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Forest type influences population densities of nocturnal lemurs in Manompana, north-eastern Madagascar

Abstract

Forest loss, fragmentation and anthropization threaten the survival of forest species all over the world. Shifting agriculture is one of these threatening processes in Madagascar. However, when its cycle is halted and the land is left to regenerate, the resulting growth of secondary forest may provide a viable habitat for folivorous and omnivorous lemur species. We aimed to identify the response of nocturnal lemurs to different successional stages of regenerating secondary forest, degraded mature and mature forest across a mosaic-type landscape. We surveyed four nocturnal lemur species (*Avahi laniger*, *Microcebus* cf. *simmonsi*, *Allocebus trichotis* and *Daubentonia madagascariensis*) in four forest types of varying habitat disturbance in north-eastern Madagascar. We estimated densities in mature and regenerating secondary forest for the eastern woolly lemur (*Avahi laniger*) and mouse lemur (*Microcebus* cf. *simmonsi*), two sympatric species with folivorous and omnivorous diets respectively. We did not estimate densities of *Allocebus trichotis* and *Daubentonia madagascariensis* due to small sample size, however, we observed both species exclusively in mature forest. We found higher population densities of *Avahi laniger* and *Microcebus* cf. *simmonsi* in secondary than in mature forest showing the potential of regenerating secondary forest for lemur conservation. Several environmental factors influenced the detectability of the two lemur species. While observer and habitat type influenced detection of the eastern woolly lemur, canopy height and vine density influenced detection of mouse lemurs. Understanding how different species with different diets interact with anthropogenically impacted habitat will aid future management decisions for the conservation of primate species.

Keywords: Anthropogenic disturbance, Mouse lemur, Eastern woolly lemur, Folivory, Omnivory, Regenerating secondary forest

Introduction

The world's forests are being rapidly depleted for timber harvest and agricultural land (Evans 2009; FAO 2011; Lambin *et al.* 2003). These unprecedented deforestation rates participate in widespread loss of biodiversity throughout forests worldwide (Brooks *et al.* 2002; de Almeida-Rocha *et al.* 2017; Mace *et al.* 2005; Sodhi *et al.* 2004). As a result of these anthropogenic influences, most tropical landscapes are matrices of mature forest remnants, agricultural land and regenerating secondary forests of varying ages (Achard *et al.* 2002; FAO 2011; Hansen and DeFries 2004; Laurance 2004; Skole and Tucker 1993; Wright 2005). As agriculture is one of the significant drivers of biodiversity decline, it is important we manage agricultural systems in ways that allow threatened species to persist within them (Maxwell 2016). Some primates exhibit tolerance and adaptability to anthropogenic landscapes (Eppley *et al.* 2015; Estrada 2006; Johns 1986), while others remain dependent on forest habitat for survival (Chapman *et al.* 2006; Schwitzer *et al.* 2011), and species responses to similar threat processes can vary (Irwin *et al.* 2010; Isaac and Cowlishaw 2004). Thus it is important that we increase our understanding of plant and animal responses to habitat disturbance, so as to not generalize responses from a few indicator species (Barlow *et al.* 2007).

Madagascar is considered a world biodiversity “hotspot” (Myers *et al.* 2000) and among its threatened forest-dwelling species, lemurs are considered to be one of the world's most endangered mammals due to habitat loss, fragmentation and environmental degradation (Green and Sussman 1990; Harper *et al.* 2007; IUCN 2014; Schwitzer *et al.* 2013; Schwitzer *et al.* 2014). The transition from mature forest (old-growth forest) to regenerating forest (i.e., younger and older growth secondary forest), that results from shifting agriculture is deeply

rooted in Madagascar's culture (Styger *et al.* 2007), and involves the development of secondary thickets after cleared land is abandoned (Lowry *et al.* 1997; Randriamalala *et al.* 2015). Very few studies have investigated the responses of lemurs to regenerating secondary forest after complete land-clearance (Ganzhorn and Schmid 1998; Ramanamanjato and Ganzhorn 2001; Schwitzer *et al.* 2007; Simmen *et al.* 2007), with the majority focusing on persistence in exotic plantations, forest fragments, and degraded forests following natural disturbances and anthropogenic disturbances such as selective logging or cyclones (Dunham *et al.* 2011; Ganzhorn 1987; Ganzhorn 1995; Ganzhorn *et al.* 2003; Herrera *et al.* 2011; Lewis and Rakotondranaivo 2011). Older growth secondary forests are particularly under-investigated but may be crucial for the persistence of forest-dwelling species in human-altered tropical landscapes (Chazdon *et al.* 2009). Thus, there is a need to broaden our focus from the remaining mature old-growth forests to include human-altered environments, such as regenerating secondary vegetation (Chazdon *et al.* 2009; Hobbs *et al.* 2006).

The responses of lemurs to human-induced habitat changes vary from population decline to species proliferation in regenerating secondary forests or forest-agriculture mosaics (Eppley *et al.* 2015; Herrera *et al.* 2011; Lehman *et al.* 2006a; Schwitzer *et al.* 2011). It is, therefore, important to investigate these responses (e.g. through population density estimates) across several species to identify macro-biogeographical and local ecological drivers of inter- and intraspecific variability in response to habitat (Setash *et al.* 2017). Low-intensity selective logging or low-intensity bush-fallow agriculture can open up a habitat allowing increased levels of light penetration, which may have a positive effect on forest productivity and/or increased leaf quality (Ganzhorn 1995; Ganzhorn *et al.* 1997; Oates 1996; Onderdonk and Chapman 2000; Skorupa 1986). Nocturnal lemurs are often largely tolerant of disturbed habitat, but diet can be a determining factor in their success (Lehman *et al.* 2006a; Lehman *et al.* 2006b; Randrianambinina *et al.* 2010; Sawyer *et al.* 2017). Some folivorous lemurs respond

