

Estimating Encounter Rates and Densities of Three Lemur Species in Northeastern Madagascar



Asia J. Murphy¹ · Zach J. Farris¹ ·
Sarah Karpanty¹ · Felix Ratelolahy² ·
Marcella J. Kelly¹

Received: 30 November 2015 / Accepted: 15 April 2016 / Published online: 21 May 2016
© Springer Science+Business Media New York 2016

Abstract Primate populations, including Madagascar’s lemurs, are threatened worldwide and conservationists need accurate population estimates to develop targeted conservation plans. We sought to fill knowledge gaps for three lemur taxa—white-fronted brown lemur (*Eulemur albifrons*); eastern woolly lemur (*Avahi laniger*); and *Allocebus/Microcebus*, a category combining observations of hairy-eared dwarf lemurs (*Allocebus trichotis*) and mouse lemurs (*Microcebus* spp.)—in northeastern Madagascar by estimating their density, examining how their encounter rates and densities vary across three different forest types, and monitoring trends in encounter rates and densities at resurveyed sites, using data from surveys at six forest sites over a 4-year period (2010–2013). Landscape density for white-fronted brown lemur, eastern woolly lemur, and *Allocebus/Microcebus* was 21.5 (SE 3.67), 57.7 (SE 9.17), and 39.1 (SE 9.55) individuals/km², respectively. There was no difference in density estimates at intact and intermediately degraded forest sites; however, we encountered white-fronted brown lemurs more often in intact forest ($1.64 \pm \text{SE } 0.40$ individuals/km) than in intermediately degraded and degraded forest ($0.15 \pm \text{SE } 0.06$ and $0.16 \pm \text{SE } 0.06$ individuals/km). In addition, we encountered white-fronted brown lemurs at lower rates in 2013 ($0.15 \pm \text{SE } 0.06$ individuals/km) compared to 2010 ($0.82 \pm \text{SE } 0.12$ individuals/km) at a resurveyed site. Our findings emphasize that primate researchers must account for variation in how lemur encounter rates and densities differ between intact

Electronic supplementary material The online version of this article (doi:10.1007/s10764-016-9906-0) contains supplementary material, which is available to authorized users.

✉ Asia J. Murphy
asia7@vt.edu

¹ Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24060, USA

² Wildlife Conservation Society Madagascar Program, Antananarivo, Madagascar

and degraded forests, and although we observed a decline in white-fronted brown lemur encounter rate at our resurveyed site, we caution that changes in lemur encounter rates may simply reflect lower detection rates rather than lower density. Future research should focus on using conventional distance sampling techniques, which are infrequently used in primate studies, to provide more robust density estimates as a way to accurately assess trends and the effects of anthropogenic pressures on lemur populations.

Keywords Distance sampling · Habitat degradation · Primate · Rainforest

Introduction

Worldwide, primate populations are highly threatened, with habitat loss and degradation presenting a major risk (Schipper *et al.* 2008). Habitat loss reduces habitat availability, while habitat degradation increases the vulnerability of primate species to further anthropogenic pressures (Brooks *et al.* 2002; Fahrig 2003), such as hunting (Laurance and Useche 2009; Peres 2001). Madagascar is a global conservation priority due to intense anthropogenic pressures threatening its endemic taxa, including numerous lemur species (Mittermeier *et al.* 2010; Myers *et al.* 2000). Lemurs are important as seed dispersers (Razafindratsima *et al.* 2014), pollinators (Kress *et al.* 1994), predictors of non-primate mammalian species diversity (Muldoon and Goodman 2015), prey to many endemic predators (Goodman 2004; Karpanty 2006), and flagships for Madagascar's endemic biodiversity (Dolins *et al.* 2010). Although low levels of habitat disturbance can be beneficial for lemurs by increasing forest productivity (Ganzhorn 1995), higher levels can be detrimental to lemur populations (Ganzhorn *et al.* 1997) and species richness (Irwin *et al.* 2010). Lemur species that are large-bodied (Irwin and Raharison 2009) or dietary/habitat specialists (Borgerson 2015) tend to be especially sensitive to habitat degradation, with folivores and omnivores tolerating higher levels of habitat degradation (Ganzhorn *et al.* 1997; Lehman *et al.* 2006a).

Lemur extinction risk is especially high in Madagascar's largest protected forest region, the Makira–Masoala landscape (Schwitzer *et al.* 2014), in part owing to increasing habitat degradation (Rakotondratsimba *et al.* 2008). There has been little primate research conducted in the area (Farris *et al.* 2014; Rakotondratsimba *et al.* 2008; Rasolofoson *et al.* 2007, 2014) although there are at least 10 threatened lemur species present in the Makira–Masoala lemur community (IUCN 2015; Mittermeier *et al.* 2010; Rasolofoson *et al.* 2007). In the face of continued habitat degradation in the region, we need an examination of how lemur abundance and detectability vary across a habitat loss and degradation gradient in the Makira–Masoala landscape.

We sought to fill knowledge gaps in lemur ecology in Makira–Masoala by estimating lemur population density and examining how lemur encounter rates and densities vary across a habitat degradation gradient. The conservation and management of threatened species depend on accurate estimates of population abundance and density (Plumptre and Cox 2006) and researchers have used distance sampling (Buckland 1985) to estimate the population density of many species (Araldi *et al.* 2014; Meyler *et al.* 2012; Rivera-Milán *et al.* 2015). This sampling method avoids biased abundance and/or density estimates by explicitly accounting for the decline in observers' ability to

detect animals as the distance to the animal from the observer/transect increases (Whitesides *et al.* 1988), providing more robust density estimates than other methods that assume all animals are detected or detected at the same rate despite distance of animal to observer/transect (Kun-Rodrigues *et al.* 2014). Such robust lemur density estimates—which the Makira–Masoala landscape lacks—are very important in the establishment of baseline information for future population monitoring and to examine species response to habitat degradation (Plumptre and Cox 2006).

We focused on the eastern woolly lemur (*Avahi laniger*, a nocturnal folivore), white-fronted brown lemur (*Eulemur albifrons*, a cathemeral frugivore), and a category combining hairy-eared dwarf lemur (*Allocebus trichotis*) and mouse lemur (*Microcebus* spp., nocturnal omnivores) observations, as we observed these species most often during surveys. Our objectives were to provide the first robust density estimates for these three taxa in the Makira–Masoala landscape and to examine how lemur encounter rates and densities vary across a habitat degradation gradient. We hypothesized that there would be no differences in encounter rates and densities of eastern woolly lemur and *Allocebus/Microcebus* across a habitat degradation gradient because folivores and omnivores tend to tolerate habitat degradation (Ganzhorn *et al.* 1997; Lehman *et al.* 2006a). In contrast, we hypothesized that encounter rate and density of white-fronted brown lemurs (frugivores) would respond to habitat degradation and be highest at intact forest sites. Our final objective was to monitor lemur encounter rates and densities at two sites that were resurveyed annually from 2010 to 2013.

