density in degraded forests. This suggests that lemurs, ground-dwelling forest birds and tenrecs might be found in lowered abundances in intermediately degraded and degraded forests. Although Farris (2014) found no responses of carnivore populations to habitat degradation, the potential lowered abundances of native lemur, bird and tenrec prey species at degraded forests might cause indirect negative effects on the populations of native carnivores at degraded forests.

Behavioral responses to habitat degradation and the presence of exotic species: Three out of seven ground-dwelling forest birds were detected less often at camera stations with high feral cat trap success. This suggests that feral cat presence might be negatively influencing their activity. This is not an isolated result. Gerber *et al.* (2012) found that the occupancy of ring-tailed vontsiras (*Galidia elegans*), a small native carnivore, decreased in the presence of feral cats, while Farris (2014) found that Malagasy civet (*Fossa fossana*) occupancy decreased in the presence of feral cats. Farris *et al.* (2014) found that mouse lemurs (*Microcebus spp.*) avoided feral cats in intact forests; together, these findings suggest that carnivores, lemurs and ground-dwelling forest birds show negative responses to the presence of feral cats.

In addition, Farris *et al.* (2015) found that the largest native predator, the fosa (*Cryptoprocta ferox*), went from strongly diurnal at intact forest site S02 to strongly nocturnal at degraded forest site S07. This change in time use between forest types was also found in my studies, with common tenrecs and cathemeral lemurs switched from diurnal to strongly nocturnal at degraded forests. This suggests that some characteristic of degraded forests—whether it is a higher abundance of exotic predators, higher vulnerability to those exotic predators, increased hunting pressure or decreased resources—is causing carnivores, tenrecs and lemurs to change their behavior.

<u>Annual trends at resurveyed sites:</u> At S02, out of 19 species that were monitored through the years (2008-2013), only four did not show consistent declines in either occupancy (ground-dwelling bird and tenrec) or encounter rate (lemur). These results are not limited to birds, tenrecs and lemurs. All six carnivore species detected at S02 also declined in occupancy probability from 2008 to 2013 (Farris, unpublished data). At S05, out of 17 species that were monitored through the years (2011-2013), only eight species did not show consistent declines in occupancy or encounter rate. Something is occurring at these resurveyed sites, whether maintained hunting pressure or increases in exotic predator presence, that might be causing these declines that we observed. In addition, lemur, ground-dwelling bird and tenrec parameter trends tended to drop in 2012 (cold-wet season), suggesting that the season wildlife surveys are conducted in might influence results.

Suggested Future Research and Conservation/Management Actions

We still know very little about the basic ecology of many species present in the Masoala-Makira landscape. Based on the declines we have observed for carnivores, lemurs, birds and tenrecs, resurveyed sites should continue to be monitored and the causes behind the declines in species' occupancy and encounter rates at these resurveyed sites should be determined. Establishing new sites for long-term monitoring will help us to determine if our observations at S02 and S05 are isolated events.

Expanding sites to include a wide range of habitat degradation, from pristine sites with very little disturbance to heavily degraded sites will provide more insight into the abilities of a variety of species to adapt to habitat disturbance. Other areas of interest would be closing the gaps regarding basic ecology—habitat use, diet, and activity patterns—of ground-dwelling birds, tenrecs and lemurs in the Masoala-Makira landscape. The interactions between exotic predators and ground-dwelling birds, tenrecs and lemurs should be investigated, as increased predation on native prey species might negatively influence native predator populations. However, based on the disturbing trends highlighted in my thesis, we cannot continue to simply gather knowledge without taking action. I suggest five actions that might help to mitigate the damages that habitat degradation, hunting pressure and exotic predator presence is causing in the Masoala-Makira landscape.

<u>Removing exotic predators from Masoala-Makira's forests:</u> The presence of feral cats had a negative effect on the occupancy probability of two native carnivores (ring-tailed vontsira and Malagasy civet), three ground-dwelling forest birds (red-breasted coua, scaly ground-roller and

Madagascar crested ibis), and mouse lemurs avoided areas with high feral cat presence in intact forest (Gerber *et al.* 2012, Farris 2014, Farris *et al.* 2014, Farris *et al.* 2015). Feral cat occupancy has only increased at our resurveyed intact forest site (S02), coinciding with a decline in carnivore, bird, tenrec and lemur occupancy and encounter rates (Farris, unpublished data). Programs that remove dogs, which are used to hunt native carnivores, tenrecs and lemurs, and feral cats from the forest, as well as trap-neuter-release programs to spay/neuter village cats, should be implemented (Farris 2014).