positively to low-medium levels of forest disturbance such as the Southern lesser bamboo lemur (*Hapalemur meridionalis*) which tolerated significant levels of habitat degradation by using an invasive species habitat for feeding and resting (Eppley *et al.* 2015). Similarly, the mostly folivorous sifaka (genus *Propithecus*) increased in numbers along census trails after logging (Ganzhorn 1995), and were frequently found using degraded, secondary and anthropized habitat (*P. coronatus* & *P. coquereli*) in western Madagascar (Salmona *et al.* 2014; Salmona *et al.* 2013). The folivorous nocturnal lemurs (*Avahi* sp., and *Lepilemur* sp.) have shown mixed responses to disturbed habitat (Ganzhorn 1987; Norscia 2008; Sawyer *et al.* 2017). The folivorous *Avahi mooreorum* and *Lepilemur scotus* were more susceptible to increasing habitat disturbance (Sawyer *et al.* 2017), and *Lepilemur grewcockorum* was less abundant in degraded forest, most likely due to the reduced availability of tree holes in old-growth trees (Randrianambinina *et al.* 2010). Omnivorous or insectivorous lemurs are often more abundant in disturbed habitats than in mature forests, potentially due to an increased light penetration and understory biomass linked with high insect abundances (Andriamandimbiarisoa *et al.* 2015; Corbin and Schmid 1995; Herrera *et al.* 2011). Omnivorous lemurs, such as mouse lemurs (*Microcebus* sp.), dwarf lemurs (*Cheirogaleus* sp.) and hairy-eared lemurs (*Allocebus trichotis*) have diverse diets, comprising insect secretions, arthropods, small vertebrates, gum, fruits, flowers, nectar, and also leaves and buds (Biebow *et al.* 2009; Ganzhorn 1988; Lahann 2007; Radespiel 2006; Radespiel *et al.* 2006; Wright and Martin 1995). Mouse lemurs have higher encounter rates in more disturbed regions of Ranomafana National Park (Herrera *et al.* 2011), and in Kirindy forest in western Madagascar, higher numbers were recorded following low-intensity logging (Ganzhorn 1995).

We aim to investigate the responses of nocturnal lemurs to a gradient of habitat types ranging from mature forest to regenerating forest (younger and older secondary), conducting surveys in different habitats in north-eastern Madagascar. We investigate the responses of four

nocturnal lemur species to anthropogenic disturbance: a folivorous lemur (eastern woolly lemur, *Avahi laniger*), omnivorous mouse lemur (cf *Microcebus simmonsi*, see *Methods: Study species* for justification of taxonomic classification), an omnivore/gumnivore (hairy-eared dwarf lemur, *Allocebus trichotis*) and an insectivore (aye-aye, *Daubentonia madagascariensis*).

We aim to answer the following questions:

1. Do different habitat types with ranging levels of disturbance affect the abundance of nocturnal lemur species?
2. Is regenerating secondary forest a viable habitat for nocturnal lemurs?

Methods

Study sites

We conducted this study in the Alan'Antanetivy forest corridor, a large tract of low-land mature rainforest in north-eastern Madagascar (Moat and Smith 2007). It is part of a community-based forest management called "KoloAla Manompana" and consists of approximately 30,000 ha of forest connecting Mananara-Nord National Park and Ambatovaky Special Reserve (Figure 1) (Rakotomavo 2009; Urech and Sorg 2013). We surveyed two lowland forests lying within the Alan'Antanetivy corridor: Ambodiriana (16°40'19.51"S, 49°42'0.63"E) and Antsahanadraitry forest (16°39'31.91"S, 49°40'56.38"E), approximately 7 and 10 km west, of the coastal town of Manompana (Analanjirifo region in north-eastern Madagascar). Both were composed of a mosaic of forest types, Ambodiriana contains low-altitude moist evergreen forest or mature forest and regenerating secondary forest regrown after shifting agriculture, and Antsahanadraitry is a mature forest punctuated by degraded sections (Table 1). Ambodiriana forest has been managed by the association ADEFA (Association de Défense de la Forêt

d'Ambodiriana) since 1999. Antsahanadraitry forest forms part of a large tract of forest of around 30,000 ha (Rakotomavo 2009), integrated into a community-based forest management national program called “KoloAla Manompana”.

Figure 1. Map of survey sites used to study nocturnal lemurs. Squares show the survey forests. Top right box shows the location of transects in two forests, Antsahanadraitry and Ambodiriana, with mature forest and regenerating secondary forest

Study species

We studied four of the five nocturnal species that occur in Ambodiriana and Antsahanadraitry forest tracts: eastern woolly lemur (*Avahi laniger*), mouse lemur (*Microcebus* sp.), hairy-eared dwarf lemur (*Allocebus trichotis*), dwarf lemur (*Cheirogaleus* sp.), and aye-aye (*Daubentonia madagascariensis*). Of these species, we observed *Avahi laniger*, *Microcebus* sp., *Allocebus trichotis* and *Daubentonia madagascariensis*.

The eastern woolly lemur is a folivorous small-bodied lemur that occurs in tropical moist forests in eastern Madagascar, with a diet consisting primarily of leaves, but also includes fruits and flowers (Faulkner 2005; Ganzhorn *et al.* 1985; Harcourt 1991; Thalmann 2003).

The closest described mouse lemurs to our study site are *M. simmonsi*, approximately 80 km to the south of the site in Tampolo (Weisrock *et al.* 2010) and *M. boraha* to the east on the island Ste. Marie (Hotaling *et al.* 2016). Preliminary analysis of genomic data of mouse lemurs in Ambodiriana suggests that they are *M. simmonsi* (J. Salmona & L. Chikhi, unpublished data), so we refer to the mouse lemur from Manompana as *M. cf. simmonsi*. Although there are currently no data available on the diet of *Microcebus simmonsi*, other *Microcebus* spp. have been reported to be omnivorous, so we assumed that *Microcebus cf. simmonsi* is also an omnivore (Mittermeier *et al.* 2010).

The hairy-eared dwarf lemur is a small-bodied lemur, frequenting moist lowland forest, often seen in tangles of brush or lianas, foraging at lower levels in the forest, with teeth and nails indicative of a gum-eating diet (Biebouw 2009; Biebouw 2012). In the wild, this species has been observed feeding on insects and gums (Biebouw *et al.* 2009).

The aye-aye is the largest fully nocturnal lemur, found in a range of habitats from mature rainforest to regenerating secondary forest and cultivated areas with an omnivorous diet, feeding on seeds, insect larvae, nectar, fruit and crops (Mittermeier *et al.* 2010).

We conducted our survey during the austral winter (May-August), which is generally characterized by low ambient temperatures and resource scarcity for many lemurs (Wright 1999). Several mouse lemur species from central and southern Madagascar enter prolonged torpor during the dry season (Schmid and Speakman 2000; 2009). If *M. cf. simmonsi* undergoes prolonged torpor during the dry season, the population may be larger than estimated in this study. In addition, *Cheirogaleus* sp. is known to hibernate during the austral winter in eastern

Madagascar (Lehman *et al.* 2006c). We make no assumptions about the habitat preferences of *Cheirogaleus* sp. at our study site as individuals may hibernate and would therefore not have been observed along transects.

