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10.1007/s10764-018-0055-5

This is an Author's Accepted Manuscript of: Miller, A., Mills, H., Ralantoharijaona, T., Volasoa, N. A., Misandeanu, C., Chikhi, L., ... & Salmona, J. (2018). Forest Type Influences Population Densities of Nocturnal Lemurs in Manompana, Northeastern Madagascar. *International Journal of Primatology*, 39(4), 646-669.

The final publication is Available [here](#).

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

3 **Abstract**

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

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

26 **Introduction**

27 The world's forests are being rapidly depleted for timber harvest and agricultural land (Evans
28 2009; FAO 2011; Lambin *et al.* 2003). These unprecedented deforestation rates participate in
29 widespread loss of biodiversity throughout forests worldwide (Brooks *et al.* 2002; de Almeida-
30 Rocha *et al.* 2017; Mace *et al.* 2005; Sodhi *et al.* 2004), As a result of these anthropogenic
31 influences, most tropical landscapes are matrices of mature forest remnants, agricultural land
32 and regenerating secondary forests of varying ages (Achard *et al.* 2002; FAO 2011; Hansen
33 and DeFries 2004; Laurance 2004; Skole and Tucker 1993; Wright 2005). As agriculture is one
34 of the significant drivers of biodiversity decline, it is important we manage agricultural systems
35 in ways that allow threatened species to persist within them (Maxwell 2016). Some primates
36 exhibit tolerance and adaptability to anthropogenic landscapes (Eppley *et al.* 2015; Estrada
37 2006; Johns 1986), while others remain dependent on forest habitat for survival (Chapman *et*
38 *al.* 2006; Schwitzer *et al.* 2011), and species responses to similar threat processes can vary
39 (Irwin *et al.* 2010; Isaac and Cowlshaw 2004). Thus it is important that we increase our
40 understanding of plant and animal responses to habitat disturbance, so as to not generalize
41 responses from a few indicator species (Barlow *et al.* 2007).

42 Madagascar is considered a world biodiversity “hotspot” (Myers *et al.* 2000) and among its
43 threatened forest-dwelling species, lemurs are considered to be one of the world's most
44 endangered mammals due to habitat loss, fragmentation and environmental degradation (Green
45 and Sussman 1990; Harper *et al.* 2007; IUCN 2014; Schwitzer *et al.* 2013; Schwitzer *et al.*
46 2014). The transition from mature forest (old-growth forest) to regenerating forest (i.e.,
47 younger and older growth secondary forest), that results from shifting agriculture is deeply

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

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

73 positively to low-medium levels of forest disturbance such as the Southern lesser bamboo
74 lemur (*Hapalemur meridionalis*) which tolerated significant levels of habitat degradation by
75 using an invasive species habitat for feeding and resting (Eppley *et al.* 2015). Similarly, the
76 mostly folivorous sifaka (genus *Propithecus*) increased in numbers along census trails after
77 logging (Ganzhorn 1995), and were frequently found using degraded, secondary and
78 anthropized habitat (*P. coronatus* & *P. coquereli*) in western Madagascar (Salmona *et al.* 2014;
79 Salmona *et al.* 2013). The folivorous nocturnal lemurs (*Avahi* sp., and *Lepilemur* sp.) have
80 shown mixed responses to disturbed habitat (Ganzhorn 1987; Norscia 2008; Sawyer *et al.*
81 2017). The folivorous *Avahi mooreorum* and *Lepilemur scotorum* were more susceptible to
82 increasing habitat disturbance (Sawyer *et al.* 2017), and *Lepilemur grewcockorum* was less
83 abundant in degraded forest, most likely due to the reduced availability of tree holes in old-
84 growth trees (Randrianambinina *et al.* 2010). Omnivorous or insectivorous lemurs are often
85 more abundant in disturbed habitats than in mature forests, potentially due to an increased light
86 penetration and understory biomass linked with high insect abundances
87 (Andriamandimbarisoa *et al.* 2015; Corbin and Schmid 1995; Herrera *et al.* 2011).
88 Omnivorous lemurs, such as mouse lemurs (*Microcebus* sp.), dwarf lemurs (*Cheirogaleous*
89 sp.) and hairy-eared lemurs (*Allocebus trichotis*) have diverse diets, comprising insect
90 secretions, arthropods, small vertebrates, gum, fruits, flowers, nectar, and also leaves and buds
91 (Biebouw *et al.* 2009; Ganzhorn 1988; Lahann 2007; Radespiel 2006; Radespiel *et al.* 2006;
92 Wright and Martin 1995). Mouse lemurs have higher encounter rates in more disturbed regions
93 of Ranomafana National Park (Herrera *et al.* 2011), and in Kirindy forest in western
94 Madagascar, higher numbers were recorded following low-intensity logging (Ganzhorn 1995).
95 We aim to investigate the responses of nocturnal lemurs to a gradient of habitat types ranging
96 from mature forest to regenerating forest (younger and older secondary), conducting surveys
97 in different habitats in north-eastern Madagascar. We investigate the responses of four

