

Environmental and anthropogenic influences of movement and foraging in a critically endangered lemur species, *Propithecus tattersalli*: implications for habitat conservation planning

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Research

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1 Environmental and anthropogenic influences of movement and foraging in a critically
2 endangered lemur species, *Propithecus tattersalli*: implications for habitat conservation
3 planning

4 Short title: Lemur space use and foraging behavior

5

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23 **Abstract**

24

25 **Background**

26 Wildlife conservation often focuses on establishing protected areas, however, these
27 conservation zones are frequently developed without adequate knowledge of the
28 movement patterns of the species they are designed to protect. Understanding movement
29 and foraging patterns of species in dynamic and diverse habitats can allow managers to
30 develop more effective conservation plans. Threatened lemurs in Madagascar are an
31 example where management plans and protected areas are typically created to encompass
32 large, remaining forests rather than the resource needs of the target species.

33

34 **Methods**

35 To gain an understanding of golden-crowned sifaka (*Propithecus tattersalli*) movement
36 patterns, including space use and habitat selection, across their range of inhabited forest
37 types, we combined behavior data with Dynamic Brownian Bridge Movement Models
38 and Resource Selection Functions. We also examined the influence of abiotic, biotic, and
39 anthropogenic factors on home range size, movement rates, and foraging patterns.

40

41 **Results**

42 We found that home range size and movement rates differed between seasons, with
43 increased core area size and movement in the rainy season. Forest type also played a role
44 in foraging behavior with lemur groups in humid forest avoiding roads in both seasons,

45 groups in the dry deciduous forest avoiding road networks in the rainy season, and groups
46 in the moderate evergreen forest displaying no selection or avoidance of road networks
47 while foraging.

48

49 **Conclusion**

50 Our study illustrates the importance of studying primate groups across seasons as well as
51 across forest types, as developing conservation plans as a single snapshot can give an
52 inaccurate assessment of their natural behavior and resources needs. More specifically,
53 by understanding how forest type influences golden-crowned sifaka movement and
54 foraging behavior, we can make conservation management plans specific to the
55 individual forest types they inhabit (humid, moderate evergreen, dry deciduous, littoral,
56 etc.), rather than the region as a whole.

57

58 **Key Words**

59 Movement; space use; foraging; resource selection; Brownian bridge modeling; home
60 range; road avoidance; primates; lemurs

61

62 **Background**

63

64 Conservation biologists have long recognized the importance of establishing protected
65 areas to facilitate population persistence in landscapes that are threatened by increasing
66 human encroachment, habitat fragmentation, and habitat loss [1–4]. However, efforts to
67 conserve wildlife and preserve biodiversity are often based on an incomplete
68 understanding of animal movement as well as variability in movement patterns among
69 groups or populations that the areas are meant to protect [5]. While a number of studies
70 have demonstrated the relevance of incorporating movement, particularly animal foraging
71 and home range size, into protected area design [6–9], integration between the disciplines
72 of conservation biology and movement (coined “conservation behavior”) is limited [10–
73 12]. Yet, knowledge of movement behavior, specifically how, when, and where animals
74 move and forage within their habitat, would illuminate how populations navigate and
75 utilize resources within their environment and thus develop better management plans
76 [13,14]. Specifically, species, populations, or even groups often respond differently to
77 factors such as seasonality, habitat characteristics, and anthropogenic pressures in
78 different ways and therefore a better understanding of their role is crucial when
79 developing management plans and establishing protected areas.

80

81 In the tropics, seasons are often divided into dry and rainy seasons, with primary
82 productivity varying seasonally as a function of rainfall. This seasonality thus influences
83 the distribution and availability of resources on the landscape and as a result animal

84 movement strategies shift to increase foraging efficiency [15–17]. For example, the
85 black-fronted titi monkey (*Callicebus nigrifrons*; Nagy-Reis and Setz, 2017) and collared
86 brown lemur (*Eulemur collaris*; Campera et al., 2014) cope with dry season food
87 shortages by reducing movement rates, while the common bumble bee (*Bombus*
88 *vosnesenskii*; Pope and Jha, 2018) and African elephant (*Loxodonta africana*; Wato et al.,
89 2018), respond by increasing foraging and movement rates. Animals can also cope with
90 dry season conditions by shifting home range size or location [22] and altering time spent
91 foraging [23]. Understanding how seasonal fluctuations influence movement and
92 foraging patterns in free-living animals can allow managers to more effectively design
93 protected areas and protect critical resources [24].

94

95 In addition to abiotic factors, biotic factors such as habitat (forest) type, strongly
96 influence animal movement and foraging [25]. Various studies demonstrate that animals
97 adjust their home range size and foraging patterns in response to habitat type and
98 structure (e.g. Roe deer (*Capreolus capreolus*); Said and Servanty, 2005) and coyote
99 (*Canis latrans*); Holzman et al., 1992)) indicating that landscape heterogeneity is a key
100 factor influencing the movement of species. While studies of canids, ungulates, and
101 primates have examined the influence of habitat type on home range size, a large
102 proportion of studies are limited to examining metrics of habitat structure (e.g. forest
103 maturity, vegetation density, food scarcity, microhabitat preference) on animal movement
104 and home range size [28,29]. The benefit of understanding movement behavior across

105 distinct habitat types is that management strategies can be designed for each habitat type
106 a species occupies.