<u>Examining the possibility of agroforestry/reforestation initiatives:</u> Reforestation is a viable way of providing new habitat in areas that have suffered from deforestation, but would require local participation and compliance (Le *et al.* 2012). Agroforestry is also a viable way of integrating human and wildlife needs (Bhagwat *et al.* 2008, Estrada *et al.* 2012). While many of Masoala-Makira's species are incredibly sensitive to habitat disturbance, there are those that could be able to adapt to community-managed buffer zones and an agroforestry ecosystem. The red-breasted coua, Madagascar crested ibis, white-fronted brown lemur and common tenrec, among others, might be able to adapt to an agroforestry landscape. However, out of the 22 species we observed and monitored, 17 species are known to be hunted (IUCN 2014). Agroforestry/reforestation initiatives can only provide habitat to Masoala-Makira's species if this hunting pressure is lessened.

<u>Increasing access to family planning services and improving food security:</u> Slowing human population growth in the Masoala-Makira landscape is a key step in lessening the anthropogenic

pressures on its wildlife. Programs that emphasize the importance of family planning and the use of birth control are needed and should be included in conservation and research-based initiatives (Allen 2007, Harris *et al.* 2012, Mohan & Shellard 2014). If such population-growth focused initiatives are not politically palatable, then there needs to be a stronger focus on improving the efficiency of agricultural practices in Madagascar, so that the amount of land needed is reduced and the gap between potential and actual crop yield is closed (Bhagwat *et al.* 2008, Estrada *et al.* 2012, Laurance *et al.* 2014). Improving food security by providing education and training in agroforestry alternatives, agricultural techniques and livestock husbandry practices could lessen habitat loss, habitat degradation, and the hunting pressure on Masoala-Makira's wildlife (Brashares *et al.* 2004, Bhagwat *et al.* 2008, Doughty *et al.* 2014, Laurance *et al.* 2014).

<u>Emphasizing local participation:</u> There needs to be a focus on improving local education, integrating conservation/ecological knowledge into primary and secondary school curriculums, and allowing for alternative employment opportunities which could allow locals to improve their livelihoods in sustainable ways (Sekercioglu 2002, Brockington *et al.* 2006, Holmes 2007, Rao *et al.* 2010, Foerster *et al.* 2011, Pfeifer *et al.* 2012, Estrada 2013). Organizations that focus on research and conservation, and governing bodies that create and enforce environmental policies, must improve the participation of and the outreach efforts to the local community, as it is only with high local participation that there can be high local compliance (Brooks *et al.* 2012, Estrada 2013, Bennett & Dearden 2014). Without providing scientific training and mentorship to locals that will allow for local grassroots environmental movements to take root and flourish, any

conservation measures enacted by outside agents will more than likely be unsustainable without continued outside interference (Danielsen *et al.* 2014, Galabuzi *et al.* 2014).

Madagascar's government already requires that outside researchers mentor local graduate students through their own research projects; however, enforcement of this policy is lax, and communication between the international researchers and their mentees can be one-way and sparse. Lindsey Rich, a PhD student in Dr. Marcella Kelly's lab, is currently conducting research on the Botswanan carnivore community, and has started a pilot program with the goal of bringing local children out in the field and teaching them about conservation. Programs like this in Madagascar could be instrumental to incorporating locals into research and conservation activities, as well as educating them on the scientific process. Overall, the wishes and the issues that the local community feels needs to be addressed must take equal precedence to any research/conservation goals and objectives, if the participation and support of the local community is desired (Brooks *et al.* 2012, Bennett & Dearden 2014).

<u>Fundraising:</u> The most important step in protecting Masoala-Makira's biodiversity, however, is obtaining the funds and human capital to empower local conservation initiatives. Without international aid, conservationists and governmental bodies will be hard-pressed improve local livelihoods or implement any of these programs, as a majority of them, if not outright paid through organization funds, are heavily subsidized (Harris *et al.* 2012, Mohan & Shellard 2014). Increased collaboration between NGOs such as the Wildlife Conservation Society (WCS) and the World Wildlife Fund (WWF), resource sharing and targeted fundraising efforts might improve the ability for these organizations to make fundamental changes in Madagascar.

My thesis has found that several species seem to have higher abundances or presence in intact forest and that time use changes from intact to degraded forest; that the presence of exotic predators can have negative effect on species detection; and that at our resurveyed sites, wildlife populations are declining. Despite the need for more research, there is also an urgent need for immediate action in Masoala-Makira, addressing both the ecological and socioeconomic causes that are threatening wildlife. Ultimately, it is only by addressing and integrating the needs of the people living in Madagascar with that of its biodiversity that we can hope to conserve its unique ecology (Adams *et al.* 2004, Brockington *et al.* 2006, Brooks *et al.* 2012, Scales 2014).