Methods

Study Area and Lemur Surveys

Located in northeastern Madagascar, the Makira–Masoala landscape is the largest contiguous area of protected forest in Madagascar (6124 km², excluding community-managed zones; Fig. 1a). We surveyed lemur populations with line transects at six sites, concurrent with a camera trapping study focused on carnivores (Farris *et al.* 2015); investigating carnivore–lemur interactions was the primary goal of the overall study and guided line transect placement (Farris *et al.* 2014). At each site we placed three to four line transects—ranging from 1.0 to 2.0 km in length—on human (0.5–2.0 m wide) and game (<0.5 m wide) trails to ensure adequate carnivore and lemur observations (Fig. 1b). We placed transects on trails because carnivores tend to be detected at higher rates on trails (Cusack *et al.* 2015). We selected trails that covered a wide range of trail types, habitat characteristics, and landscape features. We placed 83% of the line transects on human trails and the remaining 17% on game/newly cut trails. Based on camera trapping data, 58% of line transects had low rates of human activity, i.e., 0–10 human detections on camera traps over a 2-month period; 16% had moderate levels of human activity, i.e., 11–50 human detections; and 27% had high levels of human activity, i.e., >50 human detections. We placed 52% of line transects on ridges, 32% on slopes, and 16% in valleys. Finally, we placed 57% of line transects in secondary forest microhabitat, 38% in primary forest microhabitat, and 16% in highly degraded (*savoka*) microhabitat.

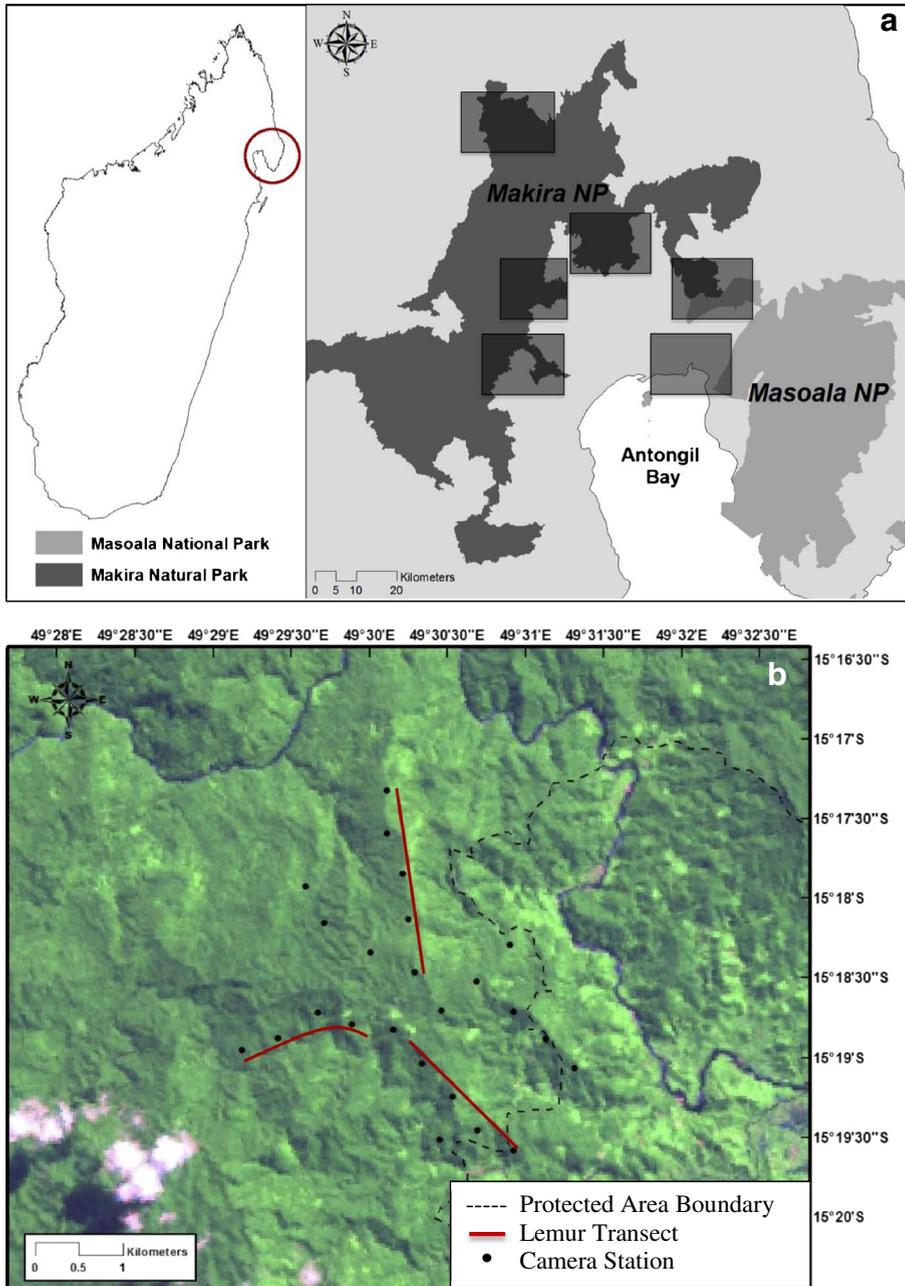


Fig. 1 Map of (a) Makira Natural Park and Masoala National Park (Makira–Masoaala protected area complex) in northeastern Madagascar and (b) an example of how a surveyed site integrated camera trap locations (dots) and line transects (lines) to examine lemur–carnivore interactions (Farris *et al.* 2014; satellite imagery from Wildlife Conservation Society Madagascar program). We surveyed six sites (S01–S05, S07), designated by rectangles on map, in the region for lemurs using line transects from 2010 to 2013. We cannot show exact locations of site because of the sensitivity of hunting data used in related publications.

We conducted diurnal (06:30–12:00 h) and nocturnal (17:30–22:00 h) lemur surveys on each transect. Local experts trained observers in lemur species identification and the second author trained observers in the lemur survey protocol. We retrained observers in survey protocol before surveys were conducted at each site and at least one observer per survey had previously conducted lemur surveys in the region. The number of observers conducting surveys ranged from one to five, with the mode being three. During surveys, the observer(s) walked slowly (<1 km/h) along transects; observers changed transects and survey partners between each line transect survey to reduce observational biases (Buckland *et al.* 2001). We conducted lemur surveys only during hours when there was no rainfall. We removed observations that were collected during the same transect survey and were <500 m apart unless we could differentiate between groups to avoid double counting individuals from mobile/fast-moving species, e.g., white-fronted brown lemur.