107

108 Importantly, anthropogenic influences affect animal movement behaviors, can have
109 deleterious effects on wildlife, and must be considered when establishing protected areas
110 [30,31]. The presence of humans and road networks may negatively influence animal
111 movement behavior by increasing human-wildlife interactions (e.g., hunting, poaching,
112 vehicle collisions) and pushing animals out of prime habitat [32,33]. Large mammals are
113 especially affected by human encroachment due to their larger home range size, lower
114 population density, more narrow geographic distributions, and large portions of their
115 distributions being shared with humans [34]. For instance, black bears (*Ursus*
116 *americanus*) have been found to avoid areas with human development during daylight
117 hours [35] and woodland caribou (*Rangifer tarandus caribou*) avoid high use roads,
118 mines, and cabins during months of high human activity [36]. Of large mammalian taxa,
119 few studies have examined the influence of human infrastructure on primate movement,
120 although they are often strongly affected by anthropogenic features [37,38].

121

122 The lemurs of Madagascar face significant anthropogenic threats [39]. Between 1953 and
123 2014, Madagascar lost 44% of its forests, with 46% of the remaining forests being
124 located within 100 m of a forest edge [40]. This high degree of forest destruction and
125 increasing presence of edge forest habitat influences lemur behavior and their ability to
126 meet their nutritional demands. While previous studies have examined lemur home range

127 size [41,42], dietary flexibility [43], species abundance [44], and reproduction in various
128 environments [45,46], our understanding of lemur movement is limited but members of
129 the genus *Propithecus* have provided some information. In regard to home range
130 characteristics, diademed sifakas (*Propithecus diadema*) in humid fragmented habitats
131 had reduced home range size and daily path length and foraged on sub-optimal food
132 items compared to sifaka groups in contiguous forest environments [41]. In contrast,
133 Milne-Edwards' sifakas (*Propithecus edwardsi*) inhabiting humid logged forests traveled
134 shorter distances each day to feed in a low-quality food environment, yet maintained
135 larger home ranges than conspecifics in contiguous forests [42]. Further, Verreaux's
136 sifakas (*Propithecus verreauxi*) in Madagascar's dry deciduous forests exhibited
137 significant home range reduction from the rainy to the dry season [47]. While these
138 studies have shed light on *Propithecus* behavioral responses to abiotic and biotic factors
139 in extremes of the humid-dry forest gradient of forest types, we do not understand how
140 species in the genus *Propithecus* respond in a moderate forest type. Knowledge of
141 *Propithecus* movement behavior in regards to these factors would enable us to predict
142 how these lemurs would use a protected area and design a reserve accordingly.

143

144 Golden-crowned sifaka (*Propithecus tattersalli*) are a critically endangered lemur
145 endemic to naturally fragmented forests of northeastern Madagascar [48]. Unlike the
146 other eight species of sifaka (*Propithecus spp.*) on Madagascar that are restricted to dry
147 or humid forest types, *P. tattersalli* inhabit a range of forest types [49,50]. Variation of
148 habitable forest types makes them a unique opportunity to examine the influence of

149 seasonality, forest type, and anthropogenic factors on movement and foraging behavior in
150 a primate. Studies of golden-crowned sifaka have documented a major decline in the
151 population in the last decade and informed researchers of the natural fragmentation of the
152 landscape, yet no previous study has examined the influence of movement on space use
153 and foraging tree selection across their range (Quéméré et al., 2012; Salmona et al.,
154 2017). An understanding of how abiotic, biotic, and anthropogenic factors influence
155 golden-crowned sifaka space use and foraging throughout their range would allow
156 species management plans to be made for populations within each particular forest type
157 occupied rather than the species as a whole.

158

159 In this study, we analyzed location and foraging behavior of six golden-crowned sifaka
160 groups to evaluate the effects of abiotic (seasonality; rainy and dry season), biotic (forest
161 type; humid, moderate evergreen, and dry deciduous forests), and anthropogenic
162 (fragmentation; edge and interior forests) factors on their movement patterns and space
163 use. Approaches to studying nonhuman primate space use typically are limited to
164 examining daily path length and home range overlap through the use of area estimators
165 (MCP, line-based kernel density, etc.; (e.g. Lehmann and Boesch, 2002; Steiniger and
166 Hunter, 2013). More modern and sophisticated approaches including Dynamic Brownian
167 Bridge movement models (DBBMM) and Bayesian methods [55,56], reduce the
168 likelihood of both Type I and Type II errors which can bias our understanding of animal
169 space use and habitat selection [57]. Thus, to estimate space use we used DBBMM which
170 incorporated temporal and behavioral characteristics of movement trajectories into

171 estimation of an animal's home range [58]. For our first objective we predicted that
172 seasonal movement rates would be greater in the rainy season, humid forests, and edge
173 forests compared to drier more interior forests. Second, we predicted that home range
174 size and core area range size would be larger in the rainy season, in edge forests, and in
175 the humid forest compared to drier and interior forests. We also predicted that sifaka
176 groups in edge forests would exhibit less core area range overlap (between the rainy and
177 dry seasons) than interior forest groups. Third, we predicted that sifakas would select the
178 largest feeding trees within their home ranges and avoid locations near human settlements
179 or manmade structures.

