

1 RH: WUESTHOFF ET AL.—MOUSE LEMUR HABITAT USE

2 **Differential habitat use by sympatric species of mouse lemurs across a mangrove–dry**
3 **forest habitat gradient**

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25 Understanding the mechanisms by which similar species coexist in sympatry is a major driver of
26 ecological research. Niche partitioning and ecological plasticity can facilitate spatial and habitat
27 use overlap between generalist and specialist species. Mouse lemurs (*Microcebus* spp.) are a
28 highly speciose group of small primates that are endemic to the forests of Madagascar. In
29 northwestern Madagascar, the relatively widespread *M. murinus* occurs sympatrically with the
30 microendemic *M. ravelobensis*. We investigated spatial distributions and densities of these two
31 species across a mangrove–dry forest habitat gradient in Mariarano commune. We used capture-
32 mark-recapture techniques and nocturnal line transect surveys along six transects during June
33 and July 2017. Spatial capture-recapture and distance sampling models were used to
34 estimate lemur densities across habitat types. The congeners displayed differential patterns of
35 spatial distribution and densities. *Microcebus murinus* was found in similar densities across all
36 habitat types, while *M. ravelobensis* was found at much higher densities in dry forests compared
37 with mangroves. This suggests that the generalist *M. murinus* uses a wider array of habitats more
38 evenly than the specialist *M. ravelobensis*. Our study provides empirical evidence of how cryptic
39 lemur species differ in their habitat use and distribution across an environmental gradient and
40 provides new insights into their ecology in an understudied habitat. Lemurs are one of the most
41 threatened groups of mammals in the world, and understanding how these species are distributed
42 across different forest types is crucial for planning and implementing conservation measures to
43 protect lemur habitat.

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45 Key words: niche, distance sampling, density, *Microcebus murinus*, *Microcebus ravelobensis*,
46 spatial capture-recapture
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48 La compréhension des mécanismes permettant à des espèces similaires de vivre en sympatrie
49 constitue un facteur important dans le domaine de la recherche en écologie. Le partage de niche
50 et la plasticité écologique pourraient faciliter la cohabitation entre espèces généralistes et
51 spécialistes. Parmi les petits primates endémiques des forêts malgaches, les microcèbes
52 (*Microcebus* spp.) constituent un genre très diversifié en termes d'espèces. Au nord-ouest de
53 Madagascar, *M. murinus*, une espèce relativement répandue, coexiste avec l'espèce micro-
54 endémique *M. ravelobensis*. Leurs distributions spatiales et leurs densités le long d'un gradient
55 d'habitat — de la mangrove à la forêt sèche caducifoliée dans la Commune Rurale de Mariarano
56 — ont fait l'objet de la présente étude. Des techniques de capture-marquage-recapture et de
57 recensements nocturnes ont été utilisées le long de six transects linéaires entre juin et juillet
58 2017. Des modèles spatiaux de capture-recapture et d'échantillonnage par transects ont été
59 utilisés pour estimer les densités de ces deux espèces de microcèbes dans différents types
60 d'habitats. Ces dernières ont montré une différence de mode de distribution spatiale et de
61 densité. L'espèce *M. murinus* a ainsi été rencontrée avec une densité relativement constante dans
62 tous les types d'habitats, tandis que *M. ravelobensis* a montré des densités plus élevées dans les
63 forêts sèches caducifoliées que dans les mangroves. Les résultats suggèrent que par comparaison
64 avec l'espèce spécialiste *M. ravelobensis*, l'espèce généraliste *M. murinus* utilise une gamme
65 plus large d'habitats, et ceci d'une façon uniforme. La présente étude montre d'une manière
66 empirique comment des espèces de lémuriers cryptiques diffèrent dans l'utilisation de leur
67 habitat et dans leur distribution le long d'un gradient environnemental, et elle apporte de

68 nouvelles informations sur leur écologie au sein d'un habitat peu étudié. Les lémuriens sont le
69 groupe de mammifères le plus menacé au monde et il est essentiel de comprendre comment ces
70 espèces sont réparties dans les différents types de forêts pour planifier et mettre en œuvre des
71 mesures de conservation en vue de protéger leur habitat.

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73 Mots clés : niche ; échantillonnage par transects ; densité ; *Microcebus murinus* ; *Microcebus*
74 *ravelobensis* ; capture-recapture

75 Understanding coexistence among ecologically similar species within communities is a long-
76 standing research focus in community ecology and biogeography (MacArthur and Levins 1967;
77 Hubbell 2005) and has important implications for conservation (Dempster 1975). In animals,
78 niche partitioning and differentiation have been proposed as mechanisms for sympatric
79 coexistence (Schoener 1974), and multiple forms of partitioning have been demonstrated across
80 taxonomic groups. These include spatial and habitat differentiation (e.g., Arlettaz 1999), diel
81 temporal partitioning (Kronfeld-Schor and Dayan 2003), seasonal separation (e.g., Alatalo
82 1980), and morphological and physiological divergence (e.g., Brown 1989). Niche breadths (e.g.,
83 dietary, resource use, habitat type use) of coexisting species are expected to influence the
84 mechanisms for niche differentiation (Büchi and Vuilleumier 2014). Generalist species, i.e.,
85 those with broad niches and wider environmental tolerance, are predicted to occupy larger
86 geographic ranges (Slatyer et al. 2013; Büchi and Vuilleumier 2014; Beaudrot et al. 2014).
87 Specialist species with narrower niches and tolerances are more geographically restricted and
88 have greater sensitivity to habitat integrity and disturbances than generalists (Clavel et al. 2011;
89 Büchi and Vuilleumier 2014).

90 Several mechanisms have been proposed to explain the widely observed overlap in the
91 distribution and habitat use between generalist and specialist species (Büchi and Vuilleumier
92 2014). Limiting biotic and abiotic factors might keep populations of one or both species below
93 carrying capacity and prevent them from competitively excluding the other from a niche (Morris
94 1996). Alternatively, generalists might use habitat that is not suitable for specialist species (e.g.,
95 Morris 1996; Bonesi and Macdonald 2004). Under this mechanism, coexistence between
96 generalist and specialist species would broaden as the habitat plasticity of the generalist increases
97 (Abrams 2006).

98 The mouse lemurs of Madagascar (*Microcebus* spp.) are an ideal model system to study
99 interspecific coexistence between congeneric generalists and specialists. This group of nocturnal
100 primates is characterized by high speciation and microendemism, with restricted distributions at
101 the species level often constrained by barriers such as rivers (Olivieri et al. 2007; Yoder et al.
102 2016; Kamilar et al. 2016). Although at least three species (*M. griseorufus*, *M. myoxinus*, and *M.*
103 *murinus*) occupy more than one inter-river system and thereby show some degree of habitat
104 plasticity (Olivieri et al. 2007; Radespiel et al. 2012; Radespiel 2016), one of these species, the
105 gray mouse lemur (*M. murinus*), has a uniquely large distribution from southern to northwestern
106 Madagascar and is found throughout a variety of forest types (Radespiel 2016). *Microcebus*
107 *murinus* exhibits adaptations that allow it to tolerate a range of environmental conditions,
108 including fat storage in its tail (Schmid 1999) and hibernation in some parts of its distribution
109 (Schmid and Kappeler 1998; Schülke and Ostner 2007). These strategies to reduce energy
110 expenditure and tolerate energetically demanding environmental conditions, coupled with its
111 large distribution and wide habitat breadth, suggest that *M. murinus* is an ecological generalist
112 among mouse lemurs (Thorén 2011; Kamilar et al. 2016; Radespiel 2016; Blanco et al. 2018).