When a lemur was visually detected, we recorded observation date and time, species, group size, sighting distance from observer to group center (m), and compass bearing from transect line to lemur(s) to compute perpendicular distances to the transect line. We determined group center by rapidly assessing the location of individuals on the periphery, visually determining group spread, and then pinpointing the center. We determined sighting distance visually because of vegetation thickness and terrain ruggedness. During nocturnal surveys, we located and then identified lemurs based on appearance, eye shine characteristics, and movement using multiple high-lumen headlamps. We lumped all observations on *Microcebus* and *Allocebus* into one *Allocebus/Microcebus* category owing to the difficulty of accurately distinguishing between the three mouse lemur species (*M. macarthurii*, *M. mittermeieri*, and *Microcebus* sp. nova; Mittermeier *et al.* 2010; Radespiel *et al.* 2008) and the hairy-eared dwarf lemur known to occur in this region (Mittermeier *et al.* 2010).

From 2010 to 2013, we conducted a total of 420 lemur surveys (224 diurnal and 196 nocturnal) at six sites and walked 823 km. In addition to observing eastern woolly lemurs, white-fronted brown lemurs, and *Allocebus/Microcebus*, we observed eight other lemur species —*Daubentonia madagascariensis*, *Eulemur rubriventer*, *Haplemur occidentalis*, *Indri indri*, *Lepilemur seali*, *Propithecus candidus*, *Varecia rubra*, and *V. variegata subcincta*— and one lemur genus (*Cheirogaleus* spp.; Electronic Supplementary Material [ESM] Appendix 1; IUCN 2015; Mittermeier *et al.* 2010). We surveyed the lemur populations of four sites (S01, S03, S04, and S07) once and two sites (S02 and S05) annually beginning in 2010 and 2011, respectively, until 2013. Because of the repeat surveys, data from S02 and S05 made up 70% of our total lemur surveys ($N = 294$ lemur surveys). As a result, we included only the first survey from the resurveyed sites (2010 for S02 and 2011 for S05) in our landscape and habitat degradation analyses to prevent biases. For these analyses, we included 196 surveys (98 diurnal and 98 nocturnal) from the six forest sites (Table I). To examine annual trends in lemur encounter rate and density, we analyzed data collected from the annual resurveys of S02 and S05 (Table II).

Site Ranking Based on Habitat Degradation

We ranked our sites from least to most degraded using a maximum likelihood estimated (MLE) principle components analysis (PCA) of landscape-level and microhabitat-level

Table 1 Details of lemur surveys conducted at six out of seven forest sites across the Makira–Masoala protected area complex, northeastern Madagascar (2010–2013)

	Study site (survey dates)	Diurnal	Nocturnal	Total no. of surveys	Distance surveyed (km)	No. of species	No. of individuals
Intact	S01 (Mar–May 2011)	15	15	30	60	9	263
	S02 (Oct–Nov 2010)	17	17	34	68	7	126
	Total	32	32	64	128	10	389
Intermediate	S03 (June–July 2011)	15	15	30	60	3	20
	S04 (June–Aug 2011)	18	18	36	72	3	95
	S05 (Mar–May 2011)	18	18	36	72	5	55
	Total	51	51	102	204	5	170
Degraded	S07 (Jan–Feb 2011)	15	15	30	60	4	47
	Total	15	15	30	60	4	47
	Total	98	98	196	392	10	606

Out of 420 lemur surveys, 196 surveys were used in landscape and habitat degradation analyses. Included is the number of diurnal and nocturnal surveys conducted, total number of surveys conducted, total distance surveyed (km), number of lemur species, and total individuals observed. Sites are ranked from least (S01) to most (S07) degraded as quantified in Farris *et al.* (2015) and described in ESM Appendices 2 and 3

Table II Details of initial surveys and resurveys of lemur populations at intact forest site S02 and intermediate forest site S05 in the Makira–Masoala protected area complex, northeastern Madagascar (2010–2013)

Study site	Survey dates	Diurnal	Nocturnal	Total no. of surveys	Distance surveyed (km)	No. of species	No. of individuals
S02	Oct–Nov 2010	17	17	34	68	7	126
	Aug–Oct 2011	17	16	33	66	4	57
	Aug–Oct 2012	24	23	47	94	3	58
	Sept–Oct 2013	30	19	49	85	7	78
	Total	88	75	163	313	9	319
S05	Mar–May 2011	18	18	36	72	5	55
	June–July 2012	14	15	29	58	4	31
	Nov–Dec 2013	41	25	66	128	8	233
	Total	73	58	131	258	8	319

Included is the number of diurnal and nocturnal surveys conducted, total number of surveys conducted, total distance surveyed (km), number of lemur species, and total individuals observed

data collected during concurrent camera trap surveys (ESM Appendices 2 and 3; Farris *et al.* 2015). Landscape-level and microhabitat-level data included, for example, percent primary rainforest cover at the site, tree density, and percent understory (ESM Appendix 2; Farris 2014). We ranked sites from least degraded (S01) to most degraded (S07) based on eigenvectors and resulting PCA biplots (ESM Appendix 3; Farris, 2014). We then visually assessed the similarities among sites using the PCA biplots and grouped them into three categories: intact (S01 and S02), intermediately degraded (hereafter, intermediate; S03, S04, and S05), and degraded (S06 and S07; ESM Appendix 3). We did not sample the lemur community at S06 because of lack of funds and transportation so our data on the lemur community at degraded forest sites come from S07. We use site codes to protect the identities of local villages near our sites, owing to the sensitivity of hunting data used in related publications.

Estimating Encounter Rates Across the Landscape and at Three Forest Types

We estimated landscape encounter rates—the number of individuals divided by the distance (km) surveyed—for each species. We included observations with no collected sighting distance/compass bearing ($N = 7$). When the true number of individuals was unknown for an observation, we assumed one individual was observed. When the number of individuals observed was a range, e.g., four or five individuals, we took the minimum number of individuals observed, e.g., four individuals. The distance surveyed for each species depended on when we assumed that species would be active; i.e., nocturnal species were divided by the total distance surveyed during nocturnal surveys only. We determined when species would be active based on the literature, i.e., nocturnal, diurnal, and cathemeral (Mittermeier *et al.* 2010). For cathemeral species, we separated observations based on whether they were collected during diurnal or nocturnal surveys. We then estimated mean encounter rates for nocturnal/diurnal surveys for each species and determined if they were different by examining 95% confidence intervals (CIs). If there was no evidence of a difference, i.e., 95% CIs overlapping, we estimated landscape encounter rates by dividing the sum of individuals of the observed species by total distance surveyed for all (nocturnal and diurnal) surveys. If there was evidence of a difference, we estimated landscape encounter rates using the total distance surveyed for the type of survey (nocturnal or diurnal) with the majority of observations.

In addition to estimating landscape encounter rates, we estimated mean encounter rates for each forest type to examine how mean lemur encounter rate varied across a habitat degradation gradient by determining encounter rates for each transect surveyed and then calculating the mean of these for each forest type (intact = six transects at two sites, intermediate = nine transects at three sites, and degraded = three transects at one site). Differences in mean encounter rate among forest types were based on 95% CIs, i.e., no difference if 95% CIs overlapped.