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Appendix A.1. Research permit issued by the Government of Madagascar granting permission to conduct photographic and line-transect sampling across the Masoala-Makira landscape for the 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 0 2 AOUT 2010

AMPLIATIONS :

- CAFF/CORE
- DCAI
- DREF concernées
- CEF Maroantsetra
- MNP
- P.N Masoala
- NAP Makira
- Communes concernées

« Pour contrôle et suivi »

- DBA

« Pour le rapport »

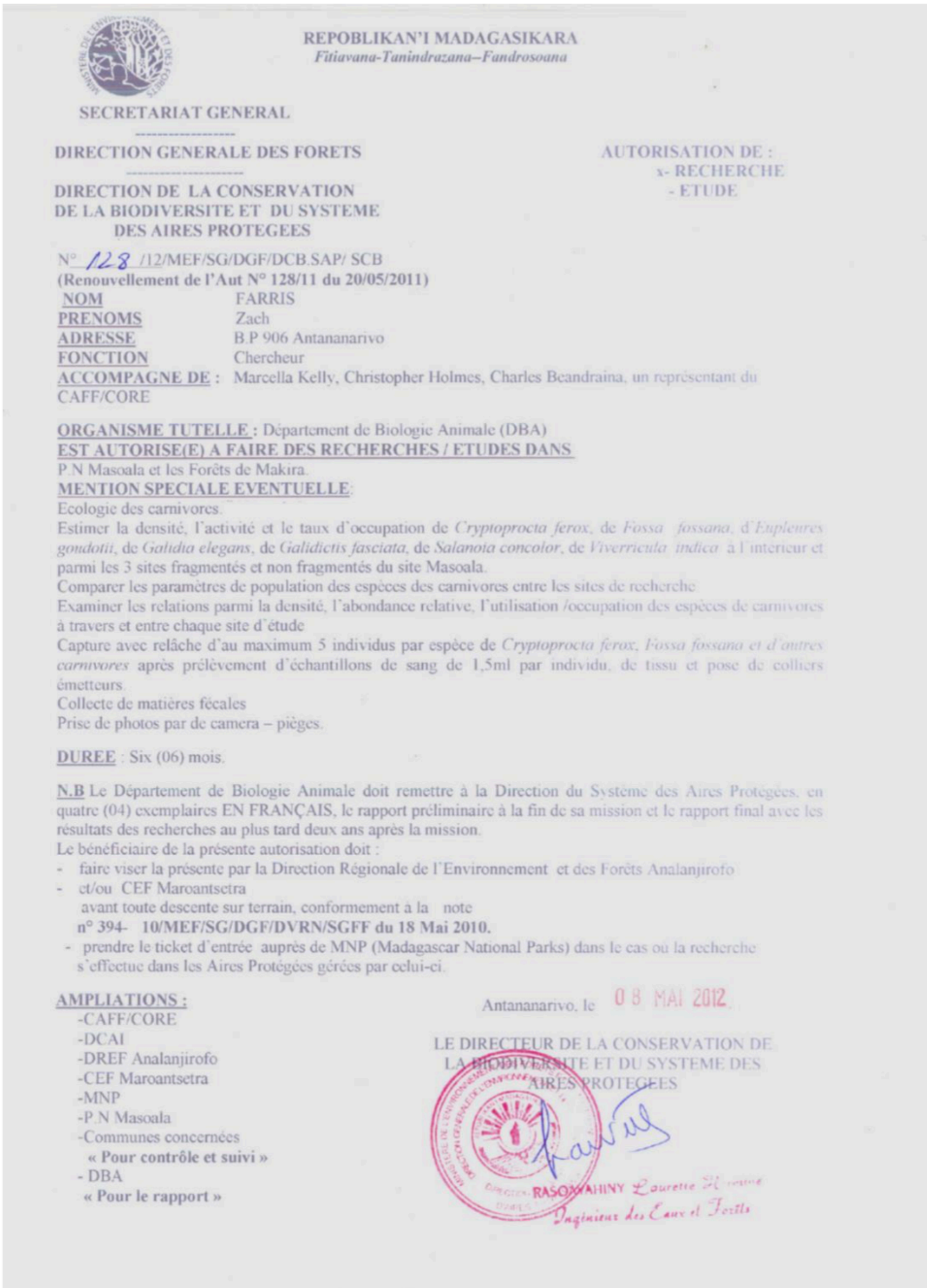
LE DIRECTEUR

DU SYSTEME D'AIRES PROTEGEES

RASOAVAHINY Laurette Hermine

Ingénieur des Eaux et Forêts

Appendix A.2. Research permit issued by the Government of Madagascar granting permission to conduct photographic and line-transect sampling across the Masoala-Makira landscape for the 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 ou la recherche s'effectue dans les Aires Protégées gérées par celui-ci.