Habitat survey

To determine the characteristics of the forest, we recorded the plant species and number of plant individuals in 3 x 0.5 m plots (Perzanowski *et al.* 1982) on either side of the transects and pre-existing trails at 10 m intervals in the two forests: Antsahanadraitry and Ambodiriana (detailed description of transects in *Methods: Distance sampling procedures*). We aligned these plots perpendicular to the trail, 3 m in length and 0.5 m in width (total of 604 plots in overall sample). We counted all plant species (exotic and native), encompassing all size classes. We recorded 112 plant species in the plot survey. We also estimated mean canopy height (one visually estimated average for each plot in meters), forest type (regenerating young secondary, regenerating older secondary, degraded mature forest and mature forest, Table 1), logging evidence (yes/no), evidence of localized fire (burnt stumps and scorched trees), and evidence of digging by humans (for minerals or tubers) (Ackermann 2004). A local guide identified trees and herbaceous species in the field. We sampled leaf specimens and photos for reference when we could not identify trees/plants immediately in the field. We later identified these specimens with the help of ADEFA's botanists or by referencing lists of local Malagasy and scientific names (north-east Madagascar) (Dokolahy 2004; Rakotondrasoa 2007). We assigned the closest plot (3 x 0.5 m) (based on GPS location) to lemur sightings along transects (≤ 10 m, mean = 5.73 m (± 2.14)).

We also measured a set of botanical variables within 5 x 5 m quadrats along transects, totalling 35 quadrats in the overall sample, (Ambodiriana n=24, Antsahanadraitry n=11). We placed quadrats every 100 m along transects and pre-existing trails (alternating sides) used for distance sampling (180-986 m in length) and started 5 m from the transect. Within quadrats we measured

plant species richness (all species present), total herbaceous plant abundance per species, total tree abundance ('tree' defined as a perennial plant with an elongated stem, or trunk, supporting branches and leaves), circumference at breast height of each tree (CBH) (<15 cm, 15-30 cm, 31-65 cm, 66-95, >95 cm), and tree height (mean tree height estimated in meters of whole quadrat) (≤ 5 m, 6-15 m, 16-25 m, 25-35 m, >35 m). We used the quadrat (5 x 5 m) information to compare the forest structure of Ambodiriana and Antsahanadraitry.

Vegetation in Ambodiriana is a mosaic of different habitat types, which we classified using the variables age (years), height (m), land use history, and dominant species (Table 1). We interviewed local people in the area (local farmers and staff at ADEFA) to gain additional information about land use history and local agricultural practices for the areas surveyed in this study.

Table 1. Characteristics used to differentiate habitat types at Ambodiriana and Antsahanadraitry forests, north-eastern Madagascar.

Habitat type	Approximated age (years) and height	Land use history and Dominant species
Herbaceous fallow 'rorongo' or secondary grassland	0-3 years (1-2 m) ^a	Areas where many years of cultivation and erosion have impoverished soils; covered with savannah; dominated by fire-resistant grasses, sedges, ferns (<i>Pteridium</i> ⁺ spp.) (Dennstaedtiaceae), <i>Clidemia hirta</i> ⁺ (Melastomataceae), <i>Erica</i> sp. (Ericaceae), and <i>Ravenala madagascariensis</i> (Strelitziaceae) ^{b c} .
Regenerating young secondary 'savoka'	3-4 years (2-4 m) ^a	After the forests is cleared but the areas is not cultivated, secondary thickets arise, dominated by heliophilous species like <i>Ravenala madagascariensis</i> , <i>Solanum mauritianum</i> ⁺ (Solanaceae), <i>Aframomum</i> sp. (Zingiberaceae), <i>Lantana camara</i> ⁺ (Verbenaceae), <i>Trema orientalis</i> (Ulmaceae), <i>Rubus</i> ⁺ sp. (Rosaceae), ferns (<i>Pteridium</i> ⁺ spp.), and tree seedling or saplings of species <i>Harungana madagascariensis</i> (Clusiaceae), <i>Albizia</i> sp. (Fabaceae), <i>Croton</i> sp., <i>Ficus</i> sp., and <i>Tambourissa</i> sp. ^{a b c d} .
Regenerating older secondary 'savoka mody' or regenerated tree fallow	~10-20 years (15-25 m) ^a	If a Savoka is left to regenerate further, it develops into a tree fallow (Savoka Mody) dominated by forest species such as <i>Croton</i> sp. (Euphorbiaceae), <i>Macaranga</i> sp. (Euphorbiaceae), <i>Dombeya</i> sp. (Sterculiaceae), <i>Ficus</i> sp.

		(Moraceae), <i>Harungana madagascariensis</i> , and <i>Trema orientalis</i> ^{d e} .
Low-altitude moist evergreen forest or mature forest	25-30 m in height with several strata and a diffuse understorey ^{e f}	<p>Intact: Mature forest rich in species; some of the dominant genera were <i>Calophyllum</i> (Calophyllaceae), <i>Ocotea</i> (Lauraceae), <i>Dalbergia</i> (Fabaceae), <i>Anthostema</i> (Euphorbiaceae), <i>Canarium</i> (Burseraceae), <i>Xylopia</i> (Annonaceae), <i>Uapacca</i> (Euphorbiaceae), <i>Dracaena</i> (Dracaenaceae), <i>Ocotea</i> (Lauraceae), <i>Dypsis</i> (Arecaceae) and <i>Pandanus</i> (Pandanaceae)^{e f g}.</p> <p>Degraded: Open canopy cover but containing still a high plant diversity and quantity^g. Species predominating degraded mature were the same as mature but characterized by large numbers of smaller, understory invasive plants^h.</p>

^a (Styger *et al.* 2007), ^b (Randrianarison *et al.* 2016), ^c (Hladik *et al.* 2000; Randrianarison *et al.* 2016), ^d (Klanderud *et al.* 2009), ^e (Gehring *et al.* 2010), ^f (Eckert *et al.* 2011), ^g (Rasolofoson *et al.* 2007), ^h (Brown and Gurevitch 2004)

⁺Exotic species

Distance sampling procedures

We carried out line transect distance sampling surveys (Buckland *et al.* 2001) in June and July 2014. We used six pre-existing trails (180–802 m) in Ambodiriana forest and two pre-existing and one new transect (500–986 m) in Antsahanadraitry forest (Figure 1). We conducted 74 nocturnal surveys totaling 51 km: 62 surveys in Ambodiriana forest (41.9 km; 25.9 km mature forest, 16 km regenerating secondary) and 12 surveys in Antsahanadraitry forest (9.1 km; mature forest). These surveys corresponded to 35 km in mature forest and 16 km in regenerating secondary forest. To avoid disturbing animals before the survey, we never conducted surveys during the 24 hours following the creation of a transect. Using existing trails can bias survey results, although one study found no significant effects of using existing trails on lemur densities (Lehman 2006). We found no direct or indirect evidence of hunting along trails, and only rare instances of disturbance in the form of cut trees. Considering topography, time constraints, and conservation restrictions, the combination of trails and transects were the best available option for our study.

