

1 The effect of habitat disturbance on the abundance of nocturnal
2 lemur species on the Masoala Peninsula, north eastern
3 Madagascar.

4

5 Sawyer, Rachel Mary^{1*}, Fenosoa, Zo Samuel Ella², Andrianarimisa, Aristide^{2,3}
6 and Donati, Giuseppe¹

7 ¹ Department of Social Sciences, Oxford Brookes University, Oxford, OX3 0BP, United
8 Kingdom.

9 ² Département Biologie Animale, Université d'Antananarivo, Antananarivo, Madagascar.

10 ³ Wildlife Conservation Society, Villa Ifanomezantsoa, Face II A 78 D, Soavimbahoaka,
11 Antananarivo 101, BP8500, Madagascar.

12 * e-mail: rachel.mary.sawyer@gmail.com; phone: +44 (0) 1865 483780; fax: +44 (0) 1865
13 483937

14

15 ABSTRACT

16 Madagascar is one of the world's 'biodiversity hotspots'. The island's past and current rates of
17 deforestation and habitat disturbance threaten its plethora of endemic biodiversity. On
18 Madagascar, *tavy* (slash and burn agriculture), land conversion for rice cultivation, illegal
19 hardwood logging and bushmeat hunting are the major contributors to habitat disturbance.
20 Understanding species specific responses to habitat disturbance across different habitat types
21 is crucial when designing conservation strategies. We surveyed three nocturnal lemur species
22 in four forest types of varying habitat disturbance on the Masoala Peninsula, north eastern
23 Madagascar. We present here updated abundance and density estimates for the Endangered

24 *Avahi mooreorum* and *Lepilemur scottorum*, and *Microcebus* sp. Distance sampling surveys
25 were conducted on 11 transects, covering a total of 33km after repeated transect walks. We
26 collected data on tree height, bole height, DBH, canopy cover and tree density using point
27 quarter sampling to characterise the four forest types (primary lowland, primary littoral,
28 selectively logged and agricultural mosaic). Median encounter rates by forest type ranged from
29 1-1.5 ind./km (*Microcebus* sp.), 0-1 ind./km (*Avahi mooreorum*) and 0-1 ind./km (*Lepilemur*
30 *scottorum*). Species density estimates were calculated at 232.31 ind./km² (*Microcebus* sp.) and
31 121.21 ind./km² (*Avahi mooreorum*), while no density estimate is provided for *Lepilemur*
32 *scottorum* due to a small sample size. *Microcebus* sp. were most tolerant to habitat
33 disturbance, exhibiting no significant effect of forest type on abundance. Their small body size,
34 omnivorous diet and generalised locomotion appear to allow them tolerate a variety of habitat
35 disturbance. Whereas both *Avahi mooreorum* and *Lepilemur scottorum* showed significant
36 effects of forest type on their respective abundance. This study suggests that the specialist
37 locomotion and diet of *Avahi mooreorum* and *Lepilemur scottorum* makes them susceptible to
38 the effects of increasing habitat disturbance.

39

40 **Keywords:** *Microcebus* sp., *Avahi mooreorum*, *Lepilemur scottorum*. anthropogenic disturbance, line
41 transects, densities.

42

43

44 INTRODUCTION

45 Primate responses to habitat disturbance are often species and site specific (Fimbel,
46 1994), and many primates have been shown to be ecologically flexible and able to
47 tolerate some level of habitat disturbance (Johns and Skorupa, 1987; Chapman and
48 Lambert, 2000; Donati et al., 2011). Large bodied frugivorous species are considered to
49 be most at risk from habitat disturbance, based on their reliance on larger trees which
50 are patchily distributed, and higher ranging area per unit biomass (Johns, 1992; Arrigo-
51 Nelson, 2006). On the contrary, small prosimians which consume insects, such as
52 Dian's tarsiers (*Tarsius diana*; Merker and Mühlenberg, 2000), and Javan slow lorises
53 (*Nycticebus javanicus*; Rode-Margono et al., 2014) have been observed at high
54 abundances in agricultural mosaic habitats, and appear more tolerant. Folivorous species
55 have also been observed to cope well with a low level of habitat disturbance, and in
56 some cases show higher abundances in selectively logged areas due to increased leaf
57 quality and productivity (Johns, 1988; Ganzhorn, 1995; Arroyo-Rodríguez and Dias,
58 2009). Much of the research which currently exists on primates in disturbed habitats is
59 focussed on forest fragments or species responses in dichotomous situations, i.e. intact
60 versus degraded areas, with research lacking comparing species responses across
61 habitats which differ in the type of disturbance they experience (Irwin et al., 2010;
62 Schwitzer et al., 2011). Just as there are few homogeneous intact forests, there are
63 equally few homogeneous degraded areas, and the continuous use of anthropogenic
64 zones makes them extremely dynamic ecosystems (Bennett et al., 2006).

65 Anthropogenic land use on Madagascar has resulted in the emergence of many
66 heterogeneous habitats which vary largely in quality over a relatively small area
67 (Herrera et al., 2011). Despite the large network of protected areas (Kaufman, 2006),

68 many wildlife populations inhabit areas outside of these zones (Irwin et al., 2010;
69 Schwitzer et al., 2011). Due to the limited financial and logistic resources of the parks'
70 management to patrol and protect Madagascar's National Parks, increasingly local
71 communities are encroaching on the parks, resulting in the alteration of these
72 'protected' habitats (Kull, 2002). Landscape alterations may have significant effects on
73 species which reside in these changing habitats. 'Domino effects' of a changing habitat
74 can include; dispersal, restricted locomotion, reduced food resources, reduction in
75 suitable sleeping sites, increased hunting risk and increased parasite loads (Golden et
76 al., 2011; 2014; Schwitzer et al., 2011; Junge et al., 2011; Lazdane et al. 2014; Balestri
77 et al., 2014).

78 In recent years' research into lemur communities living in degraded habitats has
79 increased exponentially (Irwin et al., 2010; Donati et al., 2011 Schwitzer et al., 2011;
80 Tecot, 2013; Balestri et al., 2014; Campera et al., 2014). Studies into nocturnal lemur
81 responses to habitat degradation have shown that they are ecologically flexible and
82 largely tolerant to minor habitat changes (Lehman et al., 2006a; 2006b; Radespiel,
83 2007; Meyler et al., 2012). Mixed results have been observed for folivorous nocturnal
84 lemurs (*Avahi* sp. and *Lepilemur* sp.) living in disturbed habitats. Whereas some species
85 have been found at high abundance in disturbed areas (Ganzhorn, 1987, 1999; Norscia,
86 2008), others have been found at lower densities than their conspecifics in primary
87 habitats (Randrianambinina et al., 2010; Lehman et al., 2006a). This can be attributed to
88 their specialised locomotion and diet, as heavy disturbance can reduce or eradicate
89 dispersal paths between populations (Ganzhorn, 1993; Lawes et al., 2000; Thalmann,
90 2003), and heavy tree cutting can ultimately limit leaf production and therefore dietary
91 resources (Thalmann, 2003). Small insectivorous lemurs such as *Microcebus* sp. have

92 been frequently observed in anthropogenic habitats, and particularly agricultural mosaic
93 habitats, as these ecosystems often contain a high abundance of insects (Ganzhorn,
94 1987; Lehman et al., 2006b). Their small body size and generalised locomotion allows
95 them to exploit a mixture of substrate sizes without causing major restriction to their
96 movements (Radespiel, 2007).

97 This study aims to address some of the knowledge gaps which exist in nocturnal lemur
98 responses to habitats differing in the type of disturbance. In particular, we aim to assess
99 how differing habitat disturbance affects forest structure and composition, and in turn
100 the abundance of nocturnal lemur species on the northwest Masoala Peninsula,
101 northeastern Madagascar. We will measure the habitat characteristics of four forest
102 areas of differing disturbance to characterise how different types of disturbance shape
103 vegetation structure and composition. We will do so by measuring various habitat
104 characteristics shown to affect the locomotion and resource availability of our study
105 genera (Ganzhorn, 1989; Seiler et al., 2014). Tree height and bole height, for example,
106 have been shown to be important structural characteristics for vertical clingers and
107 leapers, and could be particularly important in areas where *Avahi* spp. and *Lepilemur*
108 spp. are sympatric in terms of vertical niche separation (Thalmann, 2001).