Antananarivo, le 08 MAI 2012

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

RASOAVAHINY Laurette Hermine
Ingénieur des Eaux et Forêts

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

Appendix A.3. Research permit issued by the Government of Madagascar granting permission to conduct photographic and line-transect sampling across the Masoala-Makira landscape for the first half of the third field season (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 A.4. Research permit issued by the Government of Madagascar granting permission to conduct photographic and line-transect sampling across the Masoala-Makira landscape for the second half of the third field season (2013-2014).

MINISTERE DE L'ENVIRONNEMENT ET DES FORETS

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° 305/13/MEF/SG/DGF/DCB.SAP/ SCB
(Renouvellement de l'Aut N° 123/13 du 28/05/2013)

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

ACCOMPAGNE DE : Marcella Kelly, Christopher Holmes, 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 :
Parc National 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-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'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 13 DEC 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 A.5. Copy of Virginia Tech Institutional Animal Care and Use Committee approval issued to Sarah Karpanty, co-adviser to Asia Murphy and Zach Farris 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.

Invent the Future

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An equal opportunity, affirmative action institution

Appendix B.1. Survey details for the 15 photographic surveys across seven sites (camera trapping grids), including repeated surveys of three sites, ranked from least degraded (S01) to most degraded (S07) using a maximum-likelihood estimated (MLE) principal components analysis (PCA) of the landscape-level and station-level habitat data collected at each site. See Appendix B.2 for summary habitat information for each site. Photographic surveys occurred from 2008 to 2013 across the Masoala-Makira landscape, northeastern Madagascar.

Study Site (Survey Dates and Season)[1]	# of Camera Stations	Total # of Trap Nights	Elevation (m)
S01 (March – May 2009; HW)	20	989	1000-1400
S02 (September – November 2008; CW)	20	1315	350-706
S02 (September – November 2010; HD)	25	1230	
S02 (August – October 2011; CW)	24	1383	
S02 (July – October 2012; CW)	24	1536	
S02 (September – October 2013; CW)	24	1198	
S03 (August – October 2009; CW)	19	1067	380-550
S03 (January – February 2013; HD)	30	933	377-556
S03 (March – April 2013; HW)	25	678	453-580
S04 (June – August 2011; CW)	23	1462	21-385
S05 (March – May 2011; HW)	24	1509	308-796
S05 (June – July 2012; CW)	24	1015	
S05 (November 2013 – January 2014; HD)	24	1188	
S06 (November 2009 – January 2010; HD)	18	881	580-820
S07 (December 2010 – February 2011; HD)	24	1570	93-507

[1] Season survey was conducted: CW (cold-wet; June-September), HD (hot-dry; October-January) and HW (hot-wet; February-May).

Appendix B.2. Station-level[1] and landscape-level[2] habitat features (SE) for the seven sites in the Masoala-Makira landscape, northeastern Madagascar. Table modified and used with permission from Farris (2014).

Level	Study Site	S01	S02	S03[3]	S04	S05	S06	S07
Station	TreeDen (stems ≥ 5cm/ha)[4]	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)[5]	82 (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)[6]	16.97 (1.95)	12.50 (0.96)	7.48 (0.67)	10.55 (1.23)	12.89 (1.08)	--	9.75 (1.27)
	Percent Can Cover[7]	64.15 (5.58)	57.05 (4.89)	62.75 (3.17)	43.52 (6.82)	60.84 (4.09)	--	42.45 (5.14)
	Percent Understory Cover (0.0-2.0 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[8]	3	10	22	21	31	116	190
	Largest Patch Index[9]	60.38	52.33	44.88	51.30	39.90	43.72	50.36
	LSI[10]	1.04	1.34	2.12	1.95	2.02	3.11	6.76
	Percent Rainforest	99.94	98.89	94.48	95.19	96.87	96.06	81.07
	Percent Matrix[11]	0.05	0.66	4.38	0.59	0.76	0.19	4.07
	Tot. Core Rainforest (ha)[12]	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