113 In northwestern Madagascar, *M. murinus* occurs sympatrically with the vulnerable
114 microendemic golden-brown mouse lemur, *M. ravelobensis* (Zimmermann et al. 1998; Olivieri et
115 al. 2007). These cryptic congeners are similar in body size (Zimmermann et al. 1998), and both
116 use daily torpor (Rendigs et al. 2003). *Microcebus murinus* has not been documented hibernating
117 in sympatry with *M. ravelobensis*, likely due to the relatively high minimum temperatures in this
118 part of its distribution (Schülke and Ostner 2007). Previous studies have investigated how
119 differences in behavioral ecology of *M. murinus* and *M. ravelobensis* allow them to coexist
120 (reviewed in Radespiel 2016). Across sites in the Ankarafantsika National Park, higher densities
121 of one species are associated with lower densities of the other, suggesting possible partitioning
122 based on differential microhabitat preferences (Rakotondravony and Radespiel 2009). While
123 studies have found that *M. murinus* has a broader dietary niche with greater flexibility based on
124 seasonal availability (Radespiel et al. 2006; Thorén et al. 2011), other research suggests *M.*
125 *murinus* displays more specialization in habitat use and reduced local distribution compared with
126 *M. ravelobensis* (e.g., Radespiel et al. 2003; Rendigs et al. 2003; Rakotondravony and Radespiel
127 2009; Lutermann et al. 2010). This suggests that sympatry between these species does not exhibit
128 strict generalist–specialist dynamics (Rakotondravony and Radespiel 2009). Alternatively, *M.*
129 *murinus* might not be an ecological generalist across its distribution but instead might have
130 several specialized subpopulations (Rakotondravony and Radespiel 2009), highlighting the
131 importance of scale when assessing ecological generalists and specialists (Slayter et al. 2013).

132 While coexistence of *M. murinus* and *M. ravelobensis* has been studied in various dry
133 deciduous forests, there has been little investigation into their sympatry across a wider gradient
134 of forest types. Coastal mangrove forest represents an understudied habitat type for research on
135 many terrestrial mammals, including lemurs (Gardner 2016). Mangroves are unique in their

136 floral communities and habitat structure, which is highly dynamic due to frequent flooding
137 (Nagelkerken et al. 2008; Gardner 2016). The low plant diversity in mangroves offers limited
138 resources for some terrestrial vertebrates (Mohd-Azlan et al. 2014; Gardner 2016).
139 Consequently, species richness in terrestrial bird communities has been found to be lower in
140 mangroves than in other forest types nearby (Noske 1995; Mohd-Azlan et al. 2014). Terrestrial
141 bird communities in mangroves mostly consist of generalist feeders and, while some species are
142 mangrove specialists, there is no evidence of competitive exclusion in this habitat (Mohd-Azlan
143 et al. 2014). More than 30 primate species (e.g., capuchins, macaques, leaf monkeys, and
144 chimpanzees) have been documented using mangroves, including for feeding on novel resources,
145 dispersing between patches of other habitat, or as refuge from disturbance in other forest types
146 (Nowak and Coles 2019). Ecology of mouse lemurs within mangroves likely differs from that in
147 other forest types, as it does for other primate species (Nowak 2012). Assessing differences in
148 the spatial distribution of *M. murinus* and *M. ravelobensis* among mangroves and other nearby
149 forest types could reveal mechanisms for niche partitioning that facilitate their coexistence.

150 Our study assessed the spatial distribution of a mouse lemur community in the Mariarano
151 forest of northwestern Madagascar. Because of known differences in niche breadth and
152 microhabitat preference between *M. murinus* and *M. ravelobensis*, it was expected that these
153 congeners would display differential patterns of spatial distribution and density across a
154 mangrove–dry forest habitat gradient. We predicted that both species occurred in all habitat types
155 based on their sympatry at other sites but showed variable densities across sites due to different
156 habitat suitability. As seen with other generalist taxa, we expected *M. murinus* to occupy
157 mangroves at higher densities than the more specialized *M. ravelobensis*, a prediction also

158 supported by its known occurrence across a wide array of habitat types throughout its
159 distribution.

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MATERIALS AND METHODS

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Study taxa.—Previous research has found several ecological differences between *M. murinus* and *M. ravelobensis* in northwestern Madagascar. Studies have shown high dietary overlap between the two species (Radespiel et al. 2006; Thorén et al. 2011) but differences in seasonal feeding patterns. While both species consume arthropods, insect secretions, and gum, *M. murinus* has been shown to change to a fruit-heavy diet during the early wet season, whereas the diet of *M. ravelobensis* remains more stable throughout the year (Thorén et al. 2011). These congeners also differ in sleeping sites. *Microcebus murinus* displays strong preference for tree cavities throughout its distribution and selects large cavity trees (Radespiel et al. 2003; Lutermann et al. 2010), whereas *M. ravelobensis* uses a broader variety of sleeping sites, including tree cavities, but more often branches, tangles of lianas, and leaf nests (Radespiel et al. 2003). Availability of cavity trees likely influences habitat use and distribution for *M. murinus* (Lutermann et al. 2010). Sleeping site availability also explains the influence of microhabitat structure on distributions of the two species in sympatry (Lutermann et al. 2010, Rendigs et al. 2003). *Microcebus murinus* is found at sites with large trees that support more cavities, and *M. ravelobensis* is more associated with areas with small trees and lianas that offer more complex microhabitat structures (Rendigs et al. 2003).

Across its entire distribution, *M. murinus* is found in many forest types, including some humid forests (Rakotondranary et al. 2011), gallery forests, and spiny forest (Gligor et al. 2009) in southern Madagascar. In western and northwestern Madagascar, it occurs in dry deciduous

181 forests (Rakotondravony and Radespiel 2009) including partly degraded forest remnants and
182 secondary growth (Ganzhorn and Schmid 1998; Andriatsitohaina et al. 2020). It shows more
183 local specialization where its distribution overlaps with *M. ravelobensis* and is found at fewer
184 sites compared with this congener in the Ankarafantsika National Park. Both species occur in dry
185 deciduous forests, but *M. murinus* rarely is found in the more mesic parts that *M. ravelobensis*
186 occupies (Rakotondravony and Radespiel 2009). In sympatry, *M. ravelobensis* is found at higher
187 densities in lower elevation forests closer to surface water (Rakotondravony and Radespiel
188 2009). There is recent evidence that *M. ravelobensis* is more sensitive to fragmentation than *M.*
189 *murinus* (Andriatsitohaina et al. 2020) and that the congeners both do occasionally use grassland
190 matrix habitat (Steffens et al. 2021).