109 Specifically, we aim to answer the following questions;

110 1) Do different types of habitat disturbance affect the abundance of nocturnal lemur
111 species?

112 2) Which species are most affected, and what are the ecological correlates of lemur
113 responses to varying habitat disturbance?

114 Currently the nocturnal species studied here have no population abundance estimates
115 available on the IUCN Red List (IUCN, 2014). We will therefore present here updated
116 estimates of abundance for *Microcebus* sp., *Avahi mooreorum* and *Lepilemur scottorum*
117 on the Masoala Peninsula. The last nocturnal census was carried out on the Peninsula in
118 1994-1995, when plans were being made to create Masoala National Park (Sterling and
119 Rakotoarison, 1998). However, many species classifications have changed since this
120 time, and data on these species requires updating.

121

122 METHODS

123 Study Site & Species

124 The study was conducted on the north western coast of the Masoala Peninsula
125 surrounding the village of Ambodiforaha (S15°42.728', E049°57.839'). Masoala
126 National Park was gazetted as a National Park in 1997, the Park ranges in altitude from
127 0-1300m above sea level, and is a combination of lowland and high elevation humid
128 forest, with some small areas of remaining littoral forest (Kremen et al., 1999;
129 Schwitzer et al., 2013). Masoala National Park was contained for the conservation of
130 biodiversity, and outside of the park boundary land was set aside for multiple resource
131 use by local communities (Kremen et al., 1999). Annual rainfall in the park ranges from
132 2,200-7,000 mm and average yearly temperatures range from 21-24°C (Martinez,
133 2010). The Park has four distinct seasons 1) hot-rainy (January-March), 2) transitional
134 cold (April-May), 3) cold rainy (June-August), and 4) hot dry (October- December)
135 (Vasey, 2000).

136 Masoala National Park is home to a total of 10 species of lemur, 3 diurnal or cathemeral
137 species; *Varecia rubra*, *Eulemur albifrons*, and *Hapalemur occidentalis*, and 7
138 nocturnal species; *Microcebus* sp., *Cheirogaleus major*, *Allocebus trichotis*, *Phaner*
139 *furcifer*, *Lepilemur scottorum*, *Daubentonia madagascariensis*, and *Avahi mooreorum*.
140 This region is recognised as an area of high floristic and faunal diversity and endemism.
141 All nocturnal lemur species present at Masoala National Park were included in this
142 study, although only *Microcebus* sp., *Avahi mooreorum*, *Lepilemur scottorum* and
143 *Daubentonia madagascariensis* were observed (Table 1).

144 Vegetation Assessment

145 Nocturnal lemur censuses were carried out between 13 May and 25 June, 2014.
146 Transects were marked within an area of “primary” lowland forest, an area of “primary”
147 littoral forest, an area of agricultural mosaic forest used by local communities, and an
148 area used predominantly for selective logging for construction materials by local
149 communities. We categorised the different forest types (primary lowland, primary
150 littoral, selectively logged and agricultural mosaic) based on their vegetation structure
151 and anthropogenic uses, and although all habitats are heterogeneous, we grouped
152 transects into study areas based on their main human use and structural characteristics
153 (Herrera et al., 2011; Nekaris et al., 2014).

154 Data on habitat characteristics were collected using the point-quarter sampling method
155 (Ganzhorn et al., 2011). Botanical sampling was carried out along transect lines of
156 750m. Point-quarter samples were taken every 50m along the transect line, including
157 the start and end point, to a depth of 3m. At each point quarter sample structural tree
158 data was collected on all trees ≥ 5 cm diameter at breast height (DBH). We chose a DBH
159 of ≥ 5 cm based on the small body weight (39.5g-47.9g) of *Microcebus* sp. and their

160 inclusion in our surveys (Mittermeier et al., 2010). In order to standardise between the
161 four forest types, and to allow for comparisons within this study, we applied the DBH
162 $\geq 5\text{cm}$ to all forest types. Structural data collected in each forest type included; tree
163 height (m), bole height (m), circumference at breast height (CBH; to be later converted
164 to DBH), canopy cover (%), and tree density (Ganzhorn et al., 2007). All estimates for
165 tree height, bole height and canopy cover were made by the same observer, to reduce
166 inter-observer bias. Sampled trees were marked with flagging and vernacular names
167 provided by the local field guide. Voucher specimens were collected for each tree
168 identified. Specimens were deposited for scientific identification by botanists at the Parc
169 Botanique et Zoologique Tsimbazaza in Antananarivo.

170

171 Lemur Surveys

172 We conducted surveys using the line-transect method of distance sampling with
173 multiple observers (Buckland et al., 2001). In total we conducted 44 nocturnal surveys,
174 equating to a total survey effort of 33km. We surveyed three transects of 750m in three
175 of the study areas (primary lowland, selectively logged and agricultural mosaic forest)
176 and two transects of 750m in one area (primary littoral forest), separated by a gap of
177 250m. Fewer trails were walked in the primary littoral forest due to limited availability
178 of existing trails. We used pre-existing trails to minimize disturbance, and transects
179 were marked every 25m with flagging tape. We surveyed transect routes slowly
180 (0.25/0.5km per hour) either between 18:00-midnight or midnight-06:00 (Chapman et
181 al., 1988; Norscia, 2008; Nekaris et al., 2014). Each line transect was repeated a total of
182 4 times over the study period (Rovero et al., 2006). We walked line transects with a
183 10m distance between team members, checked both sides of the transect line, and

184 checked regularly behind ourselves to minimise our chances of missing an observation
185 (Nekaris et al., 2014). Survey routes were not repeated more than once per week. We
186 alternated the starting point on each repetition of a route to reduce bias (Fashing and
187 Cords, 2000; Ross and Reeve, 2011).

188 As *Avahi mooreorum* is a pair-living taxon observations of >1 individual were
189 considered to be a single cluster, although on occasions individuals were observed
190 alone. Upon detection of a lemur cluster, data were collected on; the date, time (hour:
191 minute), weather (rain or no rain), study area and transect number, GPS co-ordinate,
192 species, cluster size and composition, perpendicular distance from line to group
193 centre/individual, or distance from observer to individual (Fashing and Cords, 2000;
194 Lehman et al., 2006a; Marshall et al., 2008; Meyler et al., 2012).

195

196 Abundance Metrics & Density Estimates

197 We estimated lemur abundance using median encounter rates (number of individual
198 encounters/transect walk) of each taxon in each forest type. We also calculated mean
199 species-specific cluster size (number of individuals/number of observations) by forest
200 type. No statistical analyses were performed on *Daubentonia madagascariensis* due to a
201 small sample size (n=1). Overall density estimates (number of individuals/ km²) for
202 *Microcebus* sp. (n=70) and *Avahi mooreorum* (n=51) were calculated by pooling all
203 transects and repeats for each species. No density estimate is provided for *Lepilemur*
204 *scottorum* due to a small sample size (n=20). The Buckland method of distance
205 sampling was carried out using Distance 6.0 software (Buckland et al., 2001; 2010;
206 Thomas et al., 2010). We truncated our data at 5% (Meyler et al., 2012). We chose the
207 estimated strip width (ESW) which returned the lowest Akaike Information Criterion

208 (AIC) value and a high goodness-of-fit Chi-square (GOF Chi-p) value (Buckland et al.,
209 2001).

210 Statistical Analyses

211 All forest structural variables were tested for normality using the Kolmogorov-Smirnov
212 test. Any structural variables which deviated significantly from normality were log-
213 transformed to render them normally distributed and allow parametric statistical tests.
214 Analyses of variance (ANOVA) were used to compare habitat variables between the
215 four forest types. Post-hoc Tukey Least Significance Difference (LSD) tests were used
216 to identify which forest type contributed to the significant result. ANOVA were also
217 implemented to investigate differences in animal-transect perpendicular detection
218 distances between the forest types.