Estimating Density Across the Landscape and at Two Forest Types

We estimated density for eastern woolly lemurs, white-fronted brown lemurs, and *Allocebus/Microcebus* using the conventional distance sampling (CDS) engine in Distance (v. 6.2; Buckland *et al.* 2001; Thomas *et al.* 2010). We discarded all

observations that had no recorded sighting distances or compass bearings ($N = 7$). We entered observations with unknown group size as -1 , which would indicate to Distance to ignore that observation when estimating expected cluster (group) size via size-biased regression. For white-fronted brown lemurs, we examined whether detection probability and effective strip width (m) differed between nocturnal and diurnal surveys; these parameters did not differ (ESM Appendix 4), so we pooled all observations regardless of when they were collected. We calculated total line transect length (km) in Distance as the transect length (km) multiplied by the number of nocturnal surveys conducted on that transect for the eastern woolly lemur and *Allocebus/Microcebus*. We determined total line transect length for each white-fronted brown lemur observation collected during lemur surveys using the number of diurnal or nocturnal surveys conducted on the transect depending on when the observation was collected. To estimate landscape density for the three lemurs, we included observations from S07 ($N = 47$). However, we did not include observations for S07 when estimating lemur density across forest types because of high imprecision in density estimates at the degraded forest site; thus, we show density estimates only for intact and intermediate forest types.

We fit key functions, e.g., half-normal, hazard rate, and uniform, with manually selected series adjustments, e.g., cosine, simple polynomial, and hermite polynomial, to the untruncated and unbinned data during an exploratory stage. Key functions describe the shape of the diminishing detection probability as distance to the observed animal increases; we did not include the negative-exponential key function based on recommendations from Buckland *et al.* (2001). Based on histograms, we determined whether and where to right-truncate data and how to bin observations into discrete distance classes to improve key function fit. We then compared models with the three key functions and their respective series adjustments using Akaike's Information Criteria corrected for small sample sizes (AIC_c ; Akaike 1973). We discarded models that did not pass ($P \leq 0.05$) the goodness-of-fit (GOF) tests and used estimates from our top model, as model averaging made estimates less precise (Buckland *et al.* 2001; Thomas *et al.* 2010).

We stratified observations by forest type (intact or intermediate) when examining how lemur densities varied across a habitat degradation gradient; we did not stratify observations by forest type for our landscape density estimates. While estimating lemur density at intact and intermediate forest sites, in addition to comparing among the three key functions and series adjustments, we compared two types of models: global models that assumed detection probability and cluster size did not differ between intact and intermediate forest sites, and strata-specific models that assumed detection probability and cluster size did differ between forest types. Both model types estimated strata-specific and global density, with global density equaling the mean of stratum density weighed by that stratum's total survey effort (Thomas *et al.* 2010). When 95% CIs for strata-specific density estimates did not overlap, we considered this evidence for a difference in density between the two forest types.

Annual Encounter Rates at Resurveyed Sites

We conducted repeated surveys of one intact (S02; 2010–2013) and one intermediate (S05; 2011–2013) site. We surveyed S02 consistently during the months of September and October from 2010 to 2013; we surveyed S05 in different seasons each year

(March–May in 2011, June–July in 2012, and November–January in 2013; Table II). We used the same locations and lengths for line transects each year, with the addition of one new transect at each site and increased effort in 2013. We were unable to estimate density for each surveyed year because of low sample sizes, so we examined trends in mean encounter rates for eastern woolly lemur, white-fronted brown lemur, and *Allocebus/Microcebus*. We do not include annual trends in lemur encounter rate at S05 in the main text because any changes could be due to seasonal differences in lemur activity (ESM Appendix 5; Atsalis 1999; Lehman 2006). We used 95% CIs to determine whether there was evidence for a difference in encounter rates over time.

Ethical Note

The Madagascar Ministry of the Environment and Forests (permit nos. 128/11, 128/12, 123/12, and 305/13), the Wildlife Conservation Society Madagascar Program, and Antongil Conservation approved our lemur surveys. Line transects were noninvasive and no protected species were sampled (IACUC #13-100-FWC). This research complied with the International Primatological Society Code of Best Practices for Field Primatology.

Results

We found that eastern woolly lemurs had the highest encounter rate (0.90 individuals/km) and the highest density ($57.7 \pm \text{SE } 9.17$ individuals/km²) across the landscape (Fig. 2a and Table III). *Allocebus/Microcebus* had the lowest landscape encounter rate (0.47 individuals/km) and white-fronted brown lemurs had the lowest landscape density ($21.5 \pm \text{SE } 3.67$ individuals/km²). The top model for each taxon used the hazard rate-cosine key function-series expansion adjustment combination (Table IV).

There were no differences in mean eastern woolly lemur and *Allocebus/Microcebus* encounter rates at intact, intermediate, and degraded forest types (Fig. 2b), while mean white-fronted brown lemur encounter rate was higher at intact forest sites ($1.64 \pm \text{SE } 0.40$ individuals/km) than at intermediate and degraded forest types ($0.15 \pm \text{SE } 0.06$ and $0.16 \pm \text{SE } 0.06$ individuals/km, respectively; Fig. 2b). There were no differences in densities of *Allocebus/Microcebus*, eastern woolly lemur, and white-fronted brown lemur at intact and intermediate forest sites (Fig. 2a and Table IV). All three taxa had a different key function-series expansion adjustment combination in their top model, but the top model for all three taxa assumed that detection probability and cluster size did not differ between intact and intermediate forest (a “global” model; Table IV).

There were no differences in mean eastern woolly lemur and *Allocebus/Microcebus* encounter rates at S02 between 2010 and 2013. In contrast, mean white-fronted brown lemur encounter rate was higher in 2010 ($0.82 \pm \text{SE } 0.12$ individuals/km) than in 2013 ($0.15 \pm \text{SE } 0.06$ individuals/km; Fig. 3).