180

181 **Methods**

182

183 **Study Area**

184

185 Research was conducted in the Loky-Manambato Protected Area of northeastern
186 Madagascar (Fig. 1). This protected area encompasses a unique biogeographical
187 transition zone from Madagascar's northern and western dry deciduous forests to
188 southern humid forests. The Loky-Manambato region contains a mosaic of various forest
189 types including dry deciduous, dry evergreen, humid, and littoral forests separated by
190 agricultural areas and savanna (Quéméré et al., 2012). The region experiences a four-
191 month rainy season occurring from December to March followed by an eight-month dry

192 season [59]. The study sites include three distinct forest types: a humid forest, moderate
193 evergreen forest, and dry deciduous forest.

194

195 **Study Species and Subjects**

196

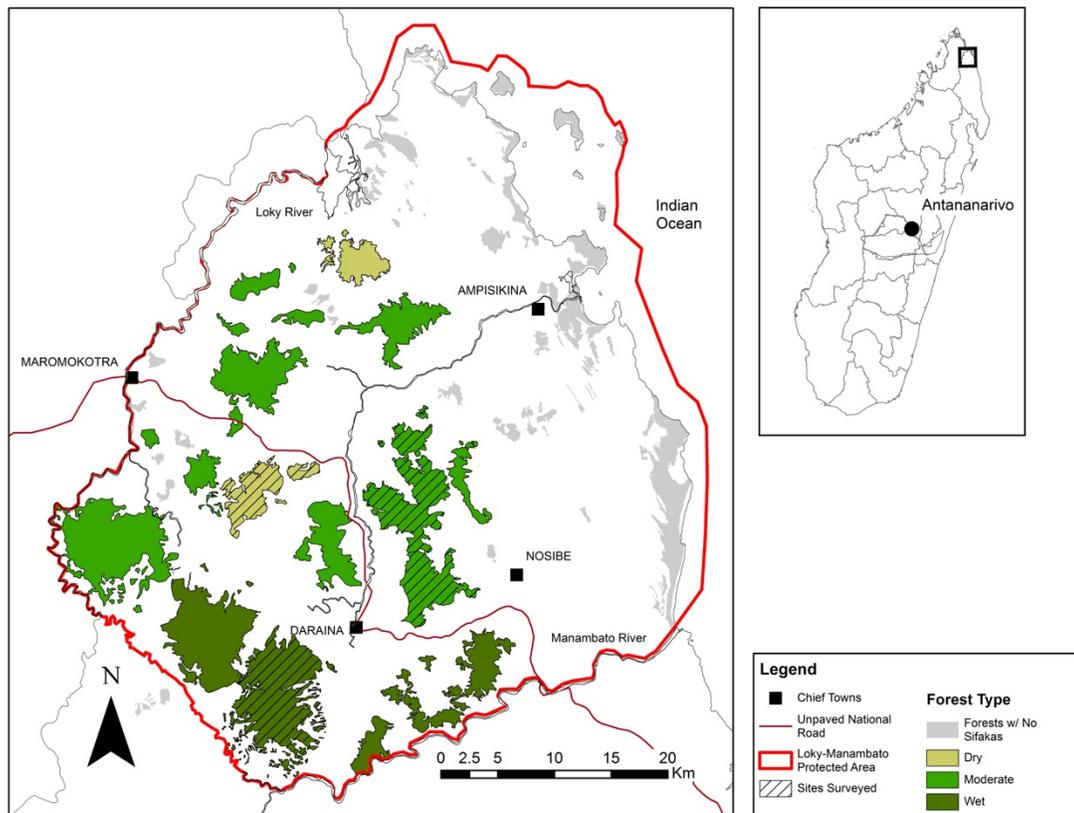
197 Golden-crowned sifaka live in semi-cohesive social groups ranging in size from 3-12
198 individuals with one or more adult males, several adult females, and several immature
199 individuals of both sexes. Group members typically travel in a coordinated fashion and
200 generally remain in visual or auditory contact with at least one other group member [59].
201 Thus, we assumed that all animals within a given social group share a home range, and
202 therefore treated each group as a unit of analysis in this study. Golden-crowned sifaka are
203 frugo-folivores, but also consume seeds, petioles, buds, flowers, and bark.

204

205 We studied six groups of habituated golden-crowned sifaka distributed across the three
206 distinct forest types (two groups each in humid, moderate evergreen, and dry deciduous
207 forests) in the Loky-Manambato Protected Area. We selected three of the 11 large forest
208 fragments containing golden-crowned sifaka due to their accessibility: Binara (humid),
209 Bekaraoka (moderate evergreen), and Solanamampilana (dry deciduous) (Figure 1).