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

103 We aim to answer the following questions:

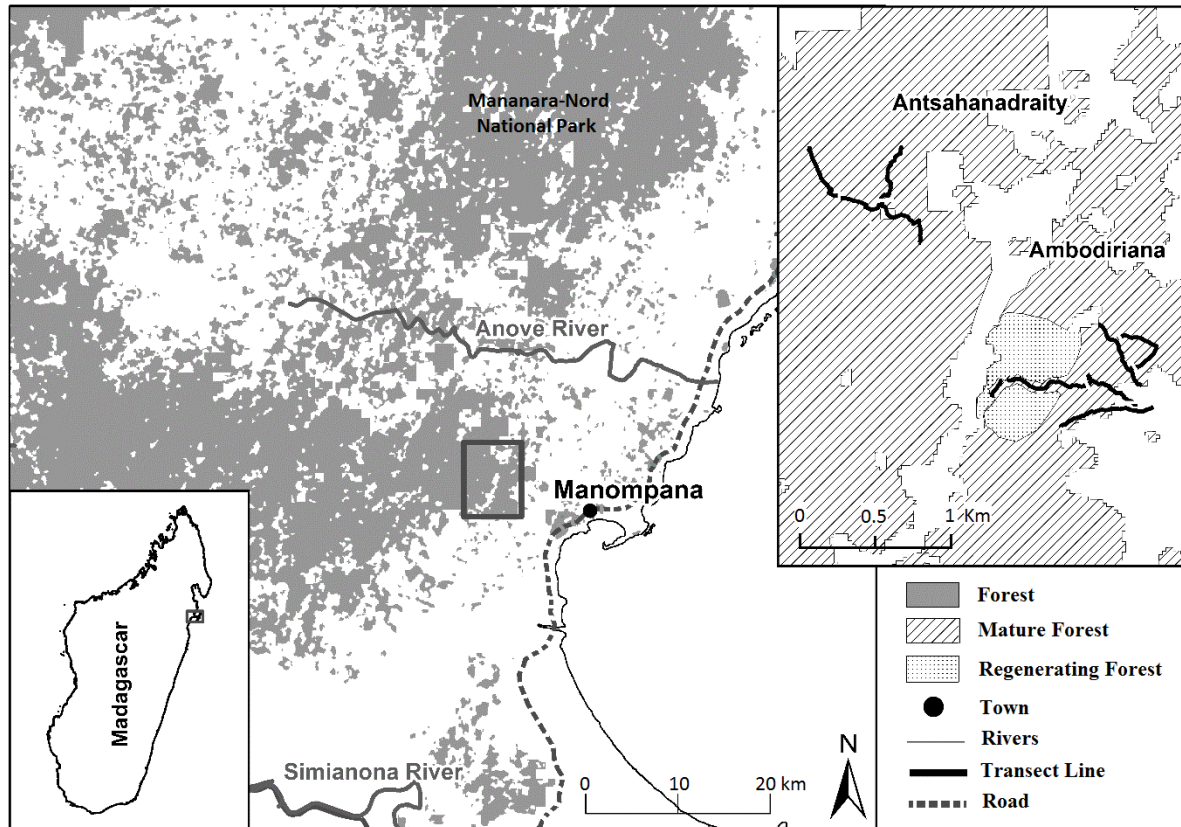
- 104 1. Do different habitat types with ranging levels of disturbance affect the abundance of
105 nocturnal lemur species?
- 106 2. Is regenerating secondary forest a viable habitat for nocturnal lemurs?