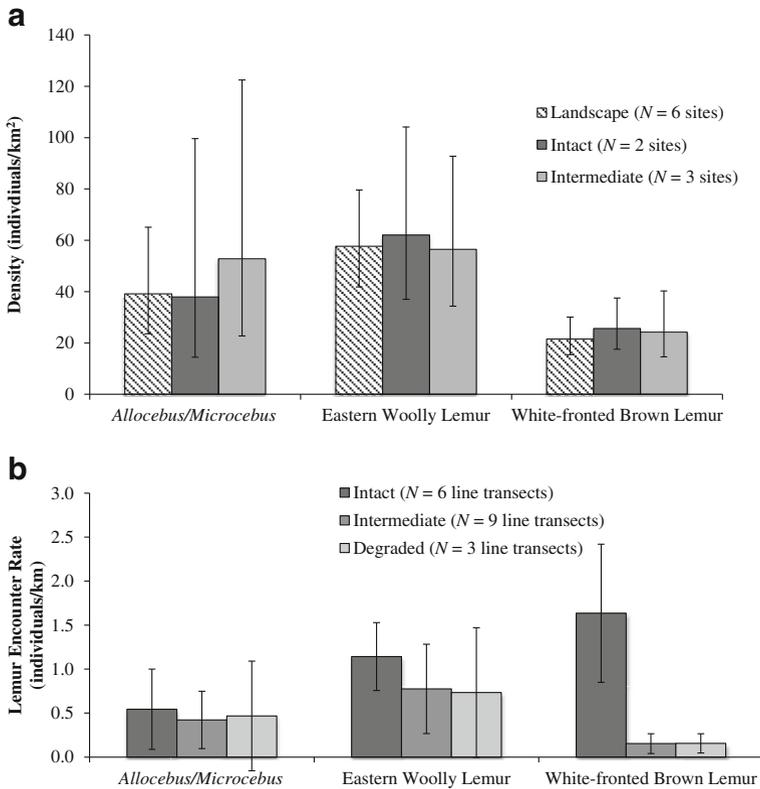


Fig. 2 Estimates of **(a)** density for *Allocebus/Microcebus*, eastern woolly lemur (*Avahi laniger*), and white-fronted brown lemur (*Eulemur albifrons*) across the landscape and at intact and intermediate forests and **(b)** mean encounter rates for *Allocebus/Microcebus*, eastern woolly lemur, and white-fronted brown lemur in intact, intermediate, and degraded forest. We conducted surveys at six forest sites in the Makira–Masoala landscape in northeastern Madagascar from 2010 to 2013. Error bars represent 95% confidence intervals.

Discussion

There were no differences in eastern woolly lemur and *Allocebus/Microcebus* mean encounter rates at intact, intermediate, and degraded forest sites, while white-fronted brown lemurs were encountered more often at intact forest sites. In addition, the white-fronted brown lemur encounter rate was lower in 2013 than in 2010 at our resurveyed intact forest site S02. Although we found differences in encounter rates, there were no differences in density estimates for all three taxa at intact and intermediate forest sites, emphasizing the need for researchers to examine trends in both encounter rates and density when determining how anthropogenic pressures influence lemur populations.

A number of our line transects occurred on rarely frequented human trails that ran along ridges in secondary forest. Distance sampling theory suggests using randomly placed transects that cover a variety habitats (Thomas *et al.* 2010), but very few studies have compared how lemur density is affected by aspects of study design such as transect characteristics. Lehman (2006) found that differences in habitat characteristics between human trails and surrounding forest might underestimate the presence of

Table III Comparisons of the number of individuals observed, landscape encounter rate (individuals/km), and mean encounter rate (SE) by forest type (intact, intermediate, and degraded) for the two lemur species and the *Allocebus/Microcebus* lemur category that were observed most often during our surveys at six forest sites across the Makira–Masoala landscape (2010–2013)

Common name (scientific name)	IUCN ^a	Activity	Diet	No. of individuals	Landscape encounter rate ^b	Mean encounter rate (SE) ^c by forest type	
						Intact	Degraded
<i>Allocebus/Microcebus</i> ^d	Vu/En	Nocturnal	Omnivore	92	0.47	0.54 (0.23)	0.42 (0.17)
Eastern woolly lemur (<i>Avahi langier</i>)	Vu	Nocturnal	Folivore	176	0.90	1.14 (0.20)	0.78 (0.26)
White-fronted brown lemur (<i>Eulemur albifrons</i>)	En	Cathemeral	Frugivore	244	0.62	1.64 (0.40)	0.15 (0.06)

Included is IUCN status (IUCN 2015), activity pattern, and dietary preference as determined by Mittermeier *et al.* (2010).

^a IUCN status: Vu = vulnerable; En = endangered.

^b Landscape encounter rate is 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.

^c Mean encounter rate by forest type is the mean encounter rate for that species over all line transects surveyed in intact ($N = 6$ line transects across two sites), intermediate ($N = 9$ line transects across 3 sites), and degraded ($N = 3$ line transects across 1 site) forest.

^d All observations that could be the three mouse lemur species present in Makira–Masoala (*Microcebus macarthurii*, *M. mittermeieri*, and *Microcebus* sp. nova) or the hairy-eared dwarf lemur (*Allocebus trichotis*) were combined

Table IV Competing ($\Delta AIC_c \leq 2.0$) landscape and habitat degradation density models from the program Distance for *Allocebus/Microcebus*, eastern woolly lemur, and white-fronted brown lemur across the Makira–Masoala landscape, northeastern Madagascar (2010–2013)

Analysis	Species	Key function—series expansion adjustment ^a	k	ΔAIC_c	CV	Detection (SE)	ESW (m; SE)	Mean cluster size (SE)
Landscape	<i>Allocebus/Microcebus</i>	Uniform rate—simple polynomial	1	0.00	0.24	0.44 (0.02)	6.65 (0.35)	1.30 (0.08)
	Eastern woolly lemur	Hazard rate—cosine	2	0.00	0.16	0.54 (0.04)	8.15 (0.61)	1.55 (0.08)
	White-fronted brown lemur	Hazard rate—cosine	2	0.00	0.17	0.50 (0.06)	10.1 (1.09)	4.20 (0.44)
Habitat ^b	<i>Allocebus/Microcebus</i>	Half-normal rate—cosine	1	1.06	0.17			
		Global uniform rate—cosine	1	0.00	0.26	IT: 0.51 (0.04) IM: 0.50 (0.03)	IT: 6.09 (0.46) IM: 6.00 (0.33)	IT: 1.32 (0.17) IM: 1.19 (0.07)
		Global half-normal rate—cosine	1	1.47	0.28			
	Eastern woolly lemur	Strata-specific uniform rate—cosine	2	1.94	0.26			
		Global hazard rate—cosine	2	1.99	0.27			
		Global hazard rate—simple polynomial	2	0.00	0.17	IT: 0.61 (0.06) IM: 0.55 (0.06)	IT: 9.16 (0.88) IM: 8.30 (0.90)	IT: 1.65 (0.16) IM: 1.44 (0.10)
		Strata-specific hazard rate—cosine	4	0.86	0.17			
White-fronted brown lemur	Global hazard rate—cosine	2	0.00	0.19	IT: 0.51 (0.08) IM: 0.57 (0.15)	IT: 10.3 (1.51) IM: 11.3 (2.98)	IT: 4.81 (0.57) IM: 2.75 (0.35)	
	Global half-normal rate—cosine	1	0.48	0.18				
	Global uniform rate—cosine	1	0.75	0.16				
		Strata-specific hazard rate—cosine	4	1.13	0.20			

Included is the key function-series expansion adjustment, estimated coefficient of variation (CV), detection probability, effective strip width (ESW), and mean cluster size. For the habitat degradation analyses, estimates are given for intact (IT) and intermediate (IM) forest type.