210 Within each forest type, we followed one group in primary forest towards the center of
211 the forest (hereafter interior; characterized by lemurs having a home range at least 300
212 meters from the forest edge) and one group on the edge of the forest fragment (hereafter

213 edge; characterized by having a home range adjacent to the forest edge). Average group
214 size was six individuals and ranged from five to eight (Table 1).



215
216 **Fig. 1.** Study area in the Loky-Manambato Protected Area of northern Madagascar. The
217 thin red line depicts the unpaved national road in the region. The three forest fragments
218 surveyed are denoted by hatched black lines and are colored based on forest type.

219
220
221
222

223

224 **Table 1.** Composition of focal groups within each forest fragment, forest type, and forest
225 fragmentation classification.

Forest Fragment	Forest Type	Forest Location	Group Size
Binara	Humid	Interior	7
Binara	Humid	Edge	5
Bekaraoka	Moderate Evergreen	Interior	7
Bekaraoka	Moderate Evergreen	Edge	8
Solanamampilana	Dry Deciduous	Interior	5
Solanamampilana	Dry Deciduous	Edge	5

226

227

228 **Group Location Data**

229

230 We collected golden-crowned sifaka group location data during two periods, February-
231 April 2019 (rainy season) and June-August 2019 (dry season). We followed groups from
232 sleep tree to sleep tree (~13 hours per day) and collected location data at 15-minute
233 intervals. In addition to daytime activity, golden-crowned sifaka are known to exhibit
234 nocturnal movements, specifically during periods of bright moon light [60], and thus
235 groups were not always located in the same sleep tree the following morning. In these
236 instances, we reestablished contact with the group as quickly as possible. Group locations
237 were recorded using a GPS receiver (Garmin 64s), using the Universal Transverse

238 Mercator coordinate system (zone 39L), and points were logged at the group's
239 approximate geometric center. If no animals were visible at the 15-minute interval,
240 observers waited to establish visual contact with the social group before recording any
241 locations.

242

243 **Foraging and Landscape Data**

244

245 We recorded foraging data at the same 15-minute intervals using scan sampling to record
246 the behavior, height in the tree, and nearest neighbor of each individual in a group [61]. If
247 an individual was actively feeding during the scan, the plant species and part (*e.g.*,
248 young/mature leaf, leaf petiole, un/ripe fruit, seed, or flower) were identified, GPS
249 location recorded, and data concerning tree species, size, and current phenology
250 collected. In addition to collecting foraging data specific to each of the lemur groups, we
251 also collected general landscape data throughout each of the six lemur home ranges in
252 both the rainy and dry season. We did this by randomly generating forty GPS points
253 within each of the six home ranges (in both seasons) and collected data from potential
254 feeding trees (species, size, phenology) within 5 meters of each location. This allowed us
255 to gain an understanding of the entire landscape of all six home ranges, not just the
256 specific feeding trees utilized by each of the groups.

257

258 **Home Range Estimation**

259

260 Utilization distributions (i.e., 95% isopleth, hereafter home ranges and 50% isopleth,
261 hereafter core area) were estimated for each golden-crowned sifaka group using Dynamic
262 Brownian Bridge Movement Models (DBBMM); [58]. Home range DBBMMs use
263 behavior and movement trajectory data of the animal group that is collected in sequential
264 relocation studies. This method provides a spatially explicit model, which describes the
265 probability of the given animal group occurring in a given location during a specified
266 period. This approach also accounts for temporal autocorrelation, spatial uncertainty,
267 irregularly sampled data, and shifts in an animal's behavior (resting, foraging,
268 thermoregulating, corridor use, etc.), making it specifically applicable to studies of group
269 living primates [57,58,62]. Using DBBMMs to estimate group home ranges requires a
270 Brownian motion variance parameter (σ^2 , in meters), which quantifies the degree of
271 diffusion or irregularity of an animal's path [58]. A moving window analysis identifies
272 changes in the movement behavior and estimates σ^2 for each step. The size of the moving
273 window must include an odd number of GPS locations, because the σ^2 parameter is
274 estimated using a "leave-one-method", and a margin of greater than three locations
275 bounding each end of the window in which no behavioral changes can occur [58]. We
276 parameterized the DBBMM with a 21-step window size, a 9-step margin size, and a 15 m
277 location error for all lemur groups, as visual inspection indicated these settings were
278 sufficient to identify changes in home range size and overall animal movement [58].
279 Home ranges were estimated for each lemur group using the DBBMM function in R
280 package 'move' [63,64]. We conducted a three-way analysis of variance (ANOVA)
281 predicting for both 50% (core area) and 95% home ranges, respectively, to determine if

282 season, forest type, interior or edge forests, and the interaction of forest type and season
283 influenced core area and home range size. All analyses were conducted in version 3.5.1
284 of program R [65]. We used Akaike's Information Criterion (AICc) to identify a top
285 model from the set of candidate ANOVA models [66].