219 We used a General Linear Mixed Model (LMM) to investigate the effect of forest type,
220 time and weather on encounter rates of *Microcebus* sp., *Avahi mooreorum* and
221 *Lepilemur scottorum* (Dytham, 1999). “Encounter rate” was used as response variable,
222 “forest type”, “time” (am or pm) as fixed effects, and “transect ID” as random effect.
223 Before running the model, we tested the effect of “weather” on species mean encounter
224 rates using a univariate ANOVA and found no significant effect; *Lepilemur scottorum*
225 ($F=0.106$, $df=1$, $p=0.746$), *Avahi mooreorum* ($F=0.66$, $df=1$, $p=0.798$), *Microcebus* sp.
226 ($F=0.143$, $df=1$, $p=0.707$). As our sample size was small ($n =24$), we did not include
227 weather in our LMM to decrease the degrees of freedom. There were no significant
228 differences shown in perpendicular detection distances for all nocturnal lemur
229 observations between forest types ($F=0.123$, $df=3$, $p= 0.944$), or in species-specific
230 perpendicular detection distances between forest types; *Microcebus* sp. ($F=1.368$, $df=3$,
231 $p=0.300$), *Avahi mooreorum* ($F= 1.640$, $df=3$, $p=0.256$), *Lepilemur scottorum* ($F=$

232 0.346, $df=2$, $p= 0.721$). We thus pooled the data to estimate overall densities. Residuals
233 from our analyses were tested for normal distribution using the Kolmogorov-Smirnov
234 test. Residuals from the *Lepilemur scottorum* LMM were not normally distributed.
235 Despite this, we opt to still report the results of the LMM as the test is acknowledged to
236 be quite robust to violations (Gelman and Hill, 2007). Post-hoc LSD tests were used to
237 identify significant differences within fixed effects from the LMM's. All statistical
238 analyses were carried out using SPSS 21.

239

240 RESULTS

241 Habitat Structure

242 No significant differences were shown in mean DBH between the four forest types
243 ($F_{3,170}= 2.597$, $p= 0.054$). Mean tree height was significantly different between the four
244 forest types ($F_{3,170}= 15.344$, $p<0.001$: Table 2). Post-hoc LSD tests showed mean tree
245 height in the primary lowland forest was significantly higher than in the agricultural
246 mosaic forest ($p<0.001$), and the primary littoral forest ($p=0.026$). Mean tree height in
247 the selectively logged forest was significantly higher than in the agricultural mosaic
248 forest ($p<0.001$), and was also significantly higher in the primary littoral forest than the
249 agricultural mosaic forest ($p<0.001$). Significant differences were also revealed in the
250 mean bole height between the four forest types ($F_{3,170}=25.689$, $p<0.001$). Post-hoc LSD
251 tests revealed the mean bole height was significantly higher between three forest types,
252 the primary lowland forest ($p<0.001$), primary littoral forest ($p<0.001$), selectively
253 logged forest ($p<0.001$) and the agricultural mosaic forest, and in addition significantly
254 higher in the primary littoral forest than the selectively logged forest ($p=0.036$).

255 Other habitat parameters which significantly differed between the four forest types
256 included mean percentage canopy cover ($F_{3,170}=9.767, p<0.001$), and mean tree density
257 per ha ($F_{3,170}=7.782, p<0.001$). Follow-up post-hoc LSD tests showed mean percentage
258 canopy cover was significantly higher in the primary forest than the three other forest
259 types; littoral forest ($p=0.001$), selectively logged forest ($p=0.004$) and the agricultural
260 mosaic forest ($p<0.001$). Post-hoc LSD tests showed that mean tree density per ha was
261 significantly lower in the agricultural mosaic forest than the three other forest types;
262 primary forest ($p=0.000$), littoral forest ($p<0.001$) and selectively logged forest
263 ($p=0.001$). We also observed variation in the floristic composition of the four forest
264 types, although there were some species which overlapped between the study areas
265 (Table 2). *Anisophyllea fallax* and *Garcinia commersonii* were the only two tree species
266 which were present in more than one forest type.

267 Lemur abundance

268 A total of 142 individuals representing four nocturnal lemur species were observed;
269 *Microcebus* sp. (n=70), *Avahi mooreorum* (n=51), *Lepilemur scottorum* (n=20) and
270 *Daubentonia madagascariensis* (n=1). There were two instances in which the
271 vocalisations of *Phaner furcifer* were heard in the primary lowland forest, although no
272 individuals were observed. No direct sightings were made of *Cheirogaleus major* or
273 *Allocebus trichotis* but we were informed of sightings of the two species (Table 1).

274 When data is pooled within sites, nocturnal lemur encounter rates and species richness
275 was highest in the primary lowland forest and lowest in the agricultural mosaic forest
276 (Table 3). Among the four forest types and between survey times we found no
277 significant effect for either factor on *Microcebus* sp. encounter rates (forest type: $F_{3,36}=$
278 $0.521, p=0.475$; time: $F_{1,36}=1.078, p=0.371$), and the interaction between forest type

279 and time also showed no significant effect on *Microcebus* sp. encounter rates ($F_{3,36}=$
280 0.044, $p=0.988$);). We found a significant effect of forest type on *Avahi mooreorum*
281 encounter rates ($F_{3,36}= 3.190$, $p=0.035$). Both time and the interaction of time and forest
282 type were found to have no significant effect on *Avahi mooreorum* encounter rates
283 (time: $F_{1,36}= 0.275$, $p= 0.603$; forest type: $F_{3,36}= 1.856$, $p=0.155$). Follow up pairwise
284 comparisons identified that *Avahi mooreorum* encounter rates were significantly higher
285 in the primary lowland forest ($p=0.008$), and selectively logged forest ($p=0.016$) than in
286 the agricultural mosaic forest (Table 3). Forest type was shown to have a strong
287 significant effect on *Lepilemur scottorum* encounter rates also ($F_{3,36}=5.542$, $p=0.003$).
288 Follow-up pairwise comparisons identified a significantly higher abundance of
289 *Lepilemur scottorum* in primary lowland forest over the selectively logged forest
290 ($p=0.018$) and the agricultural mosaic forest ($p=0.001$), and also a significantly higher
291 abundance of *Lepilemur scottorum* in primary littoral forest over the agricultural mosaic
292 forest ($p=0.007$) (Table 3). Time and the interaction between time and forest type were
293 found to not be significant predictors of *Lepilemur scottorum* encounter rates ($F_{1,36}=$
294 3.586, $p=0.066$ and $F_{3,36}=1.834$, $p=0.158$).

295 Population Density

296 Population density estimates are provided for *Microcebus* sp. and *Avahi mooreorum*
297 pooling all observations from the four forest types (Table 3). The half-normal key with
298 cosine adjustments provided the lowest AIC for *Microcebus* sp. (AIC 161.26) and *Avahi*
299 *mooreorum* (AIC 107.86) respectively, and in addition provided high goodness of fit
300 values (*Microcebus* sp.= 0.650, *Avahi mooreorum*= 0.871 GOF Chi-p). The population
301 density of *Microcebus* sp. was estimated at 232.31 individuals/km² (95% CI= 147.49-

302 365.92), while the population density of *Avahi mooreorum* was estimated at 121.21
303 individuals/km² (95% CI= 73.02- 201.20).

304

305 DISCUSSION

306

307 The primary lowland forest of the Masoala National Park exhibited the highest species
308 richness of the four study areas. Structurally the primary forest exhibited the highest
309 mean tree height, mean bole height, mean percentage canopy cover, and an intermediate
310 tree density. These characteristics were lowest in the agricultural mosaic forest, as was
311 lemur species richness, which is typical of areas with anthropogenic disturbance
312 (Ganzhorn et al., 1997; Irwin et al., 2010; Schwitzer et al., 2011). The similarities
313 observed in mean DBH between the four forest types is likely to be a consequence of
314 the methods used to collect DBH which took trees of ≥ 5 cm as the lowest value, rather
315 than the standard ≥ 10 cm DBH which is commonly used (Ganzhorn et al., 2007).