^a Key function: Global is when the detection function is fit to all observations, regardless of whether they were from intact or intermediate forest; strata-specific is when the detection function is fit to observations separately for each forest type, i.e., intact or intermediate forest.

^b Detection probabilities, effective strip width, and mean cluster size estimates for habitat degradation models come from the top strata-specific model

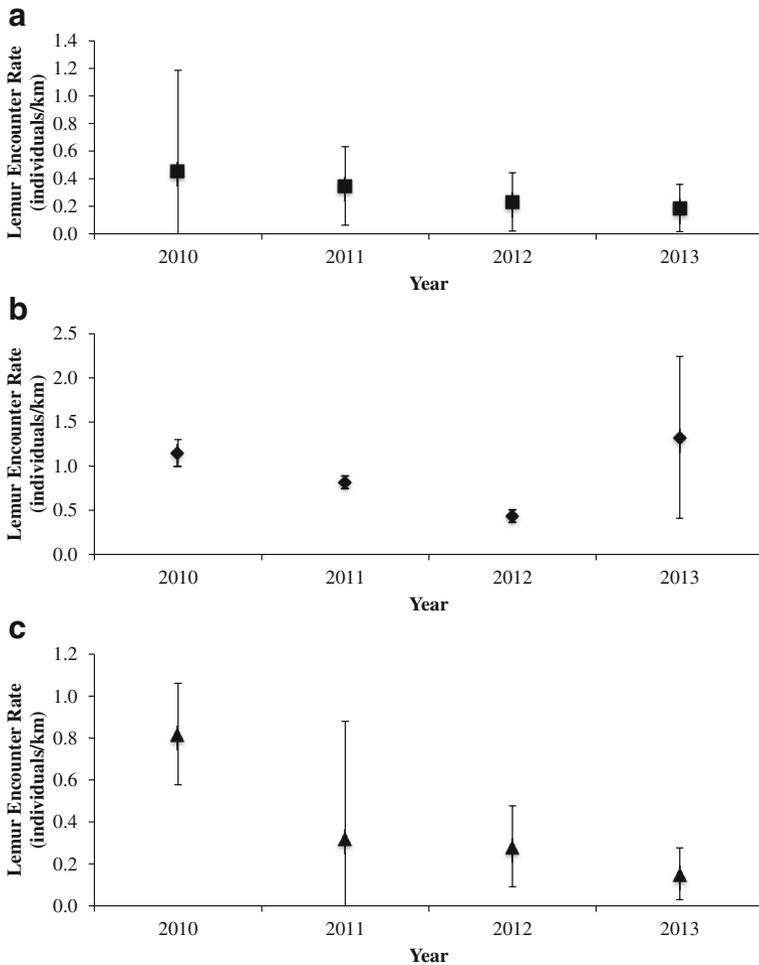


Fig. 3 Annual trends in mean encounter rate of (a) *Allocebus/Microcebus*, (b) eastern woolly lemur, and (c) white-fronted brown lemur at resurveyed site S02 (2010–2013) in the Makira–Masoala landscape, northeastern Madagascar. Error bars represent 95% confidence intervals.

habitat specialists and naturally uncommon species. In other cases, hunting pressures on existing trails can influence primate density estimates (Tagg and Willie 2013). We might have underestimated true lemur encounter rate and density by placing our line transects on trails owing to potential differences in habitat characteristics and hunting pressure between trails and surrounding forest.

In addition, our survey effort was not equal among forest types, resulting in more observations from intermediate forest sites ($N = 3$ sites and 9 transects) than intact ($N = 2$ sites and 6 transects) and degraded ($N = 1$ site and 3 transects) forest sites. Our unequal survey effort might have influenced our results in regard to degraded forest sites. As a result of the unbalanced survey effort and ongoing threats to Makira–Masoala’s lemur community (Golden 2009; Rasolofoson *et al.* 2014), we emphasize the need for additional surveys

that are dispersed equally across a gradient of anthropogenic pressure, ranging from primary, intact core forest with little to no hunting to highly degraded and exploited forest sites.

Landscape Encounter Rates and Densities

We provide important density estimates for eastern woolly lemurs in Makira–Masoala; our density estimates are similar to other estimates from other parts of their range (IUCN 2015), although eastern woolly lemurs in Makira–Masoala might exist at lower densities than in east-central Madagascar (Ganzhorn 1988). We also provide density estimates for the three newly described mouse lemur species and the hairy-eared dwarf lemur in Makira–Masoala, although our estimates should be interpreted cautiously owing to our inability to distinguish between the two genera. Rakotondratsima and Kremen (2001) found that white-fronted brown lemur density in Masoala National Park was 14.5 (SE 1.1) individuals/km² in undisturbed forest and 15.9 (SE 2.2) individuals/km² in disturbed forest. These estimates are similar to ours; however, whereas we used Distance to explicitly model how detection probability is affected by distance from animal to observer/transect, Rakotondratsima and Kremen (2001) did not. Thus, Rakotondratsima and Kremen (2001) might have underestimated white-fronted brown lemur density in Masoala National Park. As the white-fronted brown lemur is listed as Endangered (IUCN 2015) and is limited to northeastern Madagascar (Mittermeier *et al.* 2010), using Distance to provide more robust density estimates for Masoala National Park could provide researchers with a more comprehensive picture of global white-fronted brown lemur population size.

Encounter Rates and Density Across a Habitat Degradation Gradient

Lemur response to habitat degradation can vary based on many factors, including dietary preferences (Herrera *et al.* 2011; Lehman *et al.* 2006b). In general, folivores and omnivores tend to be tolerant to many measures of habitat degradation (Lehman *et al.* 2006b), while frugivores are more sensitive to habitat disturbance (Borgerson 2015; Lehman *et al.* 2006b). We found no differences in eastern woolly lemur (folivorous) and *Allocebus/Microcebus* (omnivorous) encounter rates and densities in the different forest types. Eastern woolly lemurs are not particularly sensitive to habitat disturbance (Lehman *et al.* 2006a), but there is some evidence that they prefer intact forests (Herrera *et al.* 2011). Hairy-eared dwarf lemurs and mouse lemurs also appear to tolerate some habitat disturbance (Schütz and Goodman 1998). Although there was no difference in white-fronted brown lemur density at intact and intermediate forest sites, we encountered white-fronted brown lemurs (frugivorous) less often at intermediate and degraded forest sites compared to intact forest sites. This suggests that while white-fronted brown lemur populations are able to tolerate some habitat disturbance (Borgerson 2015; Campera *et al.* 2014), there might be ecological characteristics or anthropogenic pressures at more disturbed forest sites that lower their detectability. Overall, our results

corroborate the results of studies from other regions of Madagascar in regard to how eastern woolly lemurs, white-fronted brown lemurs, and hairy-eared dwarf lemurs/mouse lemurs respond to habitat degradation.