286

287 **Core Area Overlap**

288

289 To determine the percent of joint home range overlap between the rainy and dry season
290 home ranges, we calculated the total area of each home range and then divided the area of
291 overlap between seasons by the total home range size [67]. Possible core area overlap
292 ranged from 0% overlap, indicating no shared space use between seasons, to 100%
293 overlap, indicating the dry and rainy season ranges overlapped completely. To determine
294 if the home range overlap between the rainy and dry seasons varied as a function of
295 fragmentation types (edge or interior), we conducted an unpaired two-sample t-test
296 assuming equal variances. We tested the variance assumption of our t-test using an F-test,
297 'var.test', in program R. Finally, to determine if the core area overlap between the rainy
298 and dry seasons varied as a function of forest type (humid, moderate, or dry), we
299 conducted a one-way ANOVA comparing core area and 95% home range and core area
300 as a function of degree of forest type. All analyses were conducted in version 3.6.1 of
301 program R [65].

302

303 **Movement Rates**

304

305 We calculated movement rates (meters/hour) for each lemur group using the collected
306 relocation data. The step length (i.e., the distance between sequential locations) was
307 divided by the time elapsed between each sequential location to calculate speed for each
308 golden-crowned sifaka group to characterize movement rates. To determine how
309 movement varied across season (rainy and dry), forest fragmentation (edge or interior),
310 and forest types (humid, moderate evergreen, and dry deciduous) we calculated
311 movement rates at both the daily and seasonal scale.

312

313 Daily movement rates were bootstrapped to calculate a mean for each observational day.
314 Bootstrapping is a process that involves repeatedly drawing independent samples from a
315 data set (x) to create bootstrap data sets (x^1, x^2, \dots, x^n). Our samples were performed with
316 replacement which allowed for the same observation to be sampled more than once such
317 that each bootstrapped sample was the same length as our raw lemur speed data (m/hour).
318 To calculate seasonal movement rates (\widehat{SMR}), we drew 1000 independent samples
319 ($\hat{\alpha}^1, \hat{\alpha}^2, \dots, \hat{\alpha}^B$) to calculate means and standard error (\widehat{SE}_B), which we then used to
320 generate 95% confidence intervals for comparison of means among seasons and groups,

321

$$\widehat{SE}_B = \sqrt{\frac{\sum_{b=1}^B (\hat{\alpha}^b - \bar{\alpha})^2}{(B-1)}}$$

322 where \widehat{SE}_B served as our estimate of the standard error of $\hat{\alpha}$ estimated from the raw lemur
323 speed data (m/hour). We calculated seasonal movements rates using the bootstrapping
324 approach outlined above but employed the method for each observation season.

325

326 To determine how environmental variables influenced daily movement rates, we fit linear
327 mixed effects models to predict movement rate as a function of all combinations of
328 season (rainy or dry), forest fragmentation (edge or interior), and forest type (humid,
329 moderate evergreen, and dry deciduous), while treating forest type-forest fragmentation
330 per group intercepts as random effects [68]. We used the Satterthwaite method to
331 approximate the degrees of freedom and computed p-values for direct effects and
332 interactions using t-statistics.

333

334 Finally, to determine how environmental variables influenced seasonal movement rates,
335 we conducted a three-way ANOVA seasonal movement rates as a function of forest type
336 (dry, humid, and wet), forest fragmentation (edge and interior), and season (dry and
337 rainy). All analyses were conducted in version 3.6.1 of program R [65]. We used
338 Akaike's Information Criterion corrected for small sample size (AICc) to identify a top
339 model from the set of candidate models [69]. All analyses were conducted in version
340 3.6.1 of program R [65,68].

341

342 **Habitat Selection**

343

344 To quantify habitat selection of golden-crowned sifaka groups, in relation to tree size and
345 proximity to anthropogenic factors, we fit a Resource Selection Function (RSF) using a
346 use-available design. A RSF is defined as any function producing a value proportional to

347 the probability of selection of a given habitat [70,71]. Any estimate derived from an RSF
348 is dependent on the definition of available habitats [55,70,72]. For our RSF, selection by
349 golden-crowned sifaka availability was considered within home range selection
350 (Johnson's third order; Johnson 1980) as defined by a 95% seasonal home range (i.e.,
351 95% isopleth) using DBBMMs. Within our seasonal home ranges, we characterized
352 availability by systematically identifying available locations at intervals of 10 m, as this
353 was the spatial resolution of all spatial data used in the RSF [73].

354

355 We created our RSFs by fitting generalized linear mixed-effects model (GLMM) with a
356 binomial link function, which included a group-specific (forest type and fragmentation
357 type) random intercept term to account for non-independence of habitat associations
358 within groups [74,75]. For our RSF, we used GPS locations of all feeding trees that
359 golden-crowned sifaka utilized during the rainy and dry field seasons and possible
360 locations within their known home ranges. We extracted tree basal area (cross-sectional
361 area of trees at breast height), Euclidian distance to village, road, and habitat fragment
362 edge for each golden-crowned sifaka feeding tree and each available location. These data
363 were generated using satellite imagery and habitat sampling of resources within each of
364 the six lemur home ranges.