214

215 Teams of 2-3 people, including at least one trained researcher (AM or TR) and one local guide
216 surveyed trails and transects 18:15-22:00h, five to 14 times per trail or transect within 40 days,
217 walking at ~0.5-1.0 km/h. Teams swapped between transects during the study to minimize
218 observer bias (Buckland *et al.* 2001). We also changed the order of transects surveyed each day
219 to ensure that transects were surveyed at varying times. We used head torches to spot lemurs
220 and a strong hand-held torch to confirm sightings and identify species. When we observed
221 lemurs, we recorded the observation date and time, species, group size, distance from observer
222 (m) using a digital laser rangefinder (Bosch® PLR 50; 50 m range; ± 2 mm accuracy), GPS
223 location (Garmin®Etrex-H GPS) and a compass bearing from transect to lemur/s to calculate
224 the perpendicular distances to the transect line.

225 *Data analyses*

226 We estimated population densities for the eastern woolly lemur and mouse lemur using the
227 conventional distance sampling (CDS) method implemented in DISTANCE 6.2 software,
228 which models the decreasing probability of observing animals as their distance from the
229 transect increases (Thomas *et al.* 2010). This method estimates the number of animals in a
230 survey area, taking into account the number of animals seen, the length of the transect and the
231 effective strip width (ESW), with detection being increasingly less likely as distance from
232 transect increases (Buckland 1985). A set of functions estimates the probability of detecting an
233 animal, depending on the visual conspicuousness of the species as well as habitat and sighting
234 conditions, which can vary considerably between species and habitat type. We followed
235 recommendations to truncate the extreme upper observations after a preliminary check of the
236 distribution of the data, to ensure accurate model fitting (Buckland *et al.* 2001; Meyler *et al.*
237 2012). We truncated 5% of the dataset for mouse lemurs (3 observations, >20 m from transect)

and 10% of the dataset for eastern woolly lemurs (10 observations, >20 m from transect). We compared four key functions: Uniform, Hazard Rate, Negative Exponential and Half-Normal detection models, adjusted using Cosine terms, Hermite or Simple Polynomials. We used the Akaike Information Criterion adjusted for small sample sizes (AICc), and the coefficient of variation (CV%), following the standard model selection techniques suggested by Thomas *et al.* (2010) to compare the key functions. We transformed AIC values to Akaike weights (W_i), which can be directly interpreted as conditional probabilities for each model, facilitating the interpretation of the results of AIC model comparison procedures. Given, the limited number of survey observations in Antsahanadraitry forest we did not compute the ESW independently for this site. Instead, we used the mature forest ESW estimates from Ambodiriana to compute the ESW in Antsahanadraitry forest, assuming similar detectability in both mature forest areas. We also compared median perpendicular sighting distances for each species in mature forests of both sites to ensure a global ESW was appropriate using independent sample t-tests (assuming unequal variances).

To investigate the potential effects of environmental covariates on animal detectability we used the multiple-covariate distance sampling (MCDS) analysis in DISTANCE. We first estimated the effect of each variable independently and then combined those with the lowest AIC values and a high goodness-of-fit (GOF) χ^2 value. We tested factor covariates: observer (A. Miller, T. Ralantoharijaona or A. Miller + T. Ralantoharijaona), habitat type ('mature forest & regenerating secondary', 'mature forest , regenerating young secondary & regenerating older secondary', 'mature forest, degraded mature, regenerating young secondary, regenerating older secondary'), rain during survey, and numerical covariates associated with the transects (vine density, canopy height (m), percentage of cloud cover, time (h) since last survey on transect, and lunar variables obtained from "<http://www.tides4fishing.com/af/madagascar/>" "Baie De Tintingue": intensity, duration, moon phase i.e. waxing/waning) or lemurs (group size for

Avahi, height of lemur). We combined the following covariates: observer + habitat type (all classes), observer + vine density, and observer + canopy height, to test if any environmental variables affected observer detection. For models with high GOF χ^2 values we examined histograms and investigated the Δ AIC values and Akaike weights (W_i) to select the best model(s).

We could only estimate densities for regenerating secondary vs mature forest and wanted to investigate the fine-scale differences between the four habitat types (mature, degraded mature, regenerating young secondary, regenerating older secondary). To do so, we investigated differences in encounter rates between the four habitat types using non-parametric independent samples Kruskal-Wallis test and the original non-transformed data. We initially used a one-way ANOVA approach for the mouse lemur but the Levene test result remained unsuitable when we transformed the encounter rate data (Log, LN, Arcsine, and Sqrt). We used non-parametric analyses for both species so that the results are comparable.

We used pairwise comparisons to assess the forest structure of Ambodiriana and Antsahanadraitry, and the four different habitat types (mature vs regenerating secondary, mature vs degraded mature, and regenerating young secondary vs regenerating older secondary) using independent sample t-tests (assuming unequal variances). We compared the following variables: vine number, species richness, tree species richness, and number of native species and exotic species (*Pteridium* sp., *Panicum brevifolium*, *Tristema mauritiana*, *Psidium cattleianum*, *Lantana camara*, *Aframomum angustifolium*, and *Imperata cylindrica*), canopy height, tree density, and density of *Harungana madagascariensis*. We investigated the density of *H. madagascariensis*, a pioneer species in young secondary fallow, because it is the most predominantly consumed species of *Avahi peyrierasi* and *Avahi laniger* in Ranomafana and Mantadia National Parks (Faulkner and Lehman 2006; Ganzhorn *et al.* 1985; Harcourt 1991; Klanderud *et al.* 2009).

Data availability The datasets analyzed during the current study are available from the corresponding author on reasonable request.