[1] Station-level habitat = habitat measured around a camera station using three habitat transects centered around the camera station. [2] Landscape-level habitat was measured within a 500-m buffer around a camera trapping grid (study site) using satellite imagery and ERDAS Imagine and FRAGSTATS (see **Methods**— *Landscape-level and Station-Level Habitat Sampling*).
[3] Only habitat data from S03, 2009 survey is included in this table.
[4] TreeDen = tree density averaged across all camera stations (n = 18-25) for each study site; [5] BA = average basal area; [6] Can Ht = average canopy height; [7] Percent Can Cover = average percent canopy cover; [8] #Patches: total number of habitat patches (including rainforest, degraded forest, and matrix/cultivated) within the camera grid buffer; [9] Largest patch index: the percentage of total

landscape area comprised by the largest rainforest patch; [10] LSI: landscape shape index or the standardized measure of total edge adjusted for the size of the landscape; [11] Percent Matrix: percent matrix defined as non-forest land cover consisting of cultivation, open field, or early succession; [12] 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 B.3. Representative camera trap photographs of the seven forest bird species analyzed: (A) Madagascar crested ibis (*Lophotibis cristata*), (B) Madagascar turtle-dove (*Nesoenas picturatus*), (C) Madagascar magpie-robin (female on the left and male on the right; *Copsychus albospecularis*), (D) Madagascar wood-rail (*Mentocrex kioloides*), (E) Scaly ground-roller (*Geobiastes squamiger*), (F) Red-fronted coua (*Coua reynaudii*) and (G) Red-breasted coua (*Coua serriana*).

A) Madagascar crested ibis

B) Madagascar turtle-dove

C) Madagascar magpie-robin

D) Madagascar wood-rail

E) Scaly ground-roller

F) Red-fronted coua

Appendix B.3 continued from previous page.

G) Red-breasted coua

Appendix B.4A. Competing (ΔQAIC ≤ 2.0) landscape occupancy models from single-season occupancy analyses for seven native forest bird species across the Masoala-Makira landscape, northeastern Madagascar (2008-2013). Included is model weight (w_i) and likelihood, number of parameters included in the model (k), and the estimated over dispersion value (ĉ) from the goodness of fit (GOF) test run in program PRESENCE. Covariates with strongly supported relationships with occupancy (ψ) and/or detection (p), as determined by confidence intervals on normalized beta values that do not overlap zero, are denoted positive $^{(+)}$ /negative $^{(-)}$. Red-fronted coua models are not shown due to overdispersion.

Species	Model[1]	ΔQAIC	w_i	Likelihood	k	Deviance	ĉ
Madagascar magpie-robin	ψ(%rf$^{(+)}$ + smallcarnTS$^{(+)}$), p(survey + trailtype$^{(+)}$ + bpTS$^{(-)}$)	0.00	0.49	1.00	13	742.39	1.84
	ψ(%rf$^{(+)}$), p(survey + trailtype$^{(+)}$ + bpTS^{-})	0.88	0.32	0.64	12	747.68	
Red-breasted coua	ψ(totpatches + %rf $^{(-)}$+ smallcarnTS), p(survey + egTS$^{(+)}$ + fsTS^{-})	0.00	0.79	1.00	14	1055.78	1.05
Scaly ground-roller	ψ(ffTS + %rf), p(fsTS$^{(-)}$)	0.00	0.17	1.00	5	423.67	2.67
	ψ(ffTS), p(fsTS$^{(-)}$)	0.60	0.12	0.74	4	430.60	
	ψ(ffTS + %rf), p(fsTS$^{(-)}$ + smallcarnTS)	0.67	0.12	0.72	6	420.12	
	ψ(%rf),p(fsTS$^{(-)}$)	1.10	0.10	0.58	4	431.93	
	ψ(ffTS),p(.)	1.36	0.09	0.51	3	437.96	
Madagascar crested ibis	ψ(totpatches$^{(+)}$ + ffTS), p(fsTS$^{(-)}$ + ffTS$^{(+)}$)	0.00	0.90	1.00	6	344.22	1.08
Madagascar wood-rail	ψ(totpatches$^{(+)}$), p(survey + ffTS + season$^{(-)}$)	0.00	0.46	1.00	12	674.71	1.13
	ψ(totpatches$^{(+)}$ + ffTS), p(survey + ffTS + season$^{(-)}$)	0.58	0.34	0.75	13	673.10	
	ψ(totpatches$^{(+)}$), p(survey + ffTS + season$^{(-)}$ + smallcarnTS)	1.74	0.19	0.42	13	674.41	
Madagascar turtle-dove	ψ(%rf), p(egTS$^{(+)}$ + smallcarnTS$^{(+)}$ + ffTS)	0.00	0.39	1.00	6	829.41	1.70
	ψ(.), p(egTS$^{(+)}$ + smallcarnTS$^{(+)}$ + ffTS)	1.11	0.22	0.57	5	834.71	
	ψ(.), p(egTS$^{(+)}$ + smallcarnTS$^{(+)}$)	1.96	0.14	0.38	4	839.55	