107 **Methods**

108 *Study sites*

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

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



124
125 **Figure 1. Map of survey sites used to study nocturnal lemurs. Squares show the survey**
126 **forests. Top right box shows the location of transects in two forests, Antsahanadraity**
127 **and Ambodiriana, with mature forest and regenerating secondary forest**

128 *Study species*

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

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

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

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

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

152 We conducted our survey during the austral winter (May-August), which is generally
153 characterized by low ambient temperatures and resource scarcity for many lemurs (Wright
154 1999). Several mouse lemur species from central and southern Madagascar enter prolonged
155 torpor during the dry season (Schmid and Speakman 2000; 2009). If *M. cf. simmonsi* undergoes
156 prolonged torpor during the dry season, the population may be larger than estimated in this
157 study. In addition, *Cheirogaleus* sp. is known to hibernate during the austral winter in eastern

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

161 *Habitat survey*

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

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

183 plant species richness (all species present), total herbaceous plant abundance per species, total
 184 tree abundance ('tree' defined as a perennial plant with an elongated stem, or trunk, supporting
 185 branches and leaves), circumference at breast height of each tree (CBH) (<15 cm, 15-30 cm,
 186 31-65 cm, 66-95, >95 cm), and tree height (mean tree height estimated in meters of whole
 187 quadrat) (≤ 5 m, 6-15 m, 16-25 m, 25-35 m, >35 m). We used the quadrat (5 x 5 m) information
 188 to compare the forest structure of Ambodiriana and Antsahanadraitry.

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

194 **Table 1. Characteristics used to differentiate habitat types at Ambodiriana and**
 195 **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}	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>Dyopsis</i> (Arecaceae) and <i>Pandanus</i> (Pandanaaceae) ^{e,f,g} . 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 .

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

199 ⁺Exotic species

200 *Distance sampling procedures*

201 We carried out line transect distance sampling surveys (Buckland *et al.* 2001) in June and July
202 2014. We used six pre-existing trails (180–802 m) in Ambodiriana forest and two pre-existing
203 and one new transect (500-986 m) in Antsahanadraitry forest (Figure 1). We conducted 74
204 nocturnal surveys totaling 51 km: 62 surveys in Ambodiriana forest (41.9 km; 25.9 km mature
205 forest, 16 km regenerating secondary) and 12 surveys in Antsahanadraitry forest (9.1 km;
206 mature forest). These surveys corresponded to 35 km in mature forest and 16 km in
207 regenerating secondary forest. To avoid disturbing animals before the survey, we never
208 conducted surveys during the 24 hours following the creation of a transect. Using existing trails
209 can bias survey results, although one study found no significant effects of using existing trails
210 on lemur densities (Lehman 2006). We found no direct or indirect evidence of hunting along
211 trails, and only rare instances of disturbance in the form of cut trees. Considering topography,
212 time constraints, and conservation restrictions, the combination of trails and transects were the
213 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)

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

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

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

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

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

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

290 *Ethical Note*

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

297 **Results**

298 *Habitat and botanical survey*

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

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

312 **Table 2. Results of two-sample t-tests assuming unequal variances comparing habitat**
 313 **variables measured in 3 x 0.5 m plots in mature and regenerating secondary**
 314 **forest in Ambodiriana and Antsahanadraitry forests, north-eastern Madagascar**
 315 **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

316 Variables with a significant result in bold

317 **Table 3. Results of two-sample t-tests assuming unequal variances comparing habitat**
 318 **variables in 3 x 0.5 m plots in mature and degraded mature forest in**
 319 **Ambodiriana and Antsahanadraitry forests, north-eastern Madagascar in**
 320 **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

321 Variables with a significant result in bold

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

324 secondary forest in Ambodiriana and Antsahanadraitry forests, north-eastern
 325 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

326 Variables with a significant result in bold

327 **Table 5. Results of two-sample t-tests assuming unequal variances comparing habitat**
 328 **variables measured in 5 m x 5 m quadrats in Antsahanadraitry and Ambodiriana**
 329 **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	-	-	-	-	-

330 Variables with a significant result in bold

331 *Lemur surveys*

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

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

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

Transect #	Ambodiriana						Antsahanadraitry			
	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 cf. simmonsii</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