316 Both *Avahi mooreorum* and *Lepilemur scottorum* were observed at their highest
317 abundance in the primary lowland forest, and at their lowest abundance in the
318 agricultural mosaic forest. The structural characteristics of these two study areas,
319 suggest that the abundance of the two lemur species is positively correlated with higher
320 mean tree and bole heights, which are more frequently observed in areas of lower
321 disturbance (Hitimana et al., 2004; Balko and Underwood, 2005; Malone et al., 2013).
322 A similar pattern has been observed for these genera at sites across Madagascar
323 (Herrera et al., 2011; Seiler et al., 2014). Both *A. mooreorum* and *L. scottorum* are
324 vertical clingers and leapers (VCL's), this is a postural and locomotor "habit" in which
325 the individual clings on to and leaps between predominantly vertical supports (Demes et

326 al., 1996). It is an expensive form of locomotion (Warren and Crompton, 1998), in
327 which the species often require large trees (in Madagascar trees with a DBH
328 $\geq 5\text{cm}/10\text{cm}$; Ganzhorn et al., 1999) to move around their habitat (Norscia, 2008). The
329 space between the tree crown and ground is preferred for VCL's, meaning that
330 increased tree and bole heights provide these two species with a greater space in which
331 to navigate (Ganzhorn, 1989; Warren, 1997).

332 Food resource availability can significantly influence the occurrence and abundance of
333 animal populations (Balko and Underwood, 2005). *Avahi* sp. and *Lepilemur* sp. are both
334 dedicated folivores (Ganzhorn, 1985; Nash, 1998; Thalmann, 2001), where abundance
335 is often positively correlated with the availability of preferred food tree species
336 (Ganzhorn et al., 1997). Preferred tree species of *Avahi* sp. include *Harongana*
337 *madagascariensis*, *Syzygium* sp. and *Symphonia* sp., which are often present in
338 disturbed habitats (Ganzhorn, 1985; Lowry et al., 1997; Faulkner and Lehman, 2006).
339 These were common in the selectively logged forest and agricultural mosaic forest on
340 the Masoala Peninsula (Table 2), where *A. mooreorum* individuals were present at a
341 relatively low abundance. The abundance of *Garcinia commersonii* and *Eugenia* sp. in
342 the primary lowland forest were positively associated with the highest abundance of *A.*
343 *mooreorum*. These tree species have been reported as feeding species of *A. laniger*
344 elsewhere in eastern Madagascar (Ganzhorn, 1985; Harcourt, 1991). This positive
345 association would suggest that these are preferred feeding tree species of *A. mooreorum*,
346 but may be a rarer tree species which only occur at high densities in less disturbed
347 habitats. In order to verify this hypothesis, a detailed comparative study of the feeding
348 ecology of *A. mooreorum*, including nutritional analyses of food resources, across our
349 different study habitats would be necessary.

350 *Lepilemur scottorum* appeared to be the species most affected by habitat disturbance, as
351 they occurred at the lowest abundance of all species surveyed (other than *Daubentonia*
352 *madagascariensis*). Tree species most commonly recorded to be consumed by
353 *Lepilemur* sp. include *Grewia* sp., *Garcinia* sp., and *Mangifera* sp. (Ganzhorn, 2002;
354 Seiler et al., 2014). *Lepilemur scottorum* abundance was highest in the primary lowland
355 forest where *Garcinia commersonii* was abundant, perhaps influencing this species
356 presence in this forest. *Dalbergia* sp. have also been recorded as a key dietary resource
357 for *L. ruficaudatus* in western Madagascar (Ganzhorn, 2002). It may be that the
358 continued illegal extraction of rosewood (*Dalbergia* sp.) is negatively impacting on *L.*
359 *scottorum* abundance on the Masoala peninsula.

360 As two ecologically similar species, the potential for the occurrence of competition
361 between sympatric *Avahi* sp. and *Lepilemur* sp. is high, particularly in disturbed habitats
362 where the availability of high quality resources and habitat are decreased (Huey and
363 Pianka, 1981). As *A. mooreorum* was observed at a higher abundance across all habitat
364 types, there is a possibility that this species may outcompete *L. scottorum* in our study
365 area. Additionally, our population density estimate for *A. mooreorum*, falls around the
366 mid-range of density estimates for this genera (Ganzhorn, 1988; Norscia, 2008; Herrera
367 et al., 2011), whereas our *L. scottorum* encounter rate falls on the lower end of
368 encounter rates observed for other *Lepilemur* species (Schmid and Smolker, 1998; Irwin
369 et al., 2000; Sterling and McFadden, 2000; Meyler et al., 2012). This hypothesis is
370 currently only speculation, based on a short-term study on a small sample size. Long-
371 term monitoring of the forest types and population dynamics of the nocturnal species in
372 this study area would be necessary to confidently verify this hypothesis.

373 *Microcebus* sp. were observed in all four habitats, with no significant difference in their
374 abundance between the four forest types. As a small-bodied omnivorous species,
375 *Microcebus* spp. are flexible in terms of both their behavioural and feeding ecology, and
376 as such are often abundant in secondary and anthropogenic habitats (Ganzhorn 1995;
377 Lehman et al., 2006b; Dammhahn and Kappeler, 2008a; Lahann, 2007; Herrera et al.,
378 2011). *Microcebus* spp. appear tolerant to varying habitat disturbance, and even extreme
379 habitat alteration, they occur across a range of habitats including primary and secondary
380 forests (Malone et al., 2013), and even pure garden habitats (Irwin et al., 2010). Their
381 tolerance for habitat degradation has been attributed to morphological and behavioural
382 adaptations in *Microcebus* sp. such as their small body size, diet and generalised
383 locomotion.

384 *Microcebus* sp. small body size allows them to locomote easily through disturbed
385 habitats despite low tree densities (Dammhahn and Kappeler, 2008b). At Masoala,
386 *Microcebus* sp. were observed to use a range of supports for travelling including the
387 small stems of *Afromomum angustifilium* in the agricultural mosaic forest, and larger
388 tree crown branches up to heights of *ca.* 20m in the primary lowland forest. This
389 illustrates the variety of supports they are able to exploit when compared with other
390 more specialised species. *Microcebus* sp. omnivory facilitates their ability to tolerate
391 habitat disturbance, they consume a mixture of insects, fruits, gums and flowers to
392 varying degrees (Mittermeier et al., 2010). Agricultural and secondary habitats often
393 provide high insect abundance (Losey and Vaughan, 2006), and a thick understorey
394 which provides protection from aerial predators (Mittermeier et al., 2010). Primary
395 forest may provide an “ideal” habitat for *Microcebus* sp., but they appear able to exploit
396 the opportunities which anthropogenic habitats can present. This is exemplified by the

397 density estimate of 232.31 individuals/km² observed in this study, which leans toward
398 the top range of density estimates reported elsewhere across Madagascar for other
399 *Microcebus* species (Ganzhorn, 1992; Lehman et al., 2006a; Meyler et al., 2012; IUCN,
400 2014).

401 We calculated population density estimates for our study species based on the average
402 trail-to-animal distance method also employed by Sterling and Rakotoarison (1998) on
403 the Masoala Peninsula. Density estimates were calculated based on our observations
404 from the primary lowland forest, as this was the study habitat most comparable to the
405 Iketra study site surveyed in 1994 (Sterling and Rakotoarison, 1998). We found higher
406 density estimates at our study site for *Microcebus* sp., 69.4 ind./km² compared with 39
407 ind./km² (Sterling and Rakotoarison, 1998), and *A. mooreorum*, 93.8 ind./km² compared
408 with 25 ind./km² (Sterling and Rakotoarison, 1998). We calculated a lower density
409 estimate for *L. scottorum*, 25.2 ind./km² compared with 33 ind./km² (Sterling and
410 Rakotoarison, 1998). The higher density estimates observed for *Microcebus* sp. and *A.*
411 *mooreorum* in this study from Sterling and Rakotoarison (1998) may be an indication of
412 the success that the inception of Masoala National Park since 1997 has had on the
413 populations of these species, where they are protected.