191 *Study site.*—Our study was carried out within the Mariarano Classified Forest (15°24'S,
192 46°44'E) on the Mahamavo Peninsula, located 80 km northeast of Mahajanga, Madagascar. The
193 site is located within a network of different habitat types including dry deciduous forests,
194 savannah, mangroves, and agricultural lands that is managed by a local community natural
195 resources management organization known as Vondron'Olona Ifotony (VOI). Habitat loss and
196 fragmentation have increased in the region over the last decades due to human population growth
197 and forest conversion for settlement and agriculture (Long et al. 2021). Mangroves in the area
198 also have seen increased fishing pressure (Long et al. 2021). Our study was based in the
199 mangroves and forests around the village of Antafiameva near the Antsena River.

200 Observational survey and trapping data were collected along six transects over the course
201 of four weeks June to July 2017 during the cooler dry season (Fig. 1). Transects varying in
202 length from 360 m to 1448 m (Table 1) were categorized into three habitat types: mangrove ($n =$
203 2), dry forest ($n = 3$), and “intermediate” forest ($n = 1$) that was situated in a transitional zone

204 between the other two types. Mangrove transects lines, labeled as MAN1 and MAN2, were
205 defined by the contours of the bank of the Antsena River and were sampled from a boat on the
206 water. Terrestrial transects in intermediate (INT3) and dry forest habitats (DRY4, DRY5, and
207 DRY6) were established based on existing paths used by other researchers from Operation
208 Wallacea and on established footpaths in the area. Dry forest transects were labeled by
209 increasing distance from the river (DRY4 began closest to river and DRY6 began farthest away;
210 Table 1).

211 *Capture-mark-recapture (CMR) sampling.*—Live trapping was carried out along all six
212 transects (Table 1), and each transect was sampled twice over two separate nights. Total trap
213 nights were calculated by multiplying the number of traps set by the number of sessions that each
214 was active. Trapping in mangroves along the Antsena River was done from a small motorboat.
215 Because the river was too wide (> 25 m) for mouse lemurs to cross, we only trapped along the
216 southern bank of the river. Due to difficulty navigating the river near the bank and some breaks
217 in vegetation cover, traps were placed every 20 – 40 m, one at each capture site, along the river.
218 Sherman Live Traps (type Sherman LFA: $7.6 \times 38.9 \times 22.9$ cm) always were secured with wire
219 to branches of mangrove trees 0.5 – 1.5 m above the high tide water level. Due to fluctuations in
220 water levels during daily tidal cycles, some trees were partially submerged during portions of the
221 trapping period, meaning that trap heights above the water level varied by 2 – 3 m throughout the
222 period. Trapping in dry and intermediate forests occurred along terrestrial transect lines. Traps
223 were placed in trees up to 2 m off the ground, one on each side of the transect, ~5 m apart, every
224 20 m. At every site, traps were set in the early evening (ca. 1700 – 1800 h) and baited with
225 pieces of banana. All trapping locations were marked with brightly colored flagging tape, and all

226 flag positions were mapped with GPS. Terrestrial transects were trapped on consecutive days,
227 and mangrove transects were trapped every second day due to limited access to the boat.

228 Traps were checked the following morning (ca. 0600 – 0700 h), and captured lemurs
229 were identified by species based on established characteristics (Zimmermann et al. 1998; Burke
230 and Lehman 2014). *Microcebus murinus* was identified by its gray-brown fur and a relatively
231 short tail (~12 – 13 cm) with a thick base, and *M. ravelobensis* was identified by a more rufous
232 fur color and a long tail (~14 – 15 cm) with a thinner base (Burke and Lehman 2014). Sex was
233 determined for each individual, and each animal was marked with an ear biopsy, the location of
234 which was used for individual identification (Rakotondravony and Radespiel 2009). Lemurs
235 were left to sleep in the traps during the day with some banana and then released, as appropriate
236 for a nocturnal animal, at the exact capture location in the evening on the same day. Because
237 mouse lemurs had not been trapped at our sites in previous years, there were no individuals
238 marked from previous surveys. All research followed ASM guidelines (Sikes et al. 2016), and
239 sampling was carried out with the approval of the University of Massachusetts Amherst
240 Institutional Animal Care and Use Committee (Protocol # 2017-0015), the CAFF/CORE
241 research committee, and the Water and Forests Ministry of Madagascar (Research Authorization
242 N°151/17/MEEF/SG/DGF/DSAP/SCB.Re). All institutional and permit guidelines were
243 followed, and all animals were handled by trained researchers.

244 *Nocturnal line transect surveys.*—Line transect surveys were carried out in the evening
245 (~1900 – 2200 h) along the six transects also used for trapping. Surveys were not undertaken
246 along transects where trapping was occurring on the same night to avoid disturbing trapping
247 sites. Surveys along the river were carried out from ~5 – 25 m from shore and traveling 1.0 – 5.0
248 km/h. As with the trapping, only the southern bank of the river was surveyed. On terrestrial

249 transects, nocturnal surveys were undertaken slowly (~0.5 km/h) by foot to ensure careful
250 sampling. On all transects, a headlamp was used to detect lemurs using eyeshine, and a strong
251 flashlight was used when necessary to confirm the sighting. When a lemur was detected, the
252 date, time, transect number, GPS location, estimated distance between observer and animal,
253 number of individuals, estimated perpendicular distance (90°) between animal and transect,
254 distance along the transect, height of the animal off of the ground, and behavior of the animal
255 (e.g., locomotion, feeding, resting, social) were recorded. Angle and distance measurements were
256 estimated by eye always by the same trained observers. Because the two species could not be
257 reliably distinguished during sightings in the field, observations resulted in an identification only
258 to the genus level (*Microcebus*). Each transect was surveyed twice during separate nights.
259 Surveys on the same transect were carried out 1 – 6 days apart to accommodate needs of other
260 researchers and access to the boat.

261 *Analysis and density estimates from CMR data.*—We analyzed spatially explicit
262 individual encounter histories using spatial capture-recapture (SCR—Royle et al. 2014) to
263 explore species-specific patterns in density and space use. SCR methods operate similarly to
264 traditional closed population capture-recapture methods: repeated marking events in a population
265 of interest over a short period of time produces imperfect detection histories (i.e., some marked
266 individuals are missed in some occasions) providing information about detection probability,
267 which then is used to produce error-corrected estimates of true abundance. Spatial CR extends
268 this framework explicitly to include locations of captures that generate spatial encounter histories
269 that can be used to estimate a spatial detection function that is assumed to decrease with distance
270 from an individuals' activity center. The explicit integration of a spatial detection function means
271 the effective area sampled by an array of traps is explicitly defined, and the estimate of

272 abundance is spatially referenced, i.e., SCR produces estimates of absolute density (Borchers and
273 Efford 2008; Royle et al. 2018). Thus, a SCR model has two components: (1) a submodel for the
274 spatial detection function that includes estimation of at least two parameters, the baseline
275 detection ($p\theta$: encounter probability when a trap is located in an activity center) and a space use
276 parameter (σ : scale parameter that determines the distance over which detection declines), and
277 (2) a submodel for density (D : abundance per unit area). Royle et al. (2015) demonstrated that
278 SCR analyses lend themselves easily to analyses of stratified, or class structured, populations,
279 with the most obvious application being that of estimating sex-specific parameters (density,
280 detection, and space use). This results in a third component, a submodel for the class ratio (ψ :
281 probability that an individual in a population belongs to one of two classes). Here we apply a
282 novel modification of the sex-structured model to assess the two-species structure of the
283 *Microcebus* community at our sites.