344

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

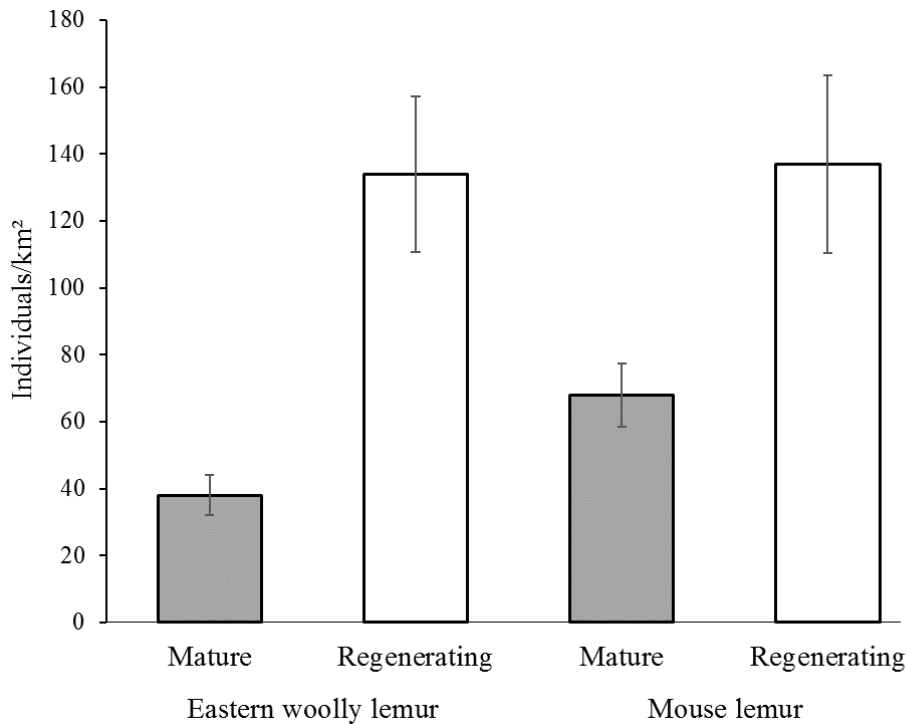
Species	Habitat type			
	Regenerating young secondary	Regenerating older secondary	Degraded mature	Mature
<i>Avahi laniger</i>	29	20	17	26
<i>Microcebus cf. simmonsii</i>	20	7	9	27
<i>Allocebus trichotis</i>	0	0	2	2
<i>Daubentonia madagascariensis</i>	0	0	0	2
Total	49	27	28	57

347

348 *Density estimates from line-transect surveys*

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

360 We estimated a density of the eastern woolly lemur of 38 ± 6.0 (SE) ind/km² in mature forest
361 and 134 ± 23.3 (SE) ind/km² in regenerating secondary forest using Multiple Covariates
362 Distance Sampling (MCDS) analyses (Figure 2). The corresponding effort was 35 km in mature
363 forest (*A. laniger* n=43), and 16 km in regenerating secondary forest (*A. laniger* n=49) (Tables
364 8 and 9). Of the variables we tested, the detection of eastern woolly lemurs was most affected
365 by a combination of habitat type and observer identity (Akaike weight (W_i)=0.72) (Table 8).
366 Detection probability was lowest in regenerating older secondary forest, and highest in mature
367 forest. Observer identity and the combination of observers affected the detection probability of
368 eastern woolly lemurs. The presence of both observers in the same team resulted in a wider
369 ESW, resulting in differing detection probabilities in different habitat types.



370

371 **Figure 2. Density (individuals/km²) of the eastern woolly lemur and mouse lemur in**
 372 **mature and regenerating secondary forest using Multiple Covariates Distance Sampling**
 373 **in Ambodiriana and Antsahanadraitry forests, north-eastern Madagascar in June/July**
 374 **2014.**

375 The eastern woolly lemur also had significantly higher encounter rates (km⁻¹) in regenerating
 376 older secondary forest than in other forest types (Table 10), Levene's Test with one-way
 377 ANOVA ($F_{3,68} = 178.46$, $p < 0.001$, effect size: partial $\eta^2 = 0.893$). Encounter rates for eastern
 378 woolly lemurs were significantly different among the four habitat types (Kruskal-Wallis, $X^2 =$
 379 58.27 , $p < 0.05$).

380

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

	K	AICc	W_i	ESW	D	95% CI	%CV
--	----------	-------------	----------------------	------------	----------	---------------	------------

						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
<i>Mouse lemur</i>	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.**