414 Whilst this paper focuses on the effect of habitat disturbance on lemur densities, another
415 aspect to consider is the effect of hunting pressure. Hunting was not previously
416 considered to be a huge threat to lemurs as many species were protected by *fady*,
417 however in recent years, research has shown that hunting is now one of the major
418 threats to the conservation of lemurs across Madagascar (Golden, 2009; Jenkins et al.,
419 2011). Research shows that lemur species targeted for bushmeat are often the larger
420 diurnal and cathemeral species, such as *Eulemur* sp., *Varecia* sp. and *Propithecus* sp.

421 (Razafimanahaka et al., 2012). Across the Masoala Peninsula and Makira Forest,
422 hunting of the red ruffed lemur (*Varecia rubra*), and white-fronted brown lemur
423 (*Eulemur albifrons*) using *laly* traps has been widely recorded (Golden, 2009;
424 Borgersen, 2015). On Makira, Golden (2009) additionally recorded the hunting of a
425 number of nocturnal lemur species including; *Avahi laniger*, *Lepilemur* sp.,
426 *Cheiroglaeus major*, *Daubentonia madagascariensis*, and *Microcebus* sp. In general,
427 the reporting of nocturnal lemur hunting is less common than that of diurnal and
428 cathemeral species, although detailed research on nocturnal lemur hunting is largely
429 lacking.

430 Research on the hunting of nocturnal primates has shown the prevalence of their use as
431 bush meat and in traditional medicine globally (Nekaris et al., 2010; Maldonado and
432 Peck, 2014; Svensson and Friant, 2014; Svensson et al., 2015). Considering global
433 patterns of bush meat hunting, it is likely that larger nocturnal species, such as *Avahi*
434 *mooreorum* and *Lepilemur scottorum*, are at risk from hunting pressure, particularly in
435 disturbed areas where high quality sleeping sites are generally less available (Seiler et
436 al., 2013), making these species more visible and accessible to hunters.

437

438 ACKNOWLEDGEMENTS

439 We are very grateful to all the staff at the following institutions; Wildlife Conservation
440 Society Madagascar, Département des Eaux et Forêts, École Supérieure des Sciences
441 Agronomiques and Madagascar National Parks for permitting the research. This
442 research was conducted under the research permit 107/14/MEF/SG/DGF/DCB.SAP/
443 SCB. We thank our local guide Be Noel, our cook Téa and the villagers of
444 Ambodiforaha. A special thank you to Olivier Fournajoux for providing logistical

445 support. We are also very grateful to the two anonymous reviewers who offered
446 suggestions which greatly improved the manuscript.

447 REFERENCES

448 Arrigo-Nelson S J (2006) The effects of habitat disturbance on ecology and behaviour
449 of *Propithecus edwardsi*, the Milne-Edwards' sifaka in Ranomafana National Park,
450 Madagascar. Unpublished PhD thesis. Stony Brook University, New York.

451 Arroyo-Rodríguez V, Dias PAD (2010) Effects of habitat fragmentation and disturbance
452 on howler monkeys: a review. *Am. J. Primatol.* 72: 1-16.

453 Balestri M, Barresi M, Campera M, Serra V, Ramanamanjato JB, Heistermann M,
454 Donati G (2014) Habitat degradation and seasonality affect physiological stress levels
455 of *Eulemur collaris* in littoral forest fragments. *PLOS One* 9: e107968.

456 Balko EA, Underwood BH (2005) Effects of forest structure and composition on food
457 availability for *Varecia variegata* at Ranomafana National Park, Madagascar. *Am. J.*
458 *Primatol.* 66: 45-70.

459 Bennett AF, Radford JQ, Haslem A (2006). Properties of land mosaics: implications for
460 nature conservation in agricultural environments. *Biol. Conserv.* 133: 250-264.

461 Borgerson C (2015) The effects of illegal hunting and habitat on two sympatric
462 endangered primates. *Int. J. Primatol.* 36: 74-93.

463 Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001)
464 Introduction to distance sampling: estimating abundance of wildlife populations. Oxford
465 University Press, Oxford.

- 466 Buckland ST, Plumptre AJ, Thomas L, Rexstad EA (2010) Design and analysis of line
467 transect surveys for primates. *Int. J. Primatol.* 31: 833-847.
- 468 Campera M, Serra V, Balestri M, Barresi M, Ravaolahy M, Randriatafika F, Donati G
469 (2014) Effects of habitat quality and seasonality on ranging patterns of collared brown
470 lemur (*Eulemur collaris*) in littoral forest fragments. *Int. J. Primatol.* 35: 957-975.
- 471 Chapman C, Fedigan LM, Fedigan L (1988) A comparison of transect methods of
472 estimating population densities of Costa Rican primates. *Brenesia* 30: 67-80.
- 473 Chapman CA, Lambert JE (2000) Habitat alteration and the conservation of African
474 Primates: case study of Kibale National Park, Uganda. *Am. J. Primatol.* 50: 169-185.
- 475 Dammhahn M, Kappeler PM (2008a) Comparative feeding ecology of sympatric
476 *Microcebus berthae* and *M. murinus*. *Int. J. Primatol.* 29: 1567-1589.
- 477 Dammhahn M, Kappeler PM (2008b) Small-scale coexistence of two mouse lemur
478 species (*Microcebus berthae* and *M. murinus*) within a homogeneous competitive
479 environment. *Oecologia* 157: 473-483.
- 480 Demes B, Jungers WL, Fleagle JG, Wunderlich RE, Richmond BG, Lemelin P (1996)
481 Body size and leaping kinematics in Malagasy vertical clingers and leapers. *J. Hum.*
482 *Evol.* 31: 367-388.
- 483 Donati G, Kesch K, Ndremifidy K, Schmidt SL, Ramanamanjato JB, Borgognini-Tarli
484 SM, Ganzhorn JU (2011) Better few than hungry: Flexible feeding ecology of collared
485 lemurs, *Eulemur collaris*, in littoral forest fragments. *PLOS One* 6: e19807.
- 486 Dufils JM (2003) Remaining forest cover. In: Goodman SM, Benstead JP (eds) *The*
487 *Natural History of Madagascar*. University of Chicago Press, Chicago, pp 88–96.

- 488 Dytham C (1999) Choosing and using statistics: a biologist's guide. Blackwell
489 Science, New York.
- 490 Fashing PJ, Cords M (2000) Diurnal primate densities and biomass in the Kakamega
491 forest: An evaluation of census methods and a comparison with other forests. Am. J.
492 Primatol. 50: 139-152.
- 493 Faulkner, AL, Lehman SM (2006) Feeding patterns in a small-bodied nocturnal folivore
494 (*Avahi laniger*) and the influence of leaf chemistry: a preliminary study. Folia
495 Primatol. 77: 218-227.
- 496 Fimbel C (1994) Ecological correlates of species success in modified habitats may be
497 disturbance-and site-specific: the primates of Tiwai Island. Cons. Biol. 8:106-113.
- 498 Ganzhorn JU (1987) A possible role of plantations for primate conservation in
499 Madagascar. Am. J. Primatol. 12: 205-215.
- 500 Ganzhorn JU (1988) Food partitioning among Malagasy primates. Oecologia 75: 436-
501 450.
- 502 Ganzhorn, JU (1989) Niche separation of seven lemur species in the eastern rainforest
503 of Madagascar. Oecologia 79: 279-286.
- 504 Ganzhorn JU (1992) Leaf chemistry and the biomass of folivorous primates in tropical
505 forests. Oecologia 91: 540-547.
- 506 Ganzhorn JU (1995) Low-level forest disturbance effects on primary production, leaf
507 chemistry, and lemur populations. Ecology 76: 2084-2096.