365

366 To relate tree basal area and crown volume to lemur GPS location data, we created
367 continuous surfaces of tree basal area and crown volume estimates across our study area
368 by using inverse distance weighting (IDW) interpolation in the package gstat [76] in

369 version 3.6.1 of program R [65]. IDW uses a weighted average of estimates from nearby
370 sampling locations to predict tree basal area and crown volume estimates to the
371 surrounding pixels of a sampling location composed of user-specified areas [77]. Our
372 user-specified areas of inference were 169 m² because it most closely matched the mean
373 distance between vegetation sampling locations (148.85 m). This interpolation process
374 provided spatially explicit estimates of tree basal area and crown volume estimates which
375 we could then associate with our lemur GPS data.

376

377 To examine if lemur habitat selection varied across forest types and seasons, we
378 developed candidate models using various combinations of distance to habitat feature
379 (i.e., village, road, and habitat fragment), and basal area, and used Akaike's Information
380 Criterion (AICc) to identify a top model from the set of candidate models [66] to
381 determine: 1) if differences in habitat selection vary as a function of forest type, and 2) if
382 differences in habitat selection vary as a function of season at each site. To account for
383 behavioral differences in lemur groups, we accounted for random effects using an
384 'animal id' that consisted of each lemur group's respective forest type (humid, dry, or
385 moderate), forest fragmentation classification (edge or interior), and season (rainy or
386 dry). No environmental variables used in model development exhibited high correlation
387 (i.e., $|r| > 0.7$). All coefficients were estimated using the "lme4" package for R 3.0.1
388 [65,68].

389

390

391 **Results**

392

393 **Home range size estimation**

394

395 Overall, home range sizes (95% utilization distribution) for golden-crowned sifaka
396 groups in the Loky-Manambato Protected Area were highly variable and ranged from
397 2.78 – 31.56 hectares (Table 2). Our top ANOVA model (Table 3), revealed that golden-
398 crowned sifaka core areas (50% home range) varied with season ($p = 0.003$, $F=14.65$,
399 $df=1$, residual $df = 10$, residual $SE = 0.004$) with core areas being larger in the rainy
400 season (average of 1.80 hectares in the rainy season, 0.81 hectares in the dry season).

401 However, while our ANOVA model candidate set for home ranges (95% home range) did
402 include season as a top model, suggesting a trend towards increased home range size in
403 the rainy season (dry or rainy; $p = 0.08$, $F=3.671$, $df=1$, residual $df = 10$, $SE = 0.08$), it
404 was no better than our null model when considering a delta AIC of 2 (Table 4).

405

406 **Seasonal Core Area Overlap**

407

408 Seasonal overlap of the 50% home range area varied from 17% to 54% overlap (Table 2,
409 Figure 2). Core area overlap between the rainy and dry season did not vary with forest
410 type (core area – $p = 0.702$, $F = 0.393$, $df = 2$, residual $df = 3$, $SE = 0.003$; home range –
411 $p = 0.394$, $F = 1.29$, $df = 2$, residual $df = 2$, residual $SE = 0.001$) or forest fragmentation

412 (core area – $p = 0.365$, $F = 1.04$, $df = 1$, residual $df = 4$, residual $SE < 0.001$; home range –
413 $p = 0.219$, $F = 2.21$, $df = 1$, residual $df = 4$, residual $SE = 0.02$).

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427

428 **Table 2.** Home range sizes (50% and 95% isopleth (UD: utilization distribution)) of
429 sifaka groups in the rainy and dry season. The three forest fragments differ in forest type
430 (Moderate; Bekaraoka, Humid; Binara, Dry; Sola) and forest fragmentation (interior;
431 edge).

432

Lemur Group ID	50% UD (ha)		50% UD	95% UD (ha)		95% UD
			(%			(%
			overlap)			overlap)
	Dry	Rainy		Dry	Rainy	
Moderate-interior	0.63	1.87	41%	2.93	9.16	55%
Moderate-edge	0.57	0.78	17%	2.78	4.83	75%
Humid-interior	0.68	1.71	29%	3.69	25.1	38%
Humid-edge	1.18	1.90	54%	12.5	11.1	61%
Dry-interior	0.88	1.91	17%	6.04	7.95	59%
Dry-edge	0.89	2.62	51%	8.19	31.6	51%

433

434

435

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440

441 **Table 3:** Models, the number of parameters (K), log-likelihood (LL), the relative
442 difference in AICc values compared to the top-ranked model ($\Delta AICc$), and the AIC
443 model weights (W) of the model-selection procedure examining core area size (50%
444 isopleth) of lemur groups.