284 We investigated specific hypotheses about whether lemur density, detection rate, and
285 movement distance varied by species, as a function of habitat type, or both. We also estimated
286 whether the species ratios varied across habitat types. We investigated models that allowed
287 density to be constant ($D\cdot$) or to vary by transect ($D_{transect}$) or by habitat ($D_{habitat}$, which also
288 accounted for potential differences in detectability due to habitat-specific trap placement); that
289 allowed detection and movement to be constant ($p\theta\cdot$ and $\sigma\cdot$, respectively) or to vary by species
290 ($p\theta_{spp}$ and σ_{spp} , respectively); and that allowed for constant ($\psi\cdot$) or transect-specific ($\psi_{transect}$)
291 species ratios. All combinations of these models resulted in a candidate set of 18 models
292 reflecting our hypotheses. The area of interest over which density was estimated (state-space)
293 was defined as a 100-m buffer around the transect lines for the dry and intermediate transects.
294 For the mangrove transects, which were on the river's edge, the buffers were clipped to only

295 include the terrestrial portions on one side of the river so that we did not overestimate the state-
296 space. Buffers and clipping were conducted in ArcMap (ESRI 2017). We compared models
297 using Akaike Information Criterion (AIC—Burnham and Anderson 2004) whereby models with
298 lower AICs were assumed to have more support. Models where the difference in AIC score
299 compared to the best-performing model (= lowest AIC) was less than 2.00 ($\Delta AIC < 2$) were
300 considered to have substantial support (Burnham and Anderson 2004). All analyses were carried
301 out in R (R Core Team 2018) using ‘oSCR’, a spatial capture-recapture package (Sutherland et
302 al. 2019). To evaluate the effect of habitat as a continuous gradient on species distributions, we
303 investigated the relationship between species identity and distance from the Antsena River using
304 generalized linear models conducted in R.

305 *Density estimates from line transect data.*—We used the Distance package in R (Miller
306 2017) to synthesize and select detection functions based on line transect survey data. This
307 program allows modelling of the probability of detection of an animal at a given distance from a
308 line (Miller et al. 2017). Using the Buckland Method (Buckland et al. 2001), the package also
309 allows for the selection of candidate models and the estimation of parameters using maximum
310 likelihood (Miller et al. 2017). These models then can be used to estimate population density and
311 abundances when survey areas are included. We generated a set of five models using uniform,
312 half-normal, and hazard-rate key functions that were either unadjusted or cosine adjusted. We
313 used AIC for model selection and set survey area using the state space in our SCR analysis to
314 facilitate comparison between the two methods. We used a two-tailed Z-test to evaluate if density
315 estimates for each transect were significantly different between modelling methods. We also
316 assessed the relationship between the density estimate rankings from SCR and distance sampling
317 models using a Spearman’s rank correlation test.

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RESULTS

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Capture-mark-recapture.—We captured 155 unique mouse lemur individuals (62 *M. murinus* and 93 *M. ravelobensis*) a total of 212 times over 856 trap nights (Table 2, Supplementary Data S1). Following our prediction, lemurs of both species were caught along all six transects, hence in all three habitat types (mangrove, intermediate, and dry forest). No individuals were captured on more than one transect, even in the case of the intermediate forest transect (INT3) intersecting with one of the dry forest sites (DRY4). Species differed significantly in their distribution relative to distance from the Antsena River (GLM: estimate = 0.003, $SE < 0.001$, $Z = 6.35$, $P < 0.001$; intercept = -1.81 , $SE = 0.377$, $Z = -4.81$, $P < 0.001$), which was used as a proxy for the underlying habitat gradient. *Microcebus murinus* made up 88% of the individuals captured within the first 250 m and 68% of the individuals captured within the first 750 m, and *M. ravelobensis* made up 88% of the individuals captured 750 – 1,570 m from the river.

Of the 18 SCR models, 9 models that tested species-specific detectability ($p0$) did not converge, likely due to low numbers of individual *M. ravelobensis* being captured in mangrove ($n = 3$) and intermediate ($n = 3$) habitats (candidate set models in Supplementary Data SD2). We evaluated the remaining models and found AIC-based support for two models: the top SCR model included constant detection, species-specific movement, transect-specific lemur densities, and transect-specific species ratios (Table 3). The second-best-performing SCR model had the same structure but with habitat-specific densities (Table 3). Our top SCR model calculated a baseline detection probability of 0.55 (95% CI : 0.29 – 0.79), which was held constant for both

340 species, and species-specific estimates of movement were 20.96 m (95% CI: 15.70 – 27.99) for
341 *M. murinus* and 17.98 m (95% CI: 14.17 – 22.81) for *M. ravelobensis*.

342 We used the top SCR model to generate density estimates for *M. murinus*, *M.*
343 *ravelobensis*, and pooled *Microcebus*, across the six transects (Table 4, Fig. 2). Densities for *M.*
344 *murinus* did not greatly vary between transects or habitat types (Table 4, Fig. 2a). In contrast, *M.*
345 *ravelobensis* density estimates (Table 4, Fig. 2b) differed between habitat types, with mangrove
346 estimates between 0.22 lemurs/ha (95% CI: 0.10 – 0.49) and 0.46 lemurs/ha (95% CI: 0.25 –
347 0.85), intermediate estimates of 1.89 lemurs/ha (95% CI: 1.06 – 3.37), and dry forest estimates of
348 2.09 lemurs/ha (95% CI: 1.36 – 3.21) to 5.45 lemurs/ha (95% CI: 3.63 – 8.18). Different density
349 estimates between species were reflective of large variations in species ratios among transects.
350 The six estimated species ratios (or probabilities that an individual in the population belongs to
351 *M. murinus*) were 0.83 (95% CI: 0.36 – 0.98) for MAN1, 0.83 (95% CI: 0.51 – 0.96) for MAN2,
352 0.62 (95% CI: 0.33 – 0.84) for INT3, 0.51 (95% CI: 0.31 – 0.71) for DRY4, 0.14 (95% CI: 0.06
353 – 0.29) for DRY5, and 0.17 (95% CI: 0.08 – 0.33) for DRY6 (Fig. 4).