- 508 Ganzhorn JU (1999) Body mass, competition and the structure of primate communities.
509 In: Fleagle JG, Janson CH, Reed K (eds). Primate communities. Cambridge University
510 Press, Cambridge, p141–157.
- 511 Ganzhorn JU, Abraham JP (1991) Possible role of plantations for lemur conservation in
512 Madagascar: food for folivorous species. *Folia Primatol.* 56: 171-176.
- 513 Ganzhorn JU, Abraham JP, Razanahoera-Rakotomalala M (1985) Some aspects of the
514 natural history and food selection of *Avahi laniger*. *Primates* 26: 452-463.
- 515 Ganzhorn JU, Jacques Rakotondrany S, Ratovonamana YR (2011) Chapter 3: Habitat
516 description and phenology. In: Setchell JM, Curtis DJ (eds) *Field and Laboratory*
517 *Methods in Primatology: A Practical Guide*. Cambridge University Press, Cambridge,
518 pp 51-68.
- 519 Ganzhorn JU, Lowry PP, Schatz GE, Sommer S (2001) The biodiversity of
520 Madagascar: one of the world's hottest hotspots on its way out. *Oryx* 35: 346-348.
- 521 Ganzhorn JU, Fietz J, Rakotovao E, Schwab D, Zinner D (1999) Lemurs and the
522 regeneration of dry deciduous forest in Madagascar. *Conserv. Biol.* 13: 794-804.
- 523 Ganzhorn JU, Andrianasolo T, Andrianjalahatra T, Donati G, Fietz J, Lahann P,
524 Norscia I, Rakotondrany J, Rakotondratsima BM, Ralison J, Ramarokoto REAF,
525 Randriamanga S, Rasarimanana S, Rakotosamimanana B, Ramanamanjato JB, Randria
526 G, Tovonanahary Rasolofoharivelo M, Razanahoera-Rakotomalala M, Schmid J,
527 Sommer S (2007) Lemurs in evergreen littoral forest fragments of different size and
528 degrees of degradation. In: Ganzhorn JU, Goodman SM, Vincelette M, (eds)
529 *Biodiversity, ecology and conservation of the littoral ecosystems of South-eastern*
530 *Madagascar*. Smithsonian Institution Press, Washington DC, pp. 223–236.

- 531 Golden CD (2009) Bushmeat hunting and use in the Makira Forest, north-eastern
532 Madagascar: a conservation and livelihoods issue. *Oryx* 43: 386-392.
- 533 Golden C D, Fernald LCH, Brashares JS, Rasolofoniaina BJR, Kremen C
534 (2011) Benefits of wildlife consumption to child nutrition in a biodiversity hotspot. *P.*
535 *Natl. Acad. Sci. U.S.A.* 108:19653-19656
- 536 Golden CD, Bonds MH, Brashares JS, Rasolofoniaina BJR, Kremen C (2014)
537 Economic valuation of subsistence harvest of wildlife in Madagascar. *Conserv.*
538 *Biol.* 28: 234-243.
- 539 Green GM, Sussman RW (1990) Deforestation History of the Eastern Rainforests of
540 Madagascar from Satellite Images. *Science* 248: 212-215.
- 541 Harcourt C (1991) Diet and behaviour of a nocturnal lemur, *Avahi laniger*, in the
542 wild. *J. Zool.* 223: 667-674.
- 543 Harper GJ, Steininger MK, Tucker CJ, Juhn D, Hawkins F (2007) Fifty years of
544 deforestation and forest fragmentation in Madagascar. *Environ. Conserv.* 34: 325-333.
- 545 Herrera JP, Wright PC, Lauterbur E, Ratovonjanahary L, Taylor LL (2011) The effects
546 of habitat disturbance on lemurs at Ranomafana National Park, Madagascar. *Int. J.*
547 *Primatol.* 32:1091-1108.
- 548 Hitimana J, Kiyiapi JL, Njunge JT (2004) Forest structure characteristics in disturbed
549 and undisturbed sites of Mt. Elgon moist lower montane forest, western Kenya. *For.*
550 *Ecol. Manag.* 194: 269-291.
- 551 Huey RB, Pianka ER (1981) Ecological consequences of foraging mode. *Ecology*: 991-
552 999.

- 553 Irwin MT, Wright PC, Birkinshaw C, Fisher BL, Gardner CJ, Glos J, Goodman SM,
554 Loiselle P, Rabeson P, Raharison J-L, Raherilalao M-J, Rakotondravony D,
555 Raselimanana A, Ratsimbazafy J, Sparks JS, Wilmé L, Ganzhorn JU (2010) Patterns of
556 species change in anthropogenically disturbed forests of Madagascar. *Biol. Cons.* 143:
557 2351-2362.
- 558 IUCN 2014. *The IUCN Red List of Threatened Species. Version 2014.2.*
559 <<http://www.iucnredlist.org>>. Accessed 27/07/2014
- 560 Jenkins RK, Keane A, Rakotoarivelo AR, Rakotomboavonjy V, Randrianandrianina
561 FH, Razafimanahaka HJ, Ralaiarimalala SR, Jones JP (2011) Analysis of patterns of
562 bushmeat consumption reveals extensive exploitation of protected species in eastern
563 Madagascar. *PLOS One* 6: e27570.
- 564 Johns AD (1988) Effects of "selective" timber extraction on rain forest structure and
565 composition and some consequences for frugivores and folivores. *Biotropica* 20: 31-37.
- 566 Johns AD (1992) Vertebrate responses to selective logging: implications for the design
567 of logging systems. *Philos. T. Roy. Soc. B* 335: 437-442.
- 568 Johns AD, Skorupa JP (1987) Responses of rain-forest primates to habitat disturbance: a
569 review. *Int. J. Primatol.* 8: 157-191.
- 570 Junge RE, Barrett MA, Yoder AD (2011) Effects of anthropogenic disturbance on indri
571 (*Indri indri*) health in Madagascar. *Am. J. Primatol.* 73: 632-642.
- 572 Kaufmann JC (2006) The sad opaqueness of the environmental crisis in
573 Madagascar. *Conserv. Soc.* 4: 179

- 574 Kremen C, Razafimahatratra V, Guillery RP, Rakotomalala J, Weiss A,
575 Ratsisompatrarivo JS (1999) Designing the Masoala National Park in Madagascar based
576 on biological and socioeconomic data. *Conserv. Biol.* 13: 1055-1068.
- 577 Kull CA (2002) Empowering pyromaniacs in Madagascar: Ideology and legitimacy in
578 community-based resource management. *Dev. Change* 33: 57-78.
- 579 Lahann P (2007) Feeding ecology and seed dispersal of sympatric cheirogaleid lemurs
580 (*Microcebus murinus*, *Cheirogaleus medius*, *Cheirogaleus major*) in the littoral
581 rainforest of south-east Madagascar. *J. Zool.* 271: 88-98.
- 582 Lazdane K, Broll A, Theisinger O, Bearder SK, Donati G (2014). A preliminary
583 assessment of nematode infections in *Eulemur collaris* (Geoffroy, 1812)(Mammalia:
584 Lemuridae) in remnant fragments of Malagasy littoral forest. *Ital. J. Zool.* 81: 374-380.
- 585 Lehman SM, Rajaonson A, Day S (2006a) Edge effects and their influence on lemur
586 density and distribution in southeast Madagascar. *Am. J. Phys. Anthropol.* 129: 232-
587 241.
- 588 Lehman SM, Rajaonson A, Day S (2006b) Lemur responses to edge effects in the
589 Vohibola III Classified Forest, Madagascar. *Am. J. Primatol.* 68: 293-299.
- 590 Lehman SM, Rajaonson A, Day S (2006c) Edge effects on the density of *Cheirogaleus*
591 *major*. *Int. J. Primatol.* 27: 1569-1588.
- 592 Losey JE, Vaughan M (2006) The economic value of ecological services provided by
593 insects. *Bioscience* 56: 311-323.
- 594 Lowry II PP, Schatz GE, Phillipson PB (1997) The classification of natural and
595 anthropogenic vegetation in Madagascar. In: Goodman SM, Patterson BD (eds.),