Model	K	LL	AICc	Δ AICc	W
season	1	48.946	-88.9	0	0.828
fragmentation + season	2	48.963	-84.2	4.68	0.08
forest type + season	2	51.882	-83.8	5.13	0.064
null	0	43.533	-81.7	7.16	0.023
fragmentation	1	43.54	-78.1	10.81	0.004
forest type	1	44.558	-75.4	13.49	0.001
forest type + season + fragmentation	3	51.91	-75	13.87	0.001
forest type + fragmentation	2	44.566	-69.1	19.76	0

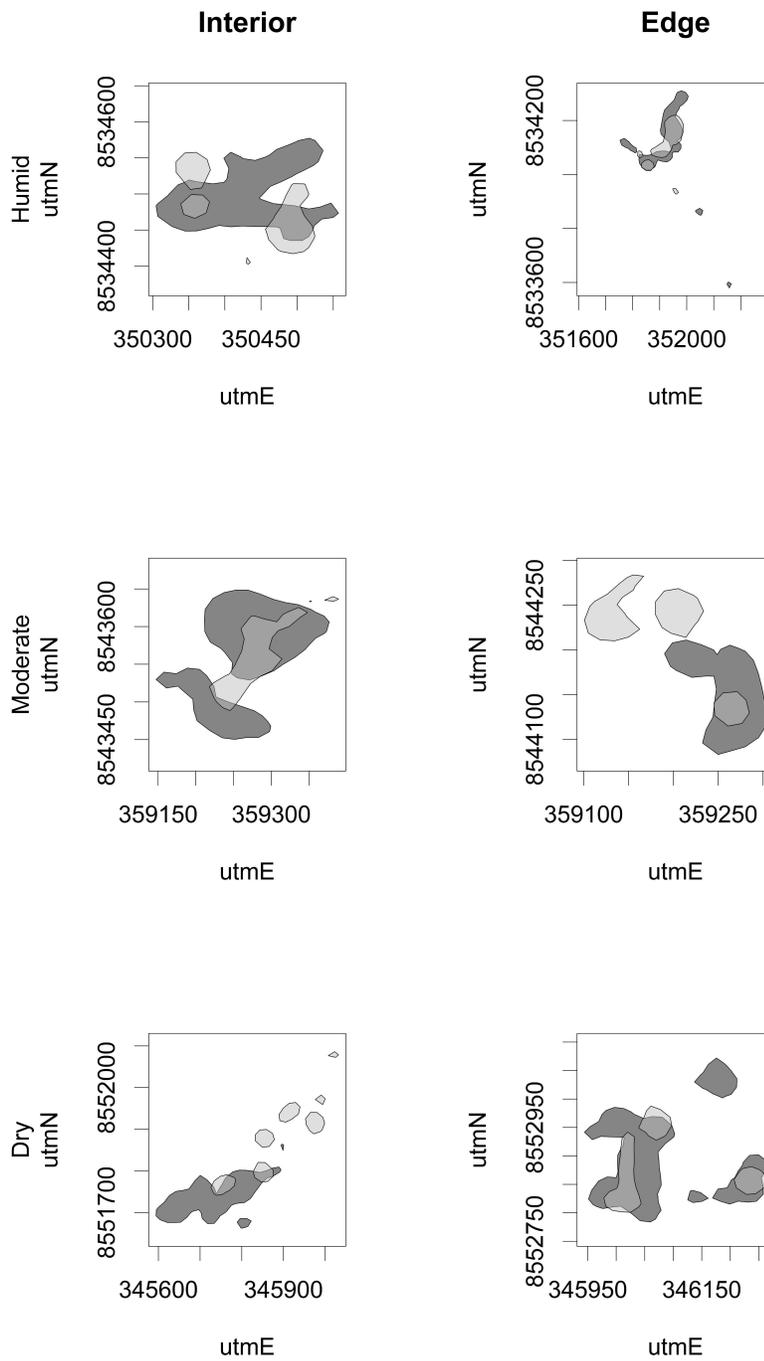
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446

447 **Table 4:** Models, the number of parameters (K), log-likelihood (LL), the relative
448 difference in AICc values compared to the top-ranked model (Δ AICc), and the AIC
449 model weights (W) of the model-selection procedure examining home range size (95%
450 isopleth) of lemur groups.

Model	K	LL	AICc	Δ AICc	W
season	1	14.266	-19.5	0	0.427
null	0	12.389	-19.4	0.09	0.409
fragmentation	1	12.535	-16.1	3.46	0.076
fragmentation + season	2	14.466	-15.2	4.31	0.049
forest type	1	13.793	-13.9	5.66	0.025
forest type + season	2	16.279	-12.6	6.97	0.013
forest type + fragmentation	2	13.978	-8	11.58	0.001
forest type + fragmentation +season	3	16.562	-4.3	15.21	0

451



454 **Fig. 2.** Brownian bridge utilization distribution (50% isopleth) depicting core area use for
455 golden-crowned sifaka groups between the rainy (dark gray) and dry (light gray) season.
456 Overlapping areas are occupied during both seasons. The six figures display the seasonal
457 home ranges for all six lemur groups followed. The columns indicate forest
458 fragmentation classification (interior or edge) and the rows indicate the occupied forest
459 type (humid, moderate, or dry) of all six lemur groups.