[1] Description of covariates included in models: %rf = percent of landscape consisting of rainforest; smallcarnTS = combined trap success of three small endemic carnivores: ring-tailed (*Galidia elegans*), brown-tailed (*Salanoia concolor*) and broad-striped (*Galidictis fasciata*) vontsiras; survey = detection varies by survey occasion; trailtype = type of trail cameras were placed on, arranged by width (human = 1, game = 2, no trail = 3); bpTS = trap success of domestic livestock, zebu (*Bos primigenius*); distedge = distance

(km) from an individual camera station to the forest edge; totpatches = total number of rainforest, degraded, and matrix habitat patches within the camera trap grid buffer; egTS = trap success of an endemic, medium-sized carnivore, the falanouc (*Eupleres goudotii*); fsTS = trap success of the exotic *Felis spp.*; ffTS = trap success of an endemic, medium-sized carnivore, the spotted fanaloka (*Fossa fossana*); season = season camera trap survey occurred in (cold-wet = 1, hot-dry = 2, hot-wet = 3).

Appendix B.4B. Competing (ΔAIC ≤ 2.0) multi-season occupancy models from multi-season occupancy analyses for seven native forest bird species at S02 and S05 (2008-2013). Included are model weight (w_i), model likelihood, and number of parameters included in the model (k). Estimated parameters include occupancy (ψ), colonization (γ), extinction (ε), and detection (p). 'Year/survey' indicates parameter varied by survey occasion or year and 0/1 indicates parameter was fixed at that value. Red-fronted coua (S02 and S05), Madagascar turtle-dove (S02), Madagascar crested ibis and Madagascar wood-rail (S05) models are not shown due to estimated overdispersion (ĉ > 3.0) or model non-convergence.

Site	Species	Model	ΔAIC	w_i	Likelihood	k	Deviance
S02	Madagascar magpie-robin	ψ, γ(0), ε(.), p(survey)	0.00	0.79	1.00	41	347.52
	Red-breasted coua	ψ, γ(year), ε(year), p(year)	0.00	1.00	1.00	14	727.11
	Scaly ground-roller	ψ, γ(.), ε(.), p(year)	0.00	0.71	1.00	8	407.49
	Madagascar crested ibis	ψ, γ(.), ε(.), p(.)	0.00	0.60	1.00	4	491.89
	Madagascar wood-rail	ψ, γ(.), ε(.), p(survey)	0.00	0.64	1.00	41	513.68
		ψ, γ(.), ε(year), p(survey)	1.29	0.34	0.52	44	508.97
S05	Madagascar magpie-robin	ψ, γ(0), ε(.), p(.)	0.00	0.53	1.00	4	134.29
		ψ, γ(0), ε(year), p(.)	1.41	0.26	0.49	5	133.70
		ψ, γ(0), ε(.), p(year)	1.78	0.22	0.41	6	132.07
	Red-breasted coua	ψ, γ(.), ε(.), p(.)	0.00	0.37	1.00	4	409.21
		ψ, γ(.), ε(.), p(year)	0.83	0.24	0.66	6	406.04
		ψ, γ(year), ε(.), p(.)	0.88	0.24	0.64	5	408.09
		ψ, γ(.), ε(year), p(.)	1.86	0.15	0.40	5	409.07
	Scaly ground-roller	ψ, γ(.), ε(1), p(year)	0.00	0.43	1.00	6	156.66
		ψ, γ(.), ε(.), p(.)	0.09	0.41	0.96	4	160.75
		ψ, γ(year), ε(1), p(year)	1.86	0.17	0.39	7	156.52
	Madagascar turtle-dove	ψ, γ(.), ε(.), p(.)	0.00	0.38	1.00	4	267.58
		ψ, γ(.), ε(year), p(.)	1.00	0.23	0.61	5	266.58
		ψ, γ(.), ε(.), p(year)	1.17	0.21	0.56	6	264.75
		ψ, γ(year), ε(.), p(.)	1.66	0.17	0.44	5	267.24

Appendix B.4C. Competing (ΔQAIC $\leq$ 2.0) landscape occupancy models and yearly estimates of occupancy (ψ) and detection (p) from single-season occupancy analyses for three native forest bird species at S03 (2009 and 2013). Included is model weight (w_i), model likelihood, number of parameters included in the model (k), and the estimated ĉ from the goodness of fit (GOF) test run in program PRESENCE. Covariates with strongly supported relationships with occupancy (ψ) and/or detection (p), as determined by confidence intervals on normalized betas that did not overlap 1, are denoted positive $^{(+)}$ /negative $^{(-)}$. Madagascar magpie-robin and Madagascar turtle-dove models are not shown due to estimated overdispersion.