Ethical Note

The Animal Ethics Committee of The University of Western Australia (UWA approval number RA-3-100-1314), the association ADEFA, the local COBA (Communauté de Base) of Antsahanadraitry, the CAFF/CORE and the “Direction Générale des Environnement et Forêts” approved this study. This research complied with the laws of the Countries of Madagascar, Australia, Portugal and France, and is in compliance with the International Society of Primatologists principles for the ethical treatment of primates.

Results

Habitat and botanical survey

Based on 0.5 x 3 m botanical plots comparing mature forest and regenerating secondary forest (Table 2), we found higher mean vine density in mature forest, higher mean density of exotic species in regenerating secondary forest, and higher mean density of *H. madagascariensis* in regenerating secondary forest. Comparing mature and degraded mature forest (Table 3), we found a higher mean density of exotic species in degraded mature forest, and a higher mean density of *H. madagascariensis* in degraded mature forest. Comparing regenerating young secondary and regenerating older secondary forest (Table 4), we found higher mean vine density in regenerating older secondary, higher mean density of native species in regenerating young secondary forest, higher mean tree density in regenerating older secondary forest and higher mean density of *H. madagascariensis* in regenerating young secondary forest.

Based on measured differences from the 5 x 5 m botanical quadrats, Antsahandraitry forest had a higher mean density of large trees than Ambodiriana forest (CBH: >95 cm, Height: 25-35 m) (Table 5).

Table 2. Results of two-sample t-tests assuming unequal variances comparing habitat variables measured in 3 x 0.5 m plots in mature and regenerating secondary forest in Ambodiriana and Antsahanadraitry forests, north-eastern Madagascar in June/July 2014.

	Mature	Regenerating secondary	t value	df	P value
Variable	Mean ($\pm$ SD)	Mean ($\pm$ SD)			
Vine density	2.06 ($\pm$ 3.99)	0.51 ($\pm$ 1.65)	4.52	186.89	0.001
Native species	7.36 ($\pm$ 2.64)	4.78 ($\pm$ 3.13)	6.13	65.34	0.129
Exotic species	0.79 ($\pm$ 1.02)	3.37 ($\pm$ 1.47)	11.95	60.26	0.001
Canopy height	22.89 ($\pm$ 5.85)	15.08 ($\pm$ 6.56)	8.51	67.31	0.161
Tree density	8.08 ($\pm$ 5.62)	5.53 ($\pm$ 6.30)	2.89	67.30	0.379
<i>Harungana</i> density	0.044 ($\pm$ 0.22)	0.25 ($\pm$ 0.87)	1.72	51.38	0.001
Species richness	8.13 ($\pm$ 2.55)	8.21 ($\pm$ 2.65)	0.21	70.21	0.798
Tree species richness	4.32 ($\pm$ 1.96)	2.78 ($\pm$ 2.05)	5.06	69.96	0.818

Variables with a significant result in bold

Table 3. Results of two-sample t-tests assuming unequal variances comparing habitat variables in 3 x 0.5 m plots in mature and degraded mature forest in Ambodiriana and Antsahanadraitry forests, north-eastern Madagascar in June/July 2014.

	Mature	Degraded mature	t value	df	P value
Variable	Mean ($\pm$ SD)	Mean ($\pm$ SD)			
Vine density	2.18 ($\pm$ 4.16)	1.11 ($\pm$ 2.00)	1.34	62.24	0.067
Native species	7.51 ($\pm$ 2.57)	6.18 ($\pm$ 2.96)	2.53	32.36	0.440
Exotic species	0.68 ($\pm$ 0.88)	1.68 ($\pm$ 1.54)	3.35	29.26	0.001
Canopy height	23.04 ($\pm$ 5.86)	21.78 ($\pm$ 5.81)	1.06	34.34	0.832
Tree density	8.27 ($\pm$ 5.72)	6.57 ($\pm$ 4.62)	1.51	38.33	0.607
<i>Harungana</i> density	0.036 ($\pm$ 0.21)	0.11 ($\pm$ 0.31)	1.16	30.12	0.003
Species richness	8.15 ($\pm$ 2.57)	8.034 ($\pm$ 2.49)	0.21	34.70	0.872
Tree species richness	4.41 ($\pm$ 1.97)	3.64 ($\pm$ 1.75)	1.95	36.32	0.492

Variables with a significant result in bold

Table 4. Results of two-sample t-tests assuming unequal variances comparing habitat variables in 3 x 0.5 m plots in regenerating young secondary and regenerating

secondary forest in Ambodiriana and Antsahanadraitry forests, north-eastern
Madagascar in June/July 2014.

	Regenerating young secondary	Regenerating secondary	t value	df	P value
Variable	Mean ($\pm$ SD)	Mean ($\pm$ SD)			
Vine density	0.18 ($\pm$ 0.48)	0.87 ($\pm$ 2.33)	1.42	24.76	0.002
Native species	5.37 ($\pm$ 2.40)	4.12 ($\pm$ 3.73)	1.40	38.46	0.034
Exotic species	3.48 ($\pm$ 1.42)	3.25 ($\pm$ 1.54)	0.56	47.16	0.550
Canopy height	12.92 ($\pm$ 6.28)	17.50 ($\pm$ 6.11)	2.63	48.59	0.977
Tree density	5.15 ($\pm$ 4.28)	5.96 ($\pm$ 8.08)	0.44	34.06	0.034
<i>Harungana</i> density	0.44 ($\pm$ 1.15)	0.042 ($\pm$ 0.20)	1.78	27.82	0.001
Species richness	8.85 ($\pm$ 2.58)	7.50 ($\pm$ 2.60)	1.86	48.20	0.756
Tree species richness	3.11 ($\pm$ 1.95)	2.41 ($\pm$ 2.14)	1.21	46.82	0.776

Variables with a significant result in bold

Table 5. Results of two-sample t-tests assuming unequal variances comparing habitat variables measured in 5 m x 5 m quadrats in Antsahanadraitry and Ambodiriana forests, north-eastern Madagascar in June/July 2014.