- 596 Natural Change and Human Impact in Madagascar. Smithsonian Institution Press,
597 Washington, DC, pp. 93– 123.
- 598 Maldonado AM, Peck MR (2014) Research and in situ conservation of owl monkeys
599 enhances environmental law enforcement at the Colombian-Peruvian border. *Am. J.*
600 *Primatol.* 76: 658-669.
- 601 Malone M, Ramanamanjato JB, Randriatafika F, Donati G (2013) Habitat structure and
602 grey mouse lemur (*Microcebus murinus*) abundance in the transitional littoral of
603 Petriky, South-East Madagascar. *Lemur News* 17: 22-27.
- 604 Marshall AR, Lovett JC, White PCL (2008) Selection of line-transect methods for
605 estimating the density of group-living animals: lessons from the Primates. *Am. J.*
606 *Primatol.* 70: 452-462
- 607 Martinez B (2010) Forest restoration in Masoala National Park, Madagascar: The
608 contribution of the red ruffed lemur (*Varecia rubra*) and the livelihoods of subsistence
609 farmers at Ambatoladama. PhD thesis, University of Minnesota.
- 610 McConnell WJ, Kull CA (2014) Deforestation in Madagascar: Debates over the island's
611 forest cover and challenges of measuring forest change. In: I. R. Scales (ed.)
612 *Conservation and Environmental Management in Madagascar*. Routledge, London and
613 New York, pp 67–104.
- 614 Merker S, Mühlenberg M (2000) Traditional land use and tarsiers–human influences on
615 population densities of *Tarsius diana*. *Folia Primatol.* 71: 426-428.
- 616 Meyler SV, Salmona J, Ibouroi MT, Besolon A, Rasolondraibe E, Radespiel U,
617 Rabarivola C, Chikhi L (2012) Density estimates of two endangered nocturnal lemur

- 618 species from Northern Madagascar: New results and a comparison of commonly used
619 methods. *Am. J. Primatol.* 74: 414-422.
- 620 Mittermeier RA, Louis Jr EE, Richardson M, Schwitzer C, Langrand O, Rylands AB,
621 Hawkins F, Rajaobelina S, Ratsimbazafy J, Rasoloarison R, Roos C, Kappeler PM,
622 Mackinnon J (2010) *Lemurs of Madagascar: Third Edition*. Conservation International,
623 Arlington, USA.
- 624 Myers N (1988) Threatened biotas: "hot spots" in tropical forests. *Environmentalist* 8:
625 187-208.
- 626 Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000).
627 Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.
- 628 Nash LT (1998) Vertical clingers and sleepers: Seasonal influences on the activities and
629 substrate use of *Lepilemur leucopus* at Beza Mahafaly Special Reserve,
630 Madagascar. *Folia Primatol.* 69: 204-217.
- 631 Nekaris KAI, Shepherd CR, Starr CR, Nijman V (2010) Exploring cultural drivers for
632 wildlife trade via an ethnoprimateological approach: a case study of slender and slow
633 lorises (*Loris* and *Nycticebus*) in South and Southeast Asia. *Am. J. Primatol.* 72: 877-
634 886.
- 635 Nekaris KAI, Pambudi JAA, Susanto D, Ahmad RD, Nijman V (2014) Densities,
636 distribution and detectability of a small nocturnal primate (Javan slow loris, *Nycticebus*
637 *javanicus*) in a montane rainforest. *Endanger. Species Res.* 24: 95-103
- 638 Norscia I (2008) Pilot survey of *Avahi* population (woolly lemurs) in littoral forest
639 fragments of southeast Madagascar. *Primates* 49: 85-88.

- 640 Patel ER (2007) Logging of Rare Rosewood and Palisandre (*Dalbergia* spp.) within
641 Marojejy National Park, Madagascar. *Madag. Conserv. Dev.* 2: 11-16.
- 642 Radespiel U (2000) Sociality in the gray mouse lemur (*Microcebus murinus*) in
643 northwestern Madagascar. *Am. J. Primatol.* 51: 21-40.
- 644 Radespiel U (2007) Ecological diversity and seasonal adaptations of mouse lemurs
645 (*Microcebus* spp.). In: Gould L, Sauther ML (eds.) *Lemurs: Ecology and adaptation*.
646 Springer, New York, pp. 211–233.
- 647 Randrianambinina B, Rasoloharijaona S, Rakotondravony R, Zimmermann E,
648 Radespiel U (2010) Abundance and conservation status of two newly described lemur
649 species in northwestern Madagascar (*Microcebus danfossi*, *Lepilemur*
650 *grewcockorum*). *Madag. Conserv. Dev.* 5: 95-102.
- 651 Razafimanahaka JH, Jenkins RK, Andriafidison D, Randrianandrianina F,
652 Rakotomboavonjy V, Keane A, Jones JP (2012) Novel approach for quantifying illegal
653 bushmeat consumption reveals high consumption of protected species in
654 Madagascar. *Oryx* 46: 584-592.
- 655 Rode-Margono EJ, Nijman V, Wirdateti, Nekaris KAI (2014) Ethology of the Critically
656 Endangered Javan slow loris *Nycticebus javanicus* É. Geoffroy Saint-Hilaire in West
657 Java. *Asian Primates* 4: 27-41.
- 658 Ross C, Reeve N (2011) Chapter 6: Survey and census methods: population distribution
659 and density. In: Setchell JM, Curtis DJ (eds) *Field and laboratory methods in*
660 *Primateology: A practical guide*. Cambridge University Press, Cambridge, pp. 111-131.

- 661 Rovero F, Struhsaker TT, Marshall AR, Rinne TA, Pedersen UB, Butynski TM, Ehardt
662 CL, Mtui AS (2006) Abundance of diurnal primates in Mwanihana forest, Udzungwa
663 Mountains, Tanzania. *Int. J. Primatol.* 27: 675-697.
- 664 Schmid J, Smolker R (1998) Lemurs of the Réserve Spéciale d'Anjanaharibe-Sud,
665 Madagascar. *Fieldiana Zool.* 90: 227.
- 666 Schuurman, D, Lowry II PP (2009) The Madagascar rosewood massacre. *Madag.*
667 *Conserv. Dev.* 4: 98-102.
- 668 Schwitzer C, Glatt L, Nekaris KAI, Ganzhorn JU (2011) Responses of animals to
669 habitat alteration: an overview focussing on primates. *Endang. Species Res.* 14: 31-38.
- 670 Schwitzer C, Mittermeier RA, Davies N, Johnson S, Ratsimbazafy J, Razafindramanana
671 J, Louis Jnr EE, Rajaobelina S (2013) Lemurs of Madagascar: a strategy for their
672 conservation 2013-2106. Bristol, UK: IUCN SSC Primate Specialist Group, Bristol
673 Conservation & Science Foundation, and Conservation International.
- 674 Schwitzer C, Mittermeier RA, Johnson SE, Donati G, Irwin M, Peacock H,
675 Ratsimbazafy J, Razafindramanana J, Louis Jr. EE, Chikhi L, Colquhoun I.C, Tinsman
676 J, Dolch R, LaFleur M, Nash S, Patel E, Randrianambinina B, Rasolofoharivelo T,
677 Wright PC (2014) Averting lemur extinctions amid Madagascar's political
678 crisis. *Science* 343: 842-843.
- 679 Seiler M, Holderied M, Schwitzer C (2013) Effects of habitat degradation on sleeping
680 site choice and use in Sahamalaza sportive lemurs (*Lepilemur sahamalazensis*). *Int. J.*
681 *Primatol.* 34: 260-280.

- 682 Seiler M, Holderied M, Schwitzer C (2014) Habitat selection and use in the Critically
683 Endangered Sahamalaza sportive lemur, *Lepilemur sahamalazensis*, in altered habitat.
684 Endang. Species Res. 24: 273-286.
- 685 Sterling E, McFadden K (2000) Rapid census of lemur populations in the Parc National
686 de Marojejy, Madagascar. Fieldiana Zool. 97: 265-274.
- 687 Sussman RW, Green GM, Sussman, LK (1994) Satellite imagery, human ecology,
688 anthropology, and deforestation in Madagascar. Hum. Ecol. 22: 333-354.
- 689 Svensson MS, Friant SC (2014) Threats from trading and hunting of pottos and
690 angwantibos in Africa resemble those faced by slow lorises in Asia. Endang. Species
691 Res. 23: 107-114.
- 692 Svensson MS, Ingram DJ, Nekaris KAI, Nijman V (2015) Trade and ethnozoological
693 use of African lorisiforms in the last 20 years. Hystrix 26: 153-161.
- 694 Tecot S (2013) Variable energetic strategies in disturbed and undisturbed rain forest
695 habitats: fecal cortisol levels in southeastern Madagascar. In: Masters J, Gamba M,
696 Génin F, Tuttle R (eds). Leaping ahead: Advances in prosimian biology (Developments
697 in Primatology: Progress and prospects). Springer, New York, pp. 185–195.
- 698 Thalmann U (2001) Food resource characteristics in two nocturnal lemurs with different
699 social behaviour: *Avahi occidentalis* and *Lepilemur edwardsi*. Int. J. Primatol. 22: 287-
700 324.
- 701 Thalmann U, Ganzhorn JU (2002) The sportive lemurs, genus *Lepilemur*. In: Goodman
702 SM, Benstead JP (eds) The natural history of Madagascar. University of Chicago Press,
703 Chicago, pp. 1336-1339.