Species	Model[1]	ΔQAIC	w_i	Likelihood	k	Deviance	ĉ
Red-breasted coua	ψ(SHC$^{(-)}$), p(fsTS)	0.00	0.86	1.00	4	143.41	1.08
Scaly ground-roller	ψ(distedge), p(survey)	0.00	0.32	1.00	10	132.53	1.00
	ψ(distedge + fsTS), p(survey)	0.96	0.20	0.62	11	131.49	
	ψ(fsTS), p(survey)	1.26	0.17	0.53	10	133.79	
	ψ(.), p(survey)	1.33	0.17	0.51	9	135.86	
Madagascar wood-rail	ψ(cancov), p(.)	0.00	0.18	1.00	3	58.30	1.77
	ψ(cancov), p(humanTS$^{(-)}$)	0.41	0.14	0.81	4	55.48	
	ψ(humanTS), p(.)	0.72	0.12	0.70	3	59.58	
	ψ(.), p(humanTS$^{(-)}$)	1.11	0.10	0.57	3	60.26	

[1] Description of covariates included in models: SHC = station-level habitat characterization based on camera station location (a qualitative assessment; primary rainforest = 1, secondary forest = 2 and *savoka* (heavily degraded) = 3); fsTS = trap success of the exotic *Felis spp.*; cancov = percent canopy cover at the camera station; distedge = distance (km) from an individual camera station to the forest edge; survey = detection varies by survey occasion; humanTS = trap success of humans (excluding researchers).

Appendix C.1. Representative camera trap photographs of the three spiny tenrec species analyzed: A) common tenrec (*Tenrec ecaudatus*), B) lowland streaked tenrec (*Hemicentetes semispinosus*) and C) greater hedgehog tenrec (*Setifer setosus*). Photographs have been cropped and edited for better viewing.

A) Common tenrec   B) Lowland streaked tenrec   C) Greater hedgehog tenrec

Appendix C.2. Station-level[1] and landscape-level habitat[2] features (SE) for the seven sites in the Masoala-Makira landscape, northeastern Madagascar. Sites are coded from least degraded (S01) to most degraded (S07). Table modified and used with permission from Farris (2014).

Level	Study Site	S01	S02	S03[3]	S04	S05	S06	S07
Station	TreeDen (stems ≥ 5cm/ha)[4]	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)[5]	82 (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)[6]	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[7]	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[8]	3	10	22	21	31	116	190
	Largest Patch Index[9]	60.38	52.33	44.88	51.30	39.90	43.72	50.36
	LSI[10]	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[11]	0.05	0.66	4.38	0.59	0.76	0.19	4.07
	Tot Core Rainforest (ha)[12]	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

[1] Station-level habitat = habitat measured around a camera station using three habitat transects centered around the camera station. [2] Landscape-level habitat measured within a 500-m buffer around a camera trapping grid (site) using satellite imagery and ERDAS Imagine and Fragstats (see Methods—Landscape-level and Station-level Habitat Sampling).
[3] Only habitat data from S03's 2009 survey is included in this table.
[4] TreeDen = tree density averaged across all camera stations (n = 18-25) for each site; [5] BA = average basal area; [6] Can Ht = average canopy height; [7] % Can Cover = average percent canopy cover; [8] #Patches: total number of rainforest, degraded forest, and matrix patches within the camera grid buffer; [9] Largest patch index: the percentage of total landscape area comprised by the largest rainforest patch; [10] LSI: landscape shape index or the standardized measure of total edge adjusted for the size of the landscape; [11] %Matrix: percent matrix defined as non-forest land cover consisting of cultivation, open field, or early succession; [12] 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 C.3. Comparison of spiny tenrec trap success rates (TS; [number of individual captures/total survey trap nights]*100) in the eastern rainforests between studies conducted with different methods: invasive baited live/pitfall trapping and noninvasive unbaited camera trapping. Included is the region and forest type that the study was conducted in, the method of capture, total trap nights and which species (lowland streaked, greater hedgehog and common tenrec) were captured.