354 *Line transect.*—We observed 150 mouse lemurs over 12 surveys (two nights per transect)
355 at perpendicular distances from transect lines of 0–25 m (data available in Supplementary Data
356 SD1). Of the 5 evaluated distance sampling models, we had substantial support based on AIC-
357 values. All of the top models used a cosine adjustment. The top distance sampling model (AIC =
358 776.91) used a hazard-rate function to model detection probability, while the second (Δ AIC =
359 0.53) and third (Δ AIC = 1.40) best-performing distance sampling models used uniform and half-
360 normal functions, respectively. Because individuals could not be identified by species during
361 transect surveys, distance sampling models only estimated densities of total mouse lemurs
362 (pooled *Microcebus*) by transect. Our top distance sampling model estimated *Microcebus* density

363 along mangrove transects between 2.63 lemurs/ha (95% *CI*: 1.15 – 5.99) and 5.40 lemurs/ha
364 (95% *CI*: 3.57 – 8.18), 10.25 lemurs/ha (95% *CI*: 6.76 – 15.54) along the intermediate forest
365 transect, and 9.52 lemurs/ha (95% *CI*: 7.34 – 12.35) to 13.60 lemurs/ha (95% *CI*: 10.91 – 16.96)
366 along dry forest transects (Fig. 3a, Table 4). Density estimates from our top SCR and distance
367 sampling models differed significantly from each other for four out of six transects (Table 4),
368 and the estimates were not correlated with one another (Spearman’s rank correlation: $\rho = 0.54$,
369 $n = 12$, $P = 0.30$).

370

371 DISCUSSION

372 Our study provides empirical evidence for differential habitat use between cryptic congeners
373 living in sympatry, as evidenced by substantial differences in spatial distribution and densities
374 between the two mouse lemur species across the mangrove–dry forest gradient. Our best-
375 performing spatial capture-recapture models suggested that the proportions and relative densities
376 of the two species varied among transects and habitat types. *Microcebus murinus* was estimated
377 to occur at densities five times greater than *M. ravelobensis* in mangroves and 1.6 times greater
378 along the intermediate transect. Along DRY4, which intersected the intermediate transect, the
379 congeners were estimated to occur at about equal densities, while *M. ravelobensis* was estimated
380 to outnumber *M. murinus* by a factor of 6.26 and 4.75 for DRY5 and DRY6, respectively. Our
381 study found that densities of these species varied differentially between forest types and that *M.*
382 *ravelobensis* reached higher maximum densities than *M. murinus*, which aligned with a previous
383 large-scale study (Rakotondravony and Radespiel 2009). Rakotondravony and Radespiel (2009)
384 also found a negative correlation between the densities of these sympatric species.

385 While our study found differential proportions of *M. murinus* and *M. ravelobensis* among
386 transects, assessing densities of each species independent of one-another across habitat types
387 revealed divergent trends independent of the presence of congeners. In the case of *M. murinus*,
388 density estimates were largely similar between mangroves, intermediate forests, and dry forest
389 transects. Meanwhile, *M. ravelobensis* estimates increased with increasing distance from the
390 river, with the dry forest transects farthest inland (DRY5 and DRY6) supporting relative
391 estimates 10 – 20 times greater than those along mangrove transects. The low variation in *M.*
392 *murinus* densities across the habitat gradient, despite the large variation in *M. ravelobensis*
393 densities, suggests that the spatial distribution of each species largely is independent of the
394 distribution of its congener and consequently not heavily influenced by interspecific competition.
395 Rather, their divergent patterns seem to reflect differences in habitat preferences or habitat
396 flexibility between the species. A recent study across varying levels of fragmentation also
397 supports the notion that densities are more heavily influenced by habitat conditions than by
398 competition between these sister species (Andriatsitohaina et al. 2020). *Microcebus murinus* is
399 found throughout an array of forest types in western Madagascar and is considered a generalist
400 with high habitat plasticity (Thorén 2011; Radespiel 2016; Blanco et al. 2018), which might
401 allow it to occupy or use a wider range of habitat types, including the mangroves at our study
402 site. The relatively low numbers of *M. ravelobensis* in mangroves compared with dry forests
403 suggests that it uses mangroves differently than *M. murinus*.

404 There are several habitat parameters that could potentially influence distributional
405 differences between these species and might therefore explain observed differences in their
406 relative densities across the gradient, particularly in mangroves. Mangroves are characterized by
407 low plant richness worldwide (Nagelkerken et al. 2008), and this is especially true in Malagasy

408 mangroves that contain one-half the number of plant species compared with mangroves on the
409 African mainland (Giri and Muhlhausen 2008). The plant communities found in mangroves
410 likely offer different food resources and microhabitat structures than those available in the dry
411 deciduous forests. Previous research has shown that *M. murinus* has a wider seasonal dietary
412 niche than *M. ravelobensis* (Thorén et al. 2011), which might allow the generalist to take
413 advantage of some food resources available in mangroves that its congener might not consume.
414 Habitat structure of mangroves also might offer preferred or more suitable sleeping sites for *M.*
415 *murinus* but less so for *M. ravelobensis*. Species of cavity-nesting birds (Monterrubio-Rico and
416 Escalante-Pliego 2006) and bats (Kunz and Lumsden 2005) are known to use large mangrove
417 trees, suggesting that tree holes also might be available as sleeping sites to *M. murinus* in
418 mangroves (Radespiel et al. 2003). Conversely, the low plant diversity in mangroves might not
419 support lianas and similarly complex structural elements that *M. ravelobensis* routinely uses as
420 sleeping sites or provide flexible leaves for nest-building (Thorén et al. 2010). Habitat structure
421 in mangroves also is highly dynamic and different from other forest types. Daily tidal cycles
422 partially submerge many trees during daily high tides even during the dry season. These changes
423 in the forest are likely to be even more dramatic during the rainy season. These dynamics may
424 impact dietary and sleeping site resources in mangroves and how this habitat is used by *M.*
425 *murinus* and *M. ravelobensis*.

426 We used spatial capture-recapture and distance sampling models to estimate lemur
427 densities across our transects. The best models for each method produced markedly different
428 results, with distance sampling predicting some densities similar to SCR (e.g., MAN2 and
429 DRY6) and others 2–3 times higher. Studies comparing estimates generated by these methods
430 have sometimes found higher densities for distance sampling compared with spatial capture-

431 recapture (de Infante Anton et al. 2013), while others have found that estimates closely align
432 (Franzetti et al. 2012; Mancini et al. 2015). A previous study estimating mouse lemur density
433 also found similar estimates between SCR and distance sampling methods (Meyler et al. 2012).
434 Our estimates are based on data from limited number of surveying and trapping sessions (two per
435 transect), which means that we might have detected individuals during surveys that we missed
436 while collecting CMR data. The relatively small dataset also limited the precision of our
437 estimates.