- 704 Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, Hedley SL, Burnham K
705 P (2010) Distance software: design and analysis of distance sampling surveys for
706 estimating population size. *J. Appl. Ecol.* 47: 5-14.
- 707 Vasey N (2000) Niche separation in *Varecia variegata rubra* and *Eulemur fulvus*
708 *albifrons*: I. Interspecific patterns. *Am. J. Phys. Anthropol.* 112: 411-431.
- 709 Warren RD (1997) Habitat use and support preference of two free-ranging saltatory
710 lemurs (*Lepilemur edwardsi* and *Avahi occidentalis*). *J. Zool.* 241: 325-341.
- 711 Warren RD, Crompton RH (1997) Locomotor ecology of *Lepilemur edwardsi* and
712 *Avahi occidentalis*. *Am. J. Phys. Anthropol.* 104: 471-486.
- 713

714 TABLES

715

716 Table 1

717

718 **Table 1.** Nocturnal lemurs present at Masoala National Park, northeastern Madagascar.

Common Name	Scientific name	Diet	IUCN Red List status	IUCN Red List Category	Observed in this study
Moore's woolly lemur	<i>Avahi mooreorum</i>	Folivore	Endangered	B1ab (iii,v)	Yes
Scott's sportive lemur	<i>Lepilemur scottorum</i>	Folivore	Endangered	B1ab (i,iii,v)	Yes
Mouse lemur	<i>Microcebus</i> sp.	Frugivore/ Insectivore	Unknown	N/A	Yes
Greater dwarf lemur	<i>Cheirogaleus major</i>	Frugivore/ Insectivore	Data deficient	N/A	No ^{ab}
Hairy-eared dwarf lemur	<i>Allocebus trichotis</i>	Frugivore/ Insectivore	Vulnerable	A2c+3c+4c	No ^b
Eastern fork-marked lemur	<i>Phaner furcifer</i>	Gummivore	Vulnerable	A2c+3c+4c	No*
Aye-aye	<i>Daubentonia madagascariensis</i>	Frugivore/ Insectivore	Endangered	A2cd + 4cd	Yes

719 # Body size is given as either XS (extra small), S (small), M (medium) or L (large). Estimated weights are
 720 given in parentheses based on weights in Mittermeier et al., 2010.

721 **Phaner furcifer* was not observed during the study, but vocalisations were heard on 2 occasions in the
 722 protected areas, which appeared to be coming from higher elevations.

723 ^a Other abundance surveys of *Cheirogaleus major* have not observed individuals between May and
 724 September as the species is known to enter torpor throughout these colder months in eastern Madagascar
 725 (Lehman et al., 2006c).

726 ^bThe presence of *Cheirogaleus major* and *Allocebus trichotis* in our study area were confirmed by local
 727 tourist guides and residents who regularly live and work in the area. Sightings of these species were
 728 reported as rare and intermittent.

729 N/A given when data is not available.

730

731

732

733 Table 2

734

735 **Table 2.** Habitat Characteristics measured in vegetation surveys.

Habitat Parameter <i>n</i>	Primary Lowland 50	Selectively Logged 50	Agricultural Mosaic 40	Primary Littoral 30
Mean Tree Height (m) *	16.38 ± 9.51 ^{A,B}	15.80 ± 6.59 ^C	10.11 ± 8.15 ^{A,C,D}	13.96 ± 6.38 ^{B,D}
Mean Bole Height (m) *	9.99 ± 7.70 ^E	9.99 ± 5.65 ^{F,H}	3.92 ± 5.16 ^{E,F,G}	8.23 ± 5.39 ^{G,H}
Mean DBH (m)	15.15 ± 10.18	17.62 ± 10.47	17.86 ± 21.33	13.62 ± 8.53
Mean Canopy Cover (%) *	75.31 ± 14.29 ^I	69.89 ± 14.75 ^J	65.10 ± 19.47 ^{L,J,K}	68.13 ± 13.46 ^K
Tree Density (> 5cm DBH per ha) *	1568.60 ± 1994.14 ^L	1015.59 ± 1496.12 ^M	591.168 ± 1309.40 ^{L,M,N}	1725.08 ± 1626.21 ^N
Top 5 tree species	<i>Cryptocarya</i> sp. <i>Homalium</i> sp. <i>Eugenia</i> sp. <i>Garcinia commersonii</i> <i>Dracaena xiphophylla</i>	<i>Anthostema madagascariensis</i> <i>Symphonia fasciculata</i> <i>Anisophyllea fallax</i> <i>Garcinia commersonii</i> <i>Diospyros</i> sp.	<i>Harongana madagascariensis</i> <i>Albizia</i> sp. <i>Mangifera indica</i> <i>Anisophyllea fallax</i> <i>Ravenala madagascariensis</i>	<i>Uapaca thouarsii</i> <i>Anisophyllea fallax</i> <i>Polyscias</i> sp. <i>Dracaena fontanesiana</i> <i>Anthostema madagascariensis</i>

736 Habitat Parameters with significant differences based on one-way ANOVA tests are marked with *($p \leq$
737 0.05). Means and standard deviations (\pm) are displayed. Cells with superscript letters in common differed
738 significantly in LSD post-hoc comparisons. ($p \leq 0.05$).

739 n = sample size

740

741

742

743 Table 3

744

745 **Table 3.** Encounter rates of lemurs (individuals/ transect walk). Values are medians with upper and lower range in parentheses (min-max).

Forest Type	Transect walks	<i>Microcebus</i> sp.	<i>Lepilemur scottorum</i>	<i>Avahi mooreorum</i>	<i>Daubentonia madagascariensis</i>	Species richness
Primary Lowland	12	1 (0-9)	1 (0-3) ^{A,B}	1 (0-8) ^D	0 (0-1)	4
<i>n</i>		25	11	26	1	
Mean cluster size		1 ± 0	1.1 ± 0.32	1.73 ± 0.80	1 ± 0	
Selectively Logged	12	1 (0-3)	0 (0-2) ^A	1 (0-3) ^E	Absent	3
<i>n</i>		13	4	15		
Mean cluster size		1 ± 0	1 ± 0	1.15 ± 0.38	-	
Primary Littoral	8	1.5 (1-4)	1 (0-1) ^C	0.5 (0-3)	Absent	3
<i>n</i>		14	5	8		
Mean cluster size		1 ± 0	1 ± 0	1.6 ± 0.55	-	
Agricultural Mosaic	12	1 (0-5)	Absent ^{B,C}	0 (0-1) ^{D,E}	Absent	2
<i>n</i>		18		2		
Mean cluster size		1.13 ± 0.34	-	1 ± 0	-	
<i>n</i>	44	70	20	51	1	4
Species density estimate (individuals/km ²)		232.31	-	121.21	-	-
95% lower-upper CI		147.49-365.92		73.02-201.20		
Estimated strip width		4.64	-	6.20	-	-
Cluster size		1.03	-	1.43		

746 Mean cluster size with standard deviation (±) is provided.

747 Species specific encounter rates with superscript letters in common differed significantly in pairwise comparisons from LMM (p≤0.05).

748 *n*= total number of individuals observed

749 Species density estimate, ESW and cluster size were calculated using Distance 6.0.

750 CI=confidence interval.

751

752