Study	Region/Forest Type	Method	Species Trapped[1]	Total Trap Nights (TN)	# of Spiny Tenrec Captures	TS
Andrianjakarivelo *et al.* (2005)	Northeastern rainforest	Baited live/pitfall traps	LS, GH	20,516	31	0.15
Goodman *et al.* (2000), Dammhahn *et al.* (2013)[2]	Eastern central rainforest	Baited live/pitfall traps and hand captures	LS, GH	5,200	9	0.17
Stephenson (1994a)	Eastern central rainforest and central plateau forest	Baited live/pitfall traps	C, GH	7,432	60	0.81
Stephenson (1995)	Northeastern rainforest	Baited live/pitfall traps	LS	5,280	1	0.02
This study	**Northeastern rainforest**	**Unbaited camera traps**	**LS, GH, C**	**16,431**	**244**	**1.49**

[1] Lowland streaked tenrec (LS), greater hedgehog tenrec (GH) and common tenrec (C).
[2] Number of spiny tenrec captures from Dammhahn *et al.* (2013) supplementary material (Table 1) and trap nights estimated from Goodman *et al.* (2000; 26 survey nights multiplied by a minimum of 100 live traps for two sites).

Appendix D.1. Survey details for the 420 lemur surveys conducted at six sites across the Masoala-Makira landscape (2010-2013). Included range of elevations that lemurs were observed, number of diurnal and nocturnal surveys conducted, total distance surveyed (km), number of species and individuals observed. Sites are ranked from least degraded (S01) to most degraded (S06) based on metrics in Appendix D.2 and as described in Farris (2014).

Study Site (Survey Dates)	Elevation (m)	# of Diurnal Surveys	# of Nocturnal Surveys	Total Distance Surveyed (km)	# of Species Detected	# of Lemur Observations
S01 (Mar – May 2011)	930-1219	15	15	60	9	263
S02 (Oct – Nov 2010)	326-616	17	17	68	7	126
S02 (Aug – Oct 2011)	354-718	17	16	66	4	57
S02 (Aug – Oct 2012)	225-641	24	23	94	4	59
S02 (Sept – Oct 2013)	389-618	30	19	85	7	87
S03 (Jun – July 2011)	454-885	15	15	60	4	31
S04 (Jun – Aug 2011)	27-692	18	18	72	3	108
S05 (Mar – May 2011)	329-809	18	18	72	6	114
S05 (Jun – July 2012)	381-708	14	15	58	5	39
S05 (Nov – Dec 2013)	354-809	41	25	128	8	241
S06 (Jan – Feb 2011)	355-483	15	15	60	4	47

Appendix D.2. Station-level[1] and landscape-level[2] habitat features (SE) for the six forest sites in the Masoala-Makira landscape, northeastern Madagascar. Sites are organized from least degraded (S01) to most (S06). Table modified and used with permission from Farris (2014).

Level	Study Site	S01	S02	S03	S04	S05	S06
Station	TreeDen (stems ≥ 5cm/ha)[3]	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)[4]	82 (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)[5]	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[6]	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[7]	3	10	22	21	31	190
	Largest Patch Index[8]	60.38	52.33	44.88	51.30	39.90	50.36
	LSI[9]	1.04	1.34	2.12	1.95	2.02	6.76
	%Rainforest	99.94	98.89	94.48	95.19	96.87	81.07
	%Matrix[10]	0.05	0.66	4.38	0.59	0.76	4.07
	Tot Core Rainforest (ha)[11]	0.88	0.99	0.85	0.87	1.14	0.59
	Tot Edge (m per ha)	0.03	0.59	1.85	1.53	2.13	7.89
	Avg. Dist. to Village (km)	10.96	2.80	3.33	2.08	4.82	1.45
	Avg. Dist. to Edge (km)	1.14	0.68	0.29	0.36	0.34	0.18

[1] Station-level = habitat measured around a camera station using three habitat transects centered around the camera station. [2] Landscape-level measured within a 500-m buffer around a camera trapping grid (study site) using satellite imagery and ERDAS Imagine and Fragstats (see Methods—Landscape-level and Station-level Habitat Sampling).
[3] TreeDen = tree density averaged across all camera stations (n = 18-25) for each study site; [4] BA = average basal area; [5] Can Ht = average canopy height; [6] % Can Cover = average percent canopy cover; [7] #Patches: total number of rainforest, degraded forest, and matrix patches within the camera grid buffer; [8] Largest patch index: the percentage of total landscape area comprised by the largest rainforest patch; [9] LSI: landscape shape index or the standardized measure of total edge adjusted for the size of the landscape; [10] %Matrix: percent matrix defined as non-forest land cover consisting of cultivation, open field, or early succession; [11] 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.