Encounter Rates over Time

White-fronted brown lemur encounter rate decreased at S02 between the first and last surveys. Our four years of sampling are likely not long enough to detect true changes in white-fronted brown lemur populations (Charnov and Berrigan 1993; Erhart and Overdorff 2008). However, this decline in white-fronted brown lemur encounter rate—despite the fixed location of our line transects and increases in survey effort throughout the years—suggests that there have been changes at S02 that are influencing our ability to detect lemurs. This might be an increase in human presence (Tagg and Willie 2013) or changes in habitat characteristics (Lehman 2006) at this site. Increased survey effort at this site is needed to provide annual density estimates and determine how changes in habitat characteristics and human use patterns affect lemur abundance and detectability.

Implications and Future Research

Although the Makira–Masoala landscape is the largest protected area complex in Madagascar, the lemur community appears to be threatened by habitat degradation (Rasolofson *et al.* 2014), overexploitation (Golden 2009), and potentially the presence of exotic predators (Farris *et al.* 2014). Our research has provided the first robust density estimates of two lemur species and one lemur category in Makira–Masoala, and shown that although habitat degradation can influence lemur encounter rate, it might not influence their density, at least as quantified during the course of this study from 2010 to 2013. Based on the richness and extinction risk of Makira–Masoala’s lemur community (Schwitzer *et al.* 2014), and the lack of research in the region, we suggest that more targeted lemur surveys on and off trails in a variety of habitats be conducted in the area to provide robust baseline density estimates of other threatened lemur species and to examine how the lemur community as a whole is affected by habitat degradation.

Acknowledgments This research was funded by the National Science Foundation (grant no. DGE 0822220), Sigma Xi, Cleveland Metroparks Zoo, European Association for Zoos and Aquaria, Idea Wild, National Geographic Society-Waits grant #W96-10, People’s Trust for Endangered Species, Virginia Tech Chapter of Sigma Xi, Virginia Tech, and Wildlife Conservation Society Madagascar Program (WCS-MP). We thank Dean Stauffer and Steig Johnson for all the advice they provided. We thank our Malagasy field assistants B. L. Donah, Marka’Helin, R. Wilson, B. J. R. Rasolofoniaina, E. J. G. Anjaraniaina, Didice, and Augustain; numerous Malagasy collaborators; and our many field volunteers and data entry volunteers. We thank WCS-MP, especially Christopher Holmes, and Antongil Conservation for logistical aid and the Madagascar Government and Madagascar National Parks (MNP) for permitting this project. We appreciate the comments of two anonymous reviewers and the editor-in-chief, which greatly improved this contribution.

This material is based on work supported by the National Science Foundation Graduate Research Fellowship. Any opinion, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

References

- Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In B. N. Petran & F. Csaki (Eds.), *Second International Symposium on Information Theory* (pp. 267–281). Budapest: Akadémiai Kiadó.
- Araldi, A., Barelli, C., Hodges, K., & Rovero, F. (2014). Density estimation of the endangered Udzungwa red colobus (*Procolobus gordonorum*) and other arboreal primates in the Udzungwa Mountains using systematic distance sampling. *International Journal of Primatology*, *35*(5), 941–956.
- Atsalis, S. (1999). Seasonal fluctuations in body fat and activity levels in a rain-forest species of mouse lemur, *Microcebus rufus*. *International Journal of Primatology*, *20*(6), 884–910.
- Borgerson, C. (2015). The effects of illegal hunting and habitat on two sympatric endangered primates. *International Journal of Primatology*, *36*, 74–93.
- Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A., Rylands, A. B., Konstant, W. R., et al. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, *16*(4), 909–923.
- Buckland, S. T. (1985). Perpendicular distance models for line transect sampling. *Biometrics*, *41*(1), 177–195.
- Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). *Introduction to distance sampling: Estimating abundance of biological populations*. Oxford: Oxford University Press.
- Campera, M., Serra, V., Balestri, M., Barresi, M., Ravaolahy, M., Randriatafika, F., et al. (2014). Effects of habitat quality and seasonality on ranging patterns of collared brown lemur (*Eulemur collaris*) in littoral forest fragments. *International Journal of Primatology*, *35*, 957–975.
- Chamov, E. L., & Berrigan, D. (1993). Why do female primates have such long lifespans and so few babies? Or life in the slow lane. *Evolutionary Anthropology*, *1*, 191–194.
- Cusack, J. J., Dickman, A. J., Rowcliffe, J. M., Carbone, C., Macdonald, D. W., & Coulson, T. (2015). Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. *PLoS ONE*, *10*(5), e0126373.
- Dolins, F. L., Jolly, A., Rasamimanana, H., Ratsimbazafy, J., Feistner, A. T., & Ravoavy, F. (2010). Conservation education in Madagascar: Three case studies in the biologically diverse island-continent. *American Journal of Primatology*, *72*(5), 391–406.
- Erhart, E. M., & Overdorff, D. J. (2008). Population demography and social structure changes in *Eulemur fulvus rufus* from 1988 to 2003. *American Journal of Physical Anthropology*, *136*(2), 183–193.
- Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 487–515.
- Farris, Z. J. (2014). *Response of Madagascar's endemic carnivores to fragmentation, hunting, and exotic carnivores across the Masoala-Makira landscape*. PhD dissertation, Virginia Polytechnic Institute and State University.
- Farris, Z. J., Karpanty, S. M., Ratelolahy, F., & Kelly, M. J. (2014). Predator–primate distribution, activity, and co-occurrence in relation to habitat and human activity across fragmented and contiguous forests in northeastern Madagascar. *International Journal of Primatology*, *35*(5), 859–880.
- Farris, Z. J., Golden, C. D., Karpanty, S., Murphy, A., Stauffer, D., Ratelolahy, F., et al. (2015). Hunting, exotic carnivores, and habitat loss: anthropogenic effects on a native carnivore community, Madagascar. *PLoS ONE*, *10*(9), e0136456.
- Ganzhorn, J. U. (1988). Food partitioning among Malagasy primates. *Oecologia*, *75*, 436–450.
- Ganzhorn, J. U. (1995). Low-level disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology*, *76*(7), 2084–2096.
- Ganzhorn, J. U., Malcomber, S., Andrianantoanina, O., & Goodman, S. M. (1997). Habitat characteristics and lemur species richness in Madagascar. *Biotropica*, *29*(3), 331–343.
- Golden, C. D. (2009). Bushmeat hunting and use in the Makira Forest, north-eastern Madagascar: a conservation and livelihoods issue. *Oryx*, *43*(3), 386.
- Goodman, S. M. (2004). Predation on lemurs. In S. M. Goodman & J. P. Benstead (Eds.), *The natural history of Madagascar* (pp. 1221–1228). Chicago: The University of Chicago Press.
- Herrera, J. P., Wright, P. C., Lauterbur, E., Ratovonjanahary, L., & Taylor, L. L. (2011). The effects of habitat disturbance on lemurs at Ranomafana National Park, Madagascar. *International Journal of Primatology*, *32*, 1091–1108.
- Irwin, M. T., & Raharison, J. L. (2009). Ecosystem in decay: factors influencing primate species extinctions in forest fragments of Tsinjoarivo, Madagascar. *American Journal of Physical Anthropology*, 155–155.