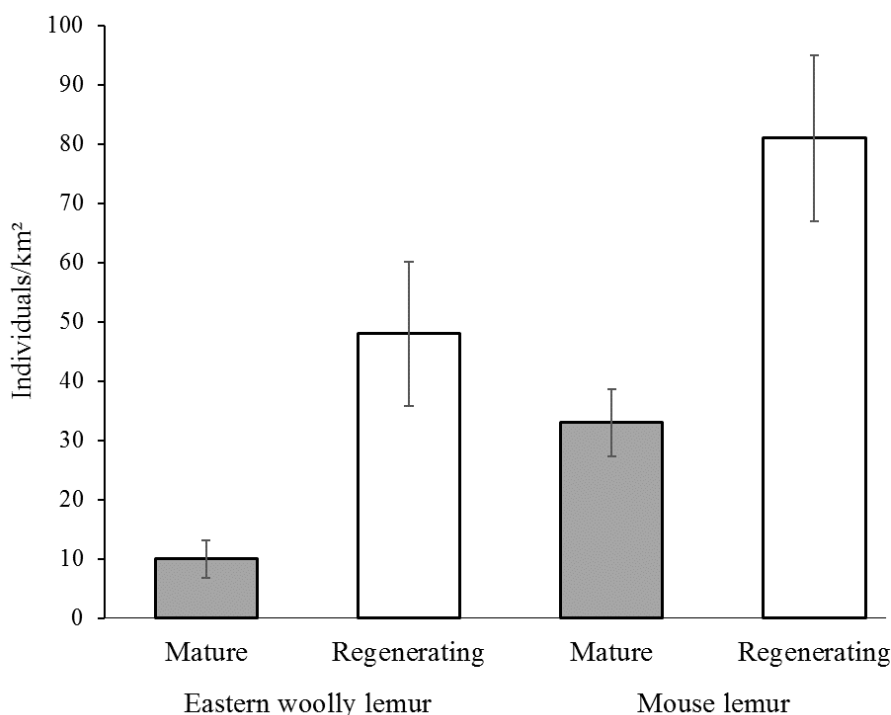
Forest type	Effort (km)	Number of sightings		Encounter rate (km ⁻¹)	
		<i>A. laniger</i>	<i>M. cf. simmonsi</i>	<i>A. laniger</i>	<i>M. cf. simmonsi</i>
Regenerating young	13.13	29	20	2.21	1.52
Regenerating older	2.94	20	7	6.80	2.38
Degraded mature	4.08	17	9	4.17	2.20
Mature	31.61	26	27	0.82	0.85

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

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

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



413

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

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

422

423 **Discussion**

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

436

437 Our results highlight the capacity of the folivorous eastern woolly lemur to persist in habitats
438 with anthropogenic disturbance, with the highest densities in regenerating secondary forest,
439 and highest encounter rates in regenerating older secondary and degraded mature forest in
440 northeastern Madagascar. The high encounter rates in degraded mature forest support the
441 hypothesis that increased leaf quality in disturbed habitats benefits folivorous species
442 (Ganzhorn 1995; Onderdonk and Chapman 2000). High densities of the favored food tree
443 (*Harungana madagascariensis*) (Faulkner and Lehman 2006; Ganzhorn *et al.* 1985; Harcourt
444 1991) in regenerating secondary forest, or the dense structure of secondary stands providing
445 substrates for clinging, leaping and sleeping may explain the higher densities of woolly lemurs.

446

447 Although previous research suggests that eastern woolly lemurs are not particularly sensitive
448 to habitat disturbance (Lehman *et al.* 2006b), our results appear to contradict a study that found
449 that woolly lemurs preferred mature forest to logged forest in Ranomafana National Park
450 (Herrera *et al.* (2011). Additionally, in Makira-Masoala region no differences in densities or
451 encounter rates were recorded for eastern woolly lemurs at intact, intermediate, and degraded
452 forest sites (Murphy *et al.* 2016), which also differs from our results and those of Herrera *et al.*
453 (2011). This suggests that other factors such as hunting pressure and other types of human
454 activities are important, beyond the dichotomy of "mature or primary" versus "secondary"
455 forests across regions of Madagascar (Golden 2009).

456

457 Our density estimates for eastern woolly lemurs in Ambodiriana forest (87 individuals/km²)
458 are similar to those of Beaucent and Fayolle (2008) (86 individuals/km²), Ferrier and Lacroix
459 (2008) (58 individuals/km²), and Sabin *et al.* (2013) (41-55 individuals/km²) in the same area.
460 However, these previous studies did not incorporate the main area of regenerating secondary

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

465

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

479

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

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

501

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

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

515

516 Our results show that regenerating secondary forest habitat can provide benefits to some
517 lemurs, and although many lemurs in Madagascar remain threatened by increasing
518 deforestation and habitat alteration, some species can persist in altered habitat. Alarming recent
519 estimates show that ~60% of primate species are threatened with extinction, and 75% have
520 declining populations mainly due to escalating anthropogenic pressure (Estrada *et al.* 2017).

521 Our results show both tolerance of the altered environment in some species and reliance on
522 mature forest habitat in others. We highlight the importance of regenerating secondary forest
523 following the abandonment of cultivated areas as a viable habitat for primates. It is important
524 we investigate further the dynamics between primates and the anthropogenic environment to
525 broaden our understanding of the scope of responses.

526

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