438 One key assumption inherent in distance sampling using line transects is that all animals
439 on the line (at distance 0) are detected (Buckland et al. 2001). Along terrestrial transects, this
440 assumption can be challenging to meet, given that mouse lemurs are small-bodied, arboreal, and
441 fast-moving animals. The nocturnal nature of the surveys presents an added challenge because
442 these animals can be difficult to see in the dark. Along our two river transects, this particular
443 assumption was impossible to meet because observers conducted surveys from water, where no
444 lemurs could occur on the transect line. Logistics of navigating the river by boat also meant that
445 we had to travel at higher speeds while surveying mangrove transects than when we surveyed
446 terrestrial transects on foot. Although we had two observers monitoring for lemurs on the same
447 side of the river, the increased speed led to instances of “swamping” where a large number of
448 sightings in a short period made it challenging to accurately count all lemurs. This could have
449 contributed to conservative estimates from boat surveys. Density estimates produced by the
450 distance sampling models also were based on data prone to human error through estimation of
451 distances among observers, lemurs, and the transect. Systemic underestimation of distance on the
452 part of the observers could, for example, have produced estimates biased toward higher densities.
453 Given these sampling biases and significant differences between values produced by the two

454 modeling techniques, the mouse lemur density estimates we report should not be taken as
455 absolute but rather as relative measurements. Despite these limitations, the models generated
456 through SCR and distance sampling techniques produced relative density estimates that were
457 similar between habitat types, with mangrove transects supporting lower mouse lemur densities
458 compared to dry forests. This suggests that while these indirect methods might not be appropriate
459 for estimating absolute densities, relative densities are comparable between methods.

460 While other mammals, including some species of monkeys (Nowak 2012) and rodents
461 (Magnusson et al. 1976), are known to specialize in mangroves, there is no analog known in
462 lemurs (Nowak 2012). Only a few published studies have documented lemurs using this habitat
463 (Gardner 2016; Donati et al. 2019), including a recent report of Coquerel’s sifaka (*Propithecus*
464 *coquereli*) feeding on mangrove leaves along the Antsena River (Chell et al. 2020). Our findings
465 show that cryptic mouse lemur species differ in their distributions along a habitat gradient that
466 includes this understudied habitat. Understanding how lemurs use different habitats has
467 important implications for conservation.

468 Madagascar is ranked as one of the top biodiversity hotspots in the world, with high
469 levels of species richness and endemism (Myers et al. 2000). Found only on the island, lemurs
470 are highly threatened by habitat loss and fragmentation and are ranked as one of the most
471 endangered group of mammals in the world (Schwitzer et al. 2013). *Microcebus ravelobensis* is
472 classified as Vulnerable by the International Union for the Conservation of Nature due to its
473 vulnerability to deforestation, limited distribution, and decreasing abundance (Blanco et al.
474 2020). Our study confirms the importance of dry deciduous forests for the maintenance of *M.*
475 *ravelobensis* populations in northwestern Madagascar as evidenced by the higher relative
476 densities of this species along dry forest transects compared to other habitat types.

477 We found *M. murinus* at similar densities across the habitat gradient and found both
478 species in mangroves, indicating that mouse lemur populations use this habitat. Due to timber
479 harvesting and land-use change, Madagascar saw a 21% net loss of mangrove forests from 1990
480 to 2010 (Giri and Muhlhausen 2008; Jones et al. 2016), including a 5% loss locally around
481 Mariarano (Jones et al., 2016). While laws and regulations prohibit timber extraction from
482 mangroves and there have been efforts to support local sustainable management of these
483 ecosystems, very few of Madagascar’s remaining mangroves are sufficiently protected from
484 degradation and loss (Jones et al. 2016). Protecting mangroves likely is important to maintain
485 mouse lemur populations, especially as other forest types decrease and become more fragmented.
486 Mangroves also provide a number of resources and ecosystem services, including fisheries,
487 storm protection, and high capacities for carbon sequestration (Jones et al., 2016). Conserving
488 these ecosystems therefore can have multiple benefits for biodiversity conservation, sustainable
489 development, and mitigating anthropogenic climate change.

490 Our study contributes strong empirical evidence of differing habitat use of sympatric
491 congeners across a habitat gradient and highlights the role of ecological flexibility and habitat
492 plasticity as mechanisms by which cryptic species might coexist. Interactions among
493 heterogeneous landscapes, dynamic habitat resources, and species-specific microhabitat
494 preferences likely drive the divergent spatial patterns of *M. murinus* and *M. ravelobensis* across
495 the mangrove–dry forest gradient.

496

497

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512

513

SUPPLEMENTARY DATA

514 Supplementary data are available at the *Journal of Mammalogy* online.

515

516 **Supplementary Data SD1.**—Project data used for CMR and distance sampling
517 modelling. The spreadsheet contains data on live trap locations, captured lemurs, and transect
518 survey detections.

519

520 **Supplementary Data SD2.**—Candidate set of spatial capture-recapture models. The
521 spreadsheet contains two ranked lists, one of models that converged and one of all models tested.