- Irwin, M. T., Wright, P. C., Birkinshaw, C., Fisher, B. L., Gardner, C. J., Glos, J., et al. (2010). Patterns of species change in anthropogenically disturbed forests of Madagascar. *Biological Conservation*, *143*(10), 2351–2362.
- IUCN. (2015). The IUCN red list of threatened species version 2015.4. Version 2015.4. Retrieved March 24, 2016 from <http://www.iucnredlist.org>.
- Karpanty, S. M. (2006). Direct and indirect impacts of raptor predation on lemurs in southeastern Madagascar. *International Journal of Primatology*, *27*(1), 239–261.
- Kress, W. J., Schatz, G. E., Andrianifahanana, M., & Morland, H. S. (1994). Pollination of *Ravenala madagascariensis* (Strelitziaceae) by lemurs in Madagascar: evidence for an archaic coevolutionary system? *American Journal of Botany*, *81*(5), 542–551.
- Kun-Rodrigues, C., Salmons, J., Besolo, A., Rasolondraibe, E., Rabarivola, C., Marques, T. A., et al. (2014). New density estimates of a threatened sifaka species (*Propithecus coquereli*) in Ankarafantsika National Park. *American Journal of Primatology*, *76*(6), 515–528.
- Laurance, W. F., & Uuseche, D. C. (2009). Environmental synergisms and extinctions of tropical species. *Conservation Biology*, *23*(6), 1427–1437.
- Lehman, S. M. (2006). Effects of transect selection and seasonality on lemur density estimates in southeastern Madagascar. *International Journal of Primatology*, *27*(4), 1041–1057.
- Lehman, S. M., Rajaonson, A., & Day, S. (2006a). Edge effects and their influence on lemur density and distribution in southeast Madagascar. *American Journal of Physical Anthropology*, *129*, 232–241.
- Lehman, S. M., Rajaonson, A., & Day, S. (2006b). Lemur responses to edge effects in the Vohibola III classified forest, Madagascar. *American Journal of Primatology*, *68*(3), 293–299.
- Meyler, S. V., Salmons, J., Ibouroy, M. T., Besolo, A., Rasolondraibe, E., Radespiel, U., et al. (2012). Density estimates of two endangered nocturnal lemur species from northern Madagascar: new results and a comparison of commonly used methods. *American Journal of Primatology*, *74*(5), 414–422.
- Mittermeier, R. A., Louis, E. E., Richardson, M., Schwitzer, C., Langrand, O., Rylands, A. B., et al. (2010). *Lemurs of Madagascar*, 3rd ed. Conservation International.
- Muldoon, K. M., & Goodman, S. M. (2015). Primates as predictors of mammal community diversity in the forest ecosystems of Madagascar. *PLoS ONE*, *10*(9), e0136787.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*, 853–858.
- Peres, C. A. (2001). Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conservation Biology*, *15*(6), 1490–1505.
- Plumptre, A. J., & Cox, D. (2006). Counting primates for conservation: primate surveys in Uganda. *Primates*, *47*(1), 65–73.
- Radespiel, U., Olivieri, G., Rasolofson, D. W., Rakotondratsimba, G., Rakotonirainy, O., Rasoloharijaona, S., et al. (2008). Exceptional diversity of mouse lemurs (*Microcebus* spp.) in the Makira region with the description of one new species. *American Journal of Primatology*, *70*(11), 1033–1046.
- Rakotondratsima, M., & Kremen, C. (2001). Suivi écologique de deux espèces de lémuriens diurnes *Varecia variegata rubra* et *Eulemur fulvus albifrons* dans la presqu'île de Masoala (1993 – 1998). *Lemur News*, *6*, 31–35.
- Rakotondratsimba, G., Rasolofson, D. W., Rakotonirainy, O., Ratsimbazafy, J., Rakotozafy, L., Rasolofoharivelo, T., et al. (2008). Les principaux facteurs menaçant les lémuriens de l'aire protégée de Makira. *Lemur News*, *13*, 32–37.
- Rasolofson, D. W., Rakotondratsimba, G., Rakotonirainy, O., Rasolofoharivelo, T., Rakotozafy, L., Ratsimbazafy, J., et al. (2007). Le bloc forestier de Makira charnière de lémuriens. *Lemur News*, *12*, 49–53.
- Rasolofson, D. W., Rakotonirainy, O., Rasolofoharivelo, T., Andrianandrasana, H., Rakotondratsimba, G., Ralisoamalala, R., et al. (2014). Prédiction de la distribution des espèces de lémuriens du Parc Naturel Makira face aux changements climatiques, implication pour la conservation. *Lemur News*, *18*, 48–52.
- Razafindratsima, O. H., Jones, T. A., & Dunham, A. E. (2014). Patterns of movement and seed dispersal by three lemur species. *American Journal of Primatology*, *76*, 84–96.
- Rivera-Milán, F. F., Bertuol, P., Simal, F., & Rusk, B. L. (2015). Distance sampling survey and abundance estimation of the critically endangered Grenada Dove (*Leptotila wellsi*). *The Condor*, *117*(1), 87–93.
- Schipper, J., Chanson, J. S., Chiozza, F., Cox, N. A., Hoffmann, M., Katariya, V., et al. (2008). The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science*, *322*(5899), 225–230.
- Schütz, H., & Goodman, S. M. (1998). Photographic evidence of *Allocebus trichotis* in the Réserve Spéciale d'Anjanaharibe-Sud. *Lemur News*, *3*, 22–23.

- Schwitzer, C., Mittermeier, R. A., Johnson, S. E., Donati, G., Irwin, M., Peacock, H., et al. (2014). Averting lemur extinctions amid Madagascar's political crisis. *Science*, *343*, 842–843.
- Tagg, N., & Willie, J. (2013). The influence of transect use by local people and reuse of transects for repeated surveys on nesting in western lowland gorillas (*Gorilla gorilla gorilla*) and central chimpanzees (*Pan troglodytes troglodytes*) in southeast Cameroon. *International Journal of Primatology*, *34*(3), 554–570.
- Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., et al. (2010). Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, *47*(1), 5–14.
- Whitesides, G. H., Oates, J. F., Green, S. M., & Kluberanz, R. P. (1988). Estimating primate densities from transects in a west African rainforest: a comparison of techniques. *Journal of Animal Ecology*, *57*(2), 345–367.