	Antsahanadraitry	Ambodiriana	t value	df	P value
Variable	Mean ($\pm$ SD)	Mean ($\pm$ SD)			
Plant species richness	10.40 ($\pm$ 2.13)	8.65 ($\pm$ 2.15)	2.39	30.51	0.946
Total Plants	109.46 ($\pm$ 41.32)	99.00 ($\pm$ 38.82)	0.77	29.23	0.989
Total Trees	79.00 ($\pm$ 36.20)	62.20 ($\pm$ 34.70)	1.39	29.59	0.773
<15 cm CBH	98.73 ($\pm$ 44.42)	89.70 ($\pm$ 33.00)	0.69	24.85	0.278
15-30 cm CBH	6.33 ($\pm$ 4.29)	8.35 ($\pm$ 4.49)	1.34	31.06	0.949
31-65 cm CBH	2.80 ($\pm$ 1.37)	2.15 ($\pm$ 1.84)	1.14	33.00	0.510
66-95 cm CBH	0.80 ($\pm$ 0.86)	0.45 ($\pm$ 1.09)	1.02	32.91	0.745
>95 cm CBH	0.80 ($\pm$ 0.86)	0.05 ($\pm$ 0.22)	3.29	15.42	0.001
$\leq$ 5 m Height	88.60 ($\pm$ 55.32)	81.15 ($\pm$ 40.36)	0.46	24.53	0.242
6-15 m Height	12.47 ($\pm$ 14.65)	10.10 ($\pm$ 6.33)	0.65	17.94	0.370
16-25 m Height	2.07 ($\pm$ 2.91)	0.85 ($\pm$ 1.04)	1.73	16.69	0.203
25-35 m Height	0.33 ($\pm$ 0.72)	0.05 ($\pm$ 0.22)	1.46	16.02	0.001
>35 m Height	-	-	-	-	-

Variables with a significant result in bold

Lemur surveys

We recorded 161 observations of four lemur species: eastern woolly lemurs, mouse lemurs, hairy-eared dwarf lemurs and aye-ayes (Table 6). We sighted four lemur species in mature forest: eastern woolly lemurs, mouse lemurs, hairy-eared dwarf lemurs, aye-ayes and only two species, eastern woolly lemurs, and mouse lemurs, in regenerating secondary forest (Table 7).

We observed most mouse lemurs in tangles of vines and in the trees *Gastonia duplicata* (Araliaceae), *Tambourissa* sp. (Monimiaceae), and *Caryophyllata aromatica* (Myrtaceae). We often observed eastern woolly lemurs feeding in stands of *Harungana madagascariensis* in regenerating secondary forest. We observed the hairy-eared dwarf lemur in the mature forest of Antsahanadraitry forest and the aye-aye in mature forest in Ambodiriana forest.

Table 6. Details of transects with numbers of nocturnal surveys and lemur sightings in Ambodiriana and Antsahanadraitry forests, north-eastern Madagascar in June/July 2014.

Ambodiriana							Antsahanadraitry			
Transect #	I	II	III	IV	V	VI	I	II	III	Total
Transect length (m)	738	802	774	668	641	180	986	520	500	-
Transect (T) or Trail (Tr)	Tr	Tr	Tr	Tr	Tr	Tr	Tr	Tr	T	10
Mature (M) or regenerating secondary (S)	M,S	M,S	M,S	M,S	M,S	M,S	M	M	M	-
Nocturnal survey #	12	13	14	10	6	7	6	5	1	74
Scientific name										
<i>Avahi laniger</i>	3	17	35	2	5	13	8	9	0	92
<i>Microcebus</i> cf. <i>simmonsi</i>	7	21	13	8	8	1	1	4	0	63
<i>Allocebus trichotis</i>	0	0	0	0	0	0	2	2	0	4
<i>Daubentonia madagascariensis</i>	0	1	0	1	0	0	0	0	0	2

Table 7. Sightings of four lemur species in different habitat types in Ambodiriana and Antsahanadraitry forests, north-eastern Madagascar in June/July 2014.

Species	Habitat type			
	Regenerating young secondary	Regenerating older secondary	Degraded mature	Mature
<i>Avahi laniger</i>	29	20	17	26
<i>Microcebus</i> cf. <i>simmonsi</i>	20	7	9	27
<i>Allocebus trichotis</i>	0	0	2	2
<i>Daubentonia madagascariensis</i>	0	0	0	2
Total	49	27	28	57

Density estimates from line-transect surveys

Of the four species we observed, only the eastern woolly and mouse lemur had sufficient observations (>40) to allow an accurate statistical estimation of the population density in mature and regenerating secondary forest. Using the CDS method, the half-normal function best fitted the data for both species. We used a global ESW to calculate densities, assuming similar detectability in Ambodiriana and Antsahanadraitry. This assumption seems reasonable since on plant metrics and habitat characteristics in mature forest habitat in Antsahanadraitry and Ambodiriana (surveyed by the same researchers and guides) were similar. In addition, there was no significant difference in perpendicular sighting distances in mature forest for *Avahi* in Ambodiriana (mean=7.49 m, SD=±7.43), and Antsahanadraitry (mean=9.94 m, SD=±7.44) forests ($t_{27}=2.05$, $P=0.25$), and for *Microcebus* in Ambodiriana (mean=5.69 m, SD=±5.99), and Antsahanadraitry (mean=4.41 m, $\pm$ SD=5.07) forests ($t_5=2.57$, $P=0.61$).

We estimated a density of the eastern woolly lemur of 38 ± 6.0 (SE) ind/km² in mature forest and 134 ± 23.3 (SE) ind/km² in regenerating secondary forest using Multiple Covariates Distance Sampling (MCDS) analyses (Figure 2). The corresponding effort was 35 km in mature forest (*A. laniger* n=43), and 16 km in regenerating secondary forest (*A. laniger* n=49) (Tables 8 and 9). Of the variables we tested, the detection of eastern woolly lemurs was most affected by a combination of habitat type and observer identity (Akaike weight (W_i)=0.72) (Table 8). Detection probability was lowest in regenerating older secondary forest, and highest in mature forest. Observer identity and the combination of observers affected the detection probability of eastern woolly lemurs. The presence of both observers in the same team resulted in a wider ESW, resulting in differing detection probabilities in different habitat types.

Figure 2. Density (individuals/km²) of the eastern woolly lemur and mouse lemur in mature and regenerating secondary forest using Multiple Covariates Distance Sampling in Ambodiriana and Antsahanadraitry forests, north-eastern Madagascar in June/July 2014.

The eastern woolly lemur also had significantly higher encounter rates (km⁻¹) in regenerating older secondary forest than in other forest types (Table 10), Levene's Test with one-way ANOVA ($F_{3,68} = 178.46$, $p < 0.001$, effect size: partial $\eta^2 = 0.893$). Encounter rates for eastern woolly lemurs were significantly different among the four habitat types (Kruskal-Wallis, $X^2 = 58.27$, $p < 0.05$).