522

523

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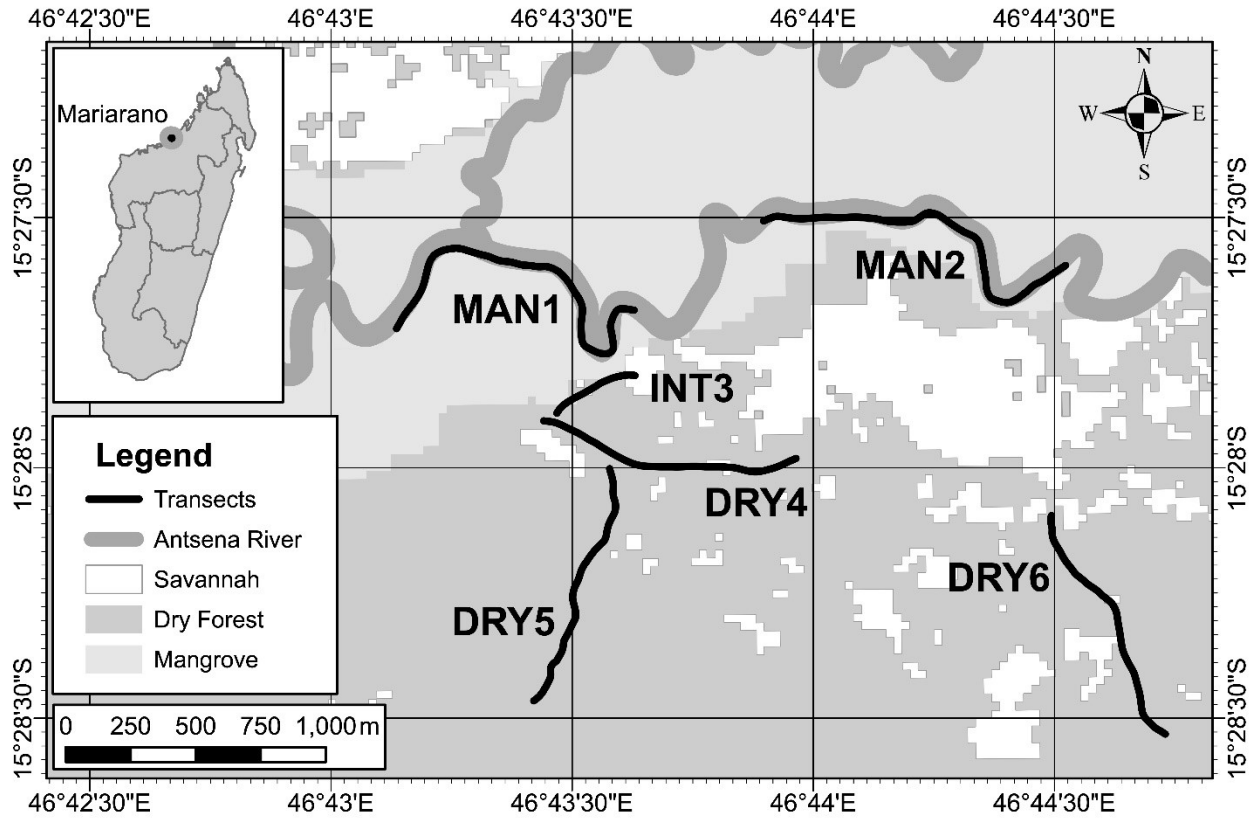
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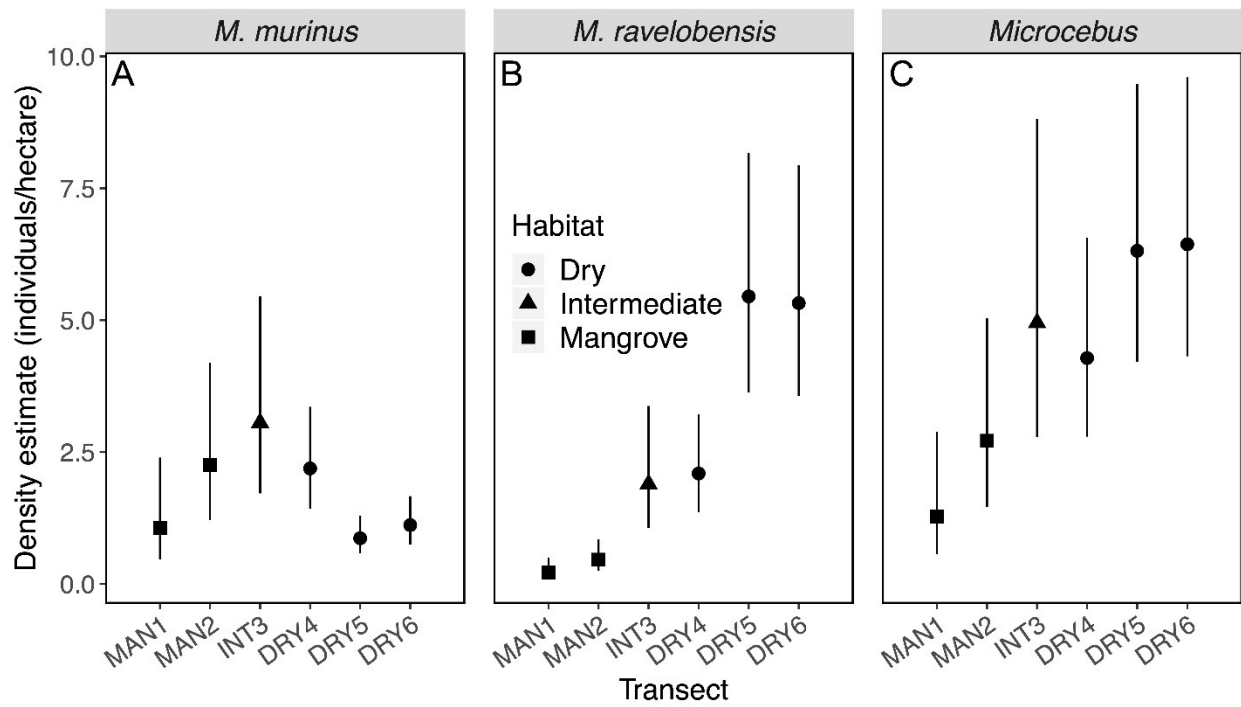
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Fig. 1.—Six transects were surveyed in the Mariarano commune, northwestern Madagascar, in June–July 2017.

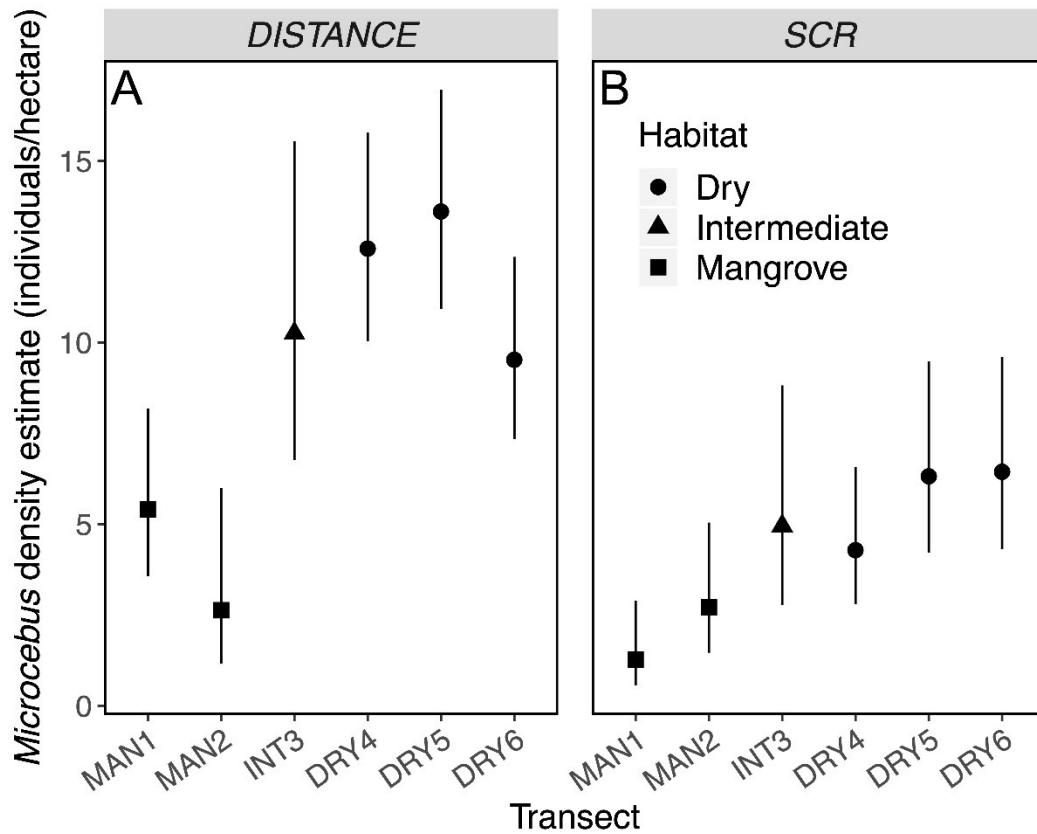


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726 **Fig. 2.**—Density estimates of (A) *Microcebus murinus*, (B) *M. ravelobensis*, and (C) pooled at
 727 the genus level across all six transects generated by the top spatial capture-recapture (SCR)
 728 model. Habitat types are represented by marker shape, and error bars delineate upper and lower
 729 95% CI.

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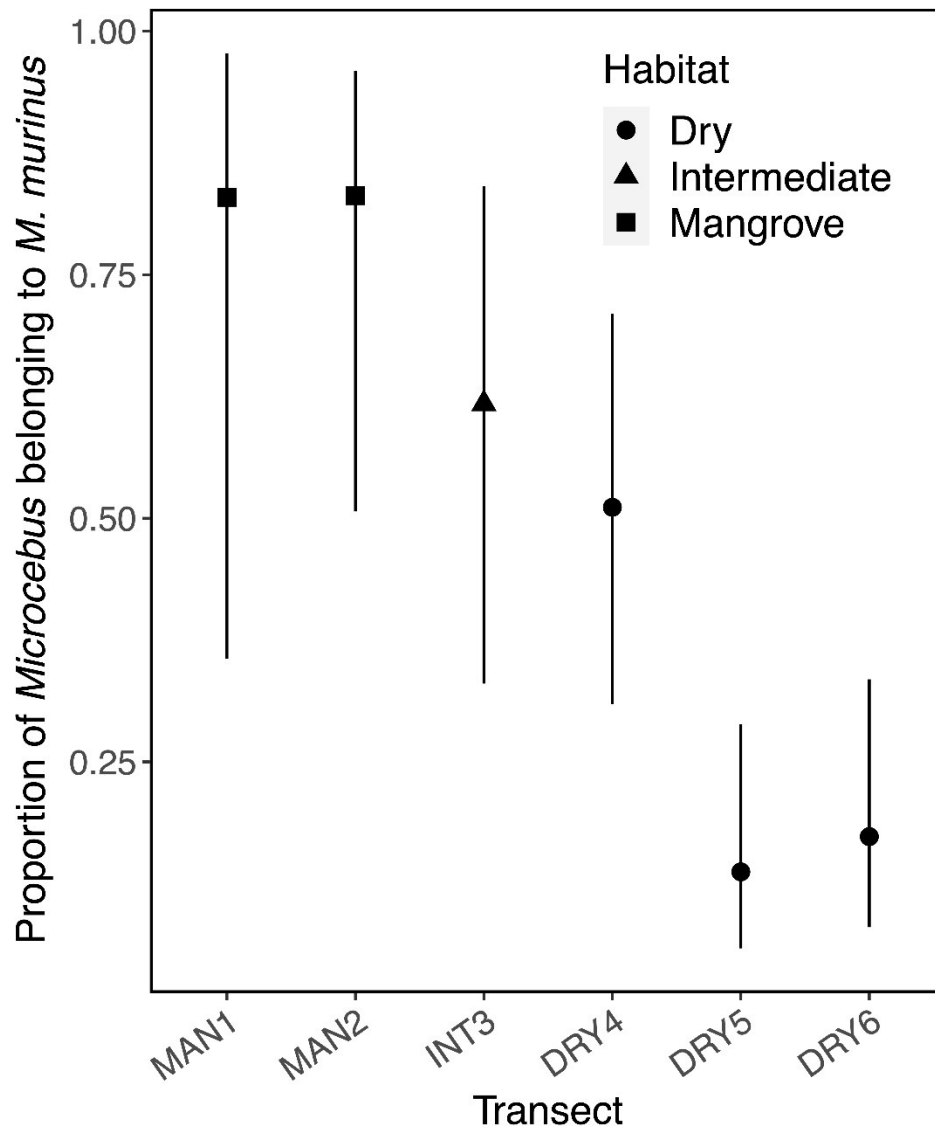


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734 **Fig. 3.**—Density estimates of mouse lemurs pooled at the genus level (*Microcebus*) across all six
 735 transects generated by (A) the top Distance Sampling model and (B) the top SCR sampling
 736 model. Habitat types are represented by marker shape, and error bars delineate upper and lower
 737 95% CI.

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742 **Fig. 4.**—Estimated proportion of mouse lemurs belonging to *Microcebus murinus* across the six
 743 transects. The species ratio estimates were generated by the top SCR model. Habitat types are
 744 represented by marker shape, and error bars delineate upper and lower 95% CI.

Table 1.—Overview of transects used for capture-mark-recapture (CMR) and line transect surveys. Distances from the river were calculated using Euclidean Distance in ArcMap (ESRI 2017).

Habitat	Transect ID	Transect Length (m)	Minimum Distance from River (m)	Maximum Distance from River (m)	Number of traps
Mangrove	MAN1	1448	0	0	41
	MAN2	1423	0	0	41
Intermediate	INT3	360	108	310	40
	DRY4	1000	310	652	102
Dry	DRY5	1000	435	1313	102
	DRY6	1000	777	1570	102

Table 2.—Comparison of capture data across transects for *M. murinus* (MUR) and *M. ravelobensis* (RAV). Trap-night is defined as number of active traps on a given transect multiplied by the number of sampling nights (two per transect).

Habitat	Transect ID	Length (m)	Trap-nights	Captures per trap night (all <i>Microcebus</i>)	MUR Captures (individuals)	RAV Captures (individuals)
Mangrove	MAN1	1448	82	0.085	6 (6)	1 (1)
	MAN2	1423	82	0.268	19 (12)	3 (2)
Intermediate	INT3	360	80	0.238	14 (10)	5 (5)
	DRY4	1000	204	0.270	9 (7)	46 (36)
Dry	DRY5	1000	204	0.211	24 (18)	19 (14)
	DRY6	1000	204	0.324	12 (9)	54 (35)

Table 3.—Comparisons of Akaike Information Criteria (AIC) for top density models for *Microcebus*. Density submodel covariates include Transect and Habitat. Species was used as a detection parameter (p_0) covariate and space-use parameter (σ) covariate. Null models are indicated by a covariate of 1. Both models listed had Transect used as the covariate for the species ratio (ψ) sub-model.

Density (D)	Detection (p_0)	Space-use (σ)	Log-likelihood	AIC	Δ AIC	Cumulative Model Weight
Transect	1	Species	687.42	1404.85	0.0	0.51
Habitat	1	Species	690.47	1404.94	0.09	0.99

Table 4.—Mouse lemur densities (individuals per hectare) across transects and habitat types using two methods of estimation. Spatial capture-recapture (SCR) models estimated density by species (*M. murinus* = MUR; *M. ravelobensis* = RAV) and pooled *Microcebus* density, while distance sampling models only estimated total *Microcebus* density. *P*-values < 0.05 from the *Z*-test comparison indicate significant differences in density estimates between best SCR and distance sampling models.

Habitat type	Transect ID	<i>Microcebus</i> Density (standard error)			MUR density (standard error)	RAV density (standard error)
		SCR	Distance Sampling	<i>P</i> value from <i>Z</i> -test comparison	SCR	SCR
Mangrove	MAN1	1.27 (0.53)	5.40 (0.67)	<0.001	1.06 (0.53)	0.22 (0.53)
	MAN2	2.71 (0.86)	2.63 (0.42)	0.933	2.25 (0.86)	0.45 (0.86)
Intermediate	INT3	4.95 (1.46)	10.25 (1.27)	0.006	3.06 (1.46)	1.89 (1.46)
	DRY4	4.28 (0.93)	12.58 (1.22)	<0.001	2.19 (0.93)	2.09 (0.93)
Dry	DRY5	6.32 (1.31)	13.60 (1.31)	<0.001	0.87 (1.31)	5.45 (1.31)
	DRY6	6.43 (1.31)	9.52 (0.98)	0.059	1.12 (1.31)	5.32 (1.31)