Table 8. Results of Conventional Distance Sampling and Multiple Covariates Distance Sampling analyses for the eastern woolly lemur and the mouse lemur, showing the top five covariate combinations for each species, in Ambodiriana and Antsahanadraitry forests, north-eastern Madagascar in June/July 2014.

K	AICc	W _i	ESW	D	95% CI	%CV
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						Lower	Upper		
<i>Eastern woolly lemur</i>		3	343.45	-	8.40	87	45	170	0.324
<i>Mouse lemur</i>		1	297.03	-	7.10	83	55	126	0.195
Covariates									
<i>Eastern woolly lemur</i>	Habitat 3 + observer ID	5	334.02	0.72	8.29	94	48	184	0.331
	Canopy height	2	338.52	0.08	10.52	71	37	137	0.316
	Habitat type 3	3	338.56	0.07	10.37	74	40	138	0.291
	Observer ID + canopy height	8	340.67	0.03	7.73	93	45	192	0.361
	Species richness	2	345.74	0.00	11.64	64	35	118	0.284
	Canopy height	2	293.41	0.27	6.61	89	58	137	0.205
	Vine density	2	293.86	0.21	6.58	89	58	137	0.206
	Observer ID + canopy height	4	296.08	0.07	6.43	91	59	141	0.209
	Species richness	2	296.11	0.07	6.83	86	56	132	0.203
	Exotic plant density	2	298.17	0.02	7.01	84	55	128	0.202

385 AICc = Akaike information criteria adjusted for small sample size; CI = 95% confidence
386 interval; % CV = coefficient of variation; Habitat 3 = three habitat types: mature, regenerating
387 young secondary, and regenerating older secondary

388 **Table 9. Estimated density of lemurs in mature and regenerating secondary forest**
389 **obtained from Multiple Covariates Distance Sampling analyses in Ambodiriana**
390 **and Antsahanadraitry forests, north-eastern Madagascar in June/July 2014.**

Forest type	Effort (km)	Species	Individuals/ km ²	95% CI	SE	%CV
Mature	35	<i>Eastern woolly lemur</i>	38	(27-52)	6.0	0.16
		<i>Mouse lemur</i>	68	(51-90)	9.4	0.14
Regenerating secondary	16	<i>Eastern woolly lemur</i>	134	(94-190)	23.3	0.17
		<i>Mouse lemur</i>	137	(92-204)	26.6	0.19

391

392 **Table 10. Sightings and encounter rates for eastern woolly lemurs (*Avahi laniger*) and**
393 **mouse lemurs (*Microcebus* cf. *simmonsi*) in different habitats in Ambodiriana**
394 **and Antsahanadraitry forests, north-eastern Madagascar in June/July 2014.**

Forest type	Effort (km)	Number of sightings		Encounter rate (km ⁻¹)	
		<i>A. laniger</i>	<i>M. cf. simmonsi</i>	<i>A. laniger</i>	<i>M. cf. simmonsi</i>
Regenerating young	13.13	29	20	2.21	1.52
Regenerating older	2.94	20	7	6.80	2.38
Degraded mature	4.08	17	9	4.17	2.20
Mature	31.61	26	27	0.82	0.85

395

396 The mouse lemur density estimates were 68 ± 9.4 (SE) ind/km² in mature forest (*Microcebus*
397 n=36), and 137 ± 26.6 (SE) ind/km² in regenerating secondary forest (*Microcebus* n=27)
398 (Figure 2). Several competing covariates affected mouse lemur detection in surveys. The top

two models included canopy height and vine density, accounting for 27% and 21% probability of being the model best describing the data (Akaike weights: W_i) (Table 8). Detection of mouse lemurs was lowest in habitats with lower canopy heights (<15 m) and highest in stands with taller canopy (>25 m).

A covariate combination containing ‘observer’ featured in the top 5 models for both the eastern woolly lemur and mouse lemur (Table 8). To tackle this confounding effect on detection probability, we estimated densities using data collected when the two observers were in the same team (*A. laniger* n=47, *Microcebus* n=38). With this approach we found higher densities of both species in regenerating secondary forest (Figure 3). The density of the eastern woolly lemur in mature forest is 10 ± 3.21 (SE) ind/km² (% CV 0.31) (95% CI 5-20) and in regenerating secondary forest; 48 ± 12.24 (SE) ind/km² (% CV 0.26) (95% CI 28-81) using MCDS analyses. For mouse lemurs in mature forest we found a density of 33 ± 5.63 (SE) ind/km² (% CV 0.17) (95% CI 23-47) and in regenerating secondary forest; 81 ± 13.96 (SE) ind/km² (% CV 0.17) (95% CI 56-116).

Figure 3. Density (individuals/km²) of the eastern woolly lemur and mouse lemur in mature and regenerating secondary forest calculated from observations with two observers present to tackle the confounding effect of observer on detection probability, using Multiple Covariates Distance Sampling in Ambodiriana and Antsahanadraitry forests, north-eastern Madagascar in June/July 2014.

The encounter rates of mouse lemurs were significantly different among the four habitat types (Kruskal-Wallis, $X^2 = 54.88$, $p < 0.05$), with the highest mean encounter rates recorded in regenerating older secondary forest (Table 10).

Discussion

We found higher densities of a folivorous and an omnivorous lemur in regenerating secondary forest than in mature forest in the Manompana region of north-eastern Madagascar. However, consistent with other research we recorded higher lemur species diversity in mature forest (Irwin *et al.* 2010; Sawyer *et al.* 2017; Schwitzer *et al.* 2011). The results highlight the importance of regenerating secondary forest as a viable habitat for the eastern woolly lemur and mouse lemur. The regenerating secondary forest was characterized by higher densities of exotic plant species (*Panicum brevifolium*, *Tristema mauritiana*, *Psidium cattleianum*, *Lantana camara*, *Imperata cylindrica*, *Aframomum angustifolium*) and higher densities of the tree *Harungana madagascariensis* than mature forest. We observed two species, the omnivorous hairy-eared dwarf lemur and insectivorous aye-aye, exclusively in mature forest, supporting the hypothesis that there is a broad scope of responses by species to disturbance (Irwin *et al.* 2010; Isaac and Cowlishaw 2004).

Our results highlight the capacity of the folivorous eastern woolly lemur to persist in habitats with anthropogenic disturbance, with the highest densities in regenerating secondary forest, and highest encounter rates in regenerating older secondary and degraded mature forest in northeastern Madagascar. The high encounter rates in degraded mature forest support the hypothesis that increased leaf quality in disturbed habitats benefits folivorous species (Ganzhorn 1995; Onderdonk and Chapman 2000). High densities of the favored food tree (*Harungana madagascariensis*) (Faulkner and Lehman 2006; Ganzhorn *et al.* 1985; Harcourt 1991) in regenerating secondary forest, or the dense structure of secondary stands providing substrates for clinging, leaping and sleeping may explain the higher densities of woolly lemurs.

Although previous research suggests that eastern woolly lemurs are not particularly sensitive to habitat disturbance (Lehman *et al.* 2006b), our results appear to contradict a study that found that woolly lemurs preferred mature forest to logged forest in Ranomafana National Park (Herrera *et al.* (2011). Additionally, in Makira-Masoala region no differences in densities or encounter rates were recorded for eastern woolly lemurs at intact, intermediate, and degraded forest sites (Murphy *et al.* 2016), which also differs from our results and those of Herrera *et al.* (2011). This suggests that other factors such as hunting pressure and other types of human activities are important, beyond the dichotomy of "mature or primary" versus "secondary" forests across regions of Madagascar (Golden 2009).

Our density estimates for eastern woolly lemurs in Ambodiriana forest (87 individuals/km²) are similar to those of Beaucent and Fayolle (2008) (86 individuals/km²), Ferrier and Lacroix (2008) (58 individuals/km²), and Sabin *et al.* (2013) (41-55 individuals/km²) in the same area. However, these previous studies did not incorporate the main area of regenerating secondary

forest area (on the southwestern edge) in their surveys. This secondary forest stand has been regenerating since 2000, and may have become a viable habitat for lemurs in recent years. By separating young (<10 years) from older secondary forest (>10 years) we were able to capture the fine-scale trends of usage at different successional stages.

Covariates of detectability greatly influence aspects of detection for a range of taxa in different forest types, affecting the ESW (Buckland *et al.* 2015). In particular, mammals who move quietly and call rarely may not be detected reliably at the transect midline, e.g. lorises *Nycticebus* spp., lemurs *Cheirogaleus* spp. and *Avahi* spp., common palm civet *Paradoxurus hermaphroditus* and colugo *Cynocephalus variegatus* (Duckworth 1998). In mature forests, researchers often overlook the vertical component because animals sitting higher up might be less likely to move and there could be more branches to block eye-shine, and this may confound our results. Furthermore, our results show that different environmental factors affected the lateral visibility of woolly lemurs during line-transect surveys, highlighting a critical consideration when estimating densities during multi-species surveys of lemurs in eastern rainforests in Madagascar. While the thick understorey foliage may explain the lower detectability of eastern woolly lemurs in mature secondary habitat, the observer effect calls for systematic integration of multiple effects in density estimates models.

Our results show that mouse lemurs were present at a density twice as high in regenerating secondary than in mature forest, with the highest encounter rates in regenerating older secondary forest. These results reflect previous studies showing that mouse lemurs use degraded habitat (Dammhahn and Kappeler 2010; Herrera *et al.* 2011; Knoop *et al.* in press; Lehman *et al.* 2006b; Randrianambinina *et al.* 2010), including rural and garden environments

(Ganzhorn 1987; Ganzhorn *et al.* 2003; Irwin *et al.* 2010; Radespiel *et al.* 2012). In some cases, populations in disturbed mature forest are at higher densities than recorded for undisturbed mature forest (Burke and Lehman 2014; Corbin and Schmid 1995; Herrera *et al.* 2011; Schaffler 2012). For example, lemurs were distributed mainly along the forest edge where secretions of the *Homopteran* insect *Flatidia coccinea* were significantly more abundant than in the forest interior (Corbin and Schmid (1995). In both the dry forests of western Madagascar and tropical forests of eastern Madagascar, understorey and shrub layers are important for food resources and protection from aerial predators for mouse lemurs (Ganzhorn 1995; Ganzhorn and Schmid 1998). Mouse lemurs often use the shrub understorey (Ganzhorn 1988; 1989; Ganzhorn 1995). We found the highest densities of mouse lemurs in regenerating forest stands, which were characterized by low canopy height and a thick understorey layer. Additionally, we found the invasive plant *Clidemia hirta*, a crucial food resource for mouse lemurs (Ganzhorn 1987; 1988) associated with perturbed and degraded areas (Lowry *et al.* 1997), at high densities at the edges of transects and throughout the regenerating savoka areas. Further research on the diet of Simmons' mouse lemur may shed light on the cause and the potential seasonality of its habitat preferences.

We only observed the hairy-eared dwarf lemur and aye-aye in intact mature forest, suggesting that they are most affected by habitat degradation and alteration out of the nocturnal lemurs observed in Manompana. Aye-ayes feed on insect larvae extracted from deadwood, hard seeds of *Canarium madagascariensis* and forage in cultivated areas on coconuts, litchis and mangoes (Iwano and Iwakawa 1988; Petter *et al.* 1977; Thompson *et al.* 2016), food sources which would be scarce in younger secondary forest. Additionally, this species builds nests high in the crowns of trees and, although it can travel to forage outside of mature forest, research suggests this species requires mature forest areas, or habitat containing suitable trees for resting

(Ancrenaz *et al.* 1994). The aye-aye is classified as Endangered throughout Madagascar as this species is hunted/and or killed due to local beliefs or *fady* and is widely believed to be a bad omen (Simons and Meyers 2001). Similarly, hairy-eared dwarf lemurs are restricted to mature forest, using tree hollows as sleeping sites, and our results reflect earlier studies suggesting that secondary forest is unsuitable for this species (Biebow *et al.* 2009; Meier and Albignac 1991).

Our results show that regenerating secondary forest habitat can provide benefits to some lemurs, and although many lemurs in Madagascar remain threatened by increasing deforestation and habitat alteration, some species can persist in altered habitat. Alarming recent estimates show that ~60% of primate species are threatened with extinction, and 75% have declining populations mainly due to escalating anthropogenic pressure (Estrada *et al.* 2017). Our results show both tolerance of the altered environment in some species and reliance on mature forest habitat in others. We highlight the importance of regenerating secondary forest following the abandonment of cultivated areas as a viable habitat for primates. It is important we investigate further the dynamics between primates and the anthropogenic environment to broaden our understanding of the scope of responses.

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