460

461 **Daily and Seasonal Movement Rates**

462

463 Our top model (Table 5) indicated that seasonal movement rates varied as a function of
464 season (Sum Squares = 0.405, 95% CI [0.13, 0.65], $F=11.27$, $df=1$, $p=0.007$, residual $df =$
465 10, residual SE = 0.04), with higher rates in the rainy season (rainy season: 83.47 m/h;
466 dry season: 56.70 m/h). When investigating daily movement rates, our mixed effects
467 linear model analysis supported our seasonal movement results, as the top model
468 included season; however, there was not support for effects of forest type or forest
469 fragmentation ($\beta = 0.36$, 95% CI [0.11, 0.60]; $p=0.019$; Table 6, Figure 3).

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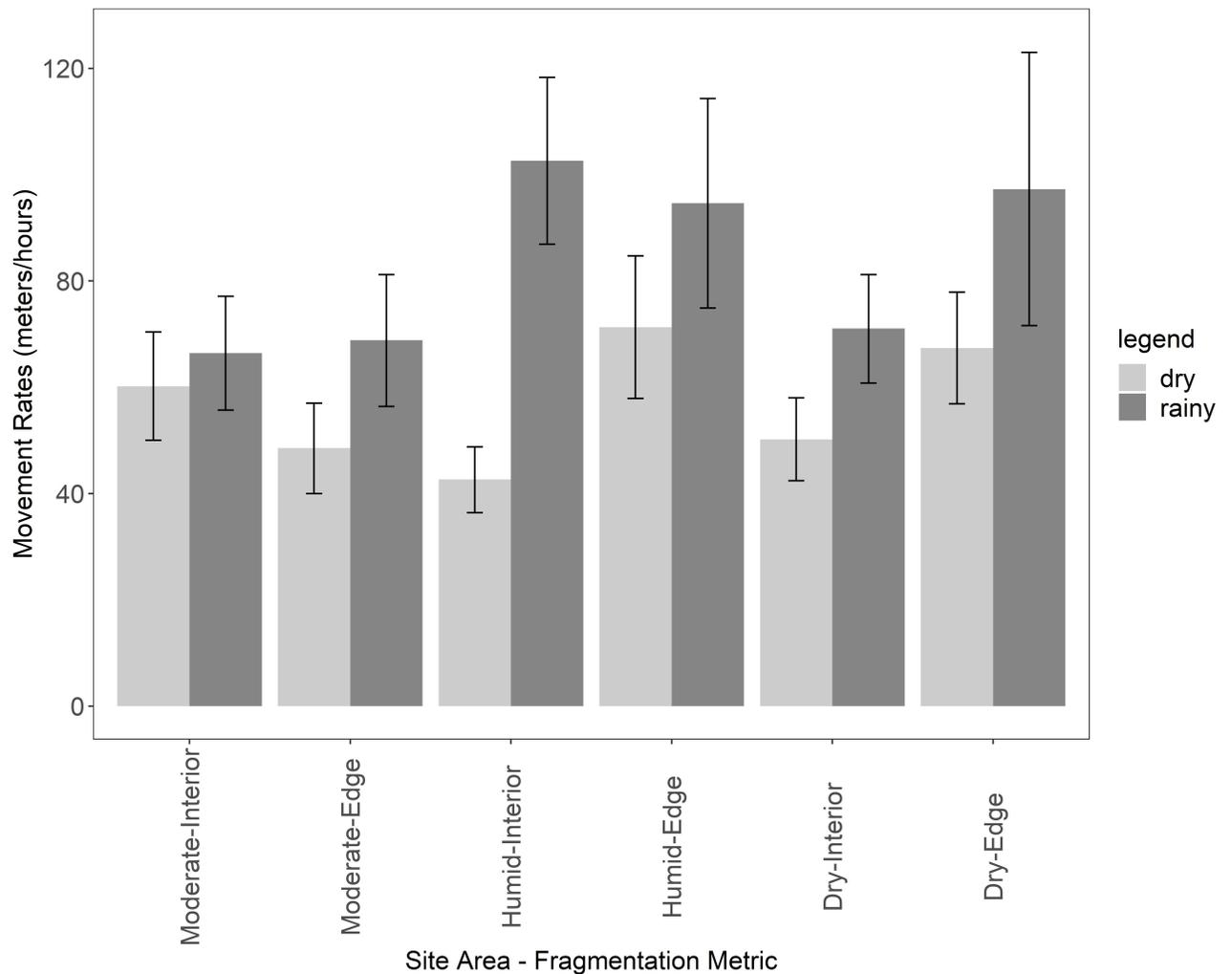
476 **Table 5:** Competing models, the log-likelihood (LL), the number of parameters in the
 477 model (K), the relative difference in AICc values compared to the top-ranked model
 478 (Δ AICc), and the AIC model weights (W) of the model-selection procedure examining
 479 seasonal movement rates of lemur groups.

Model	LL	AICc	Δ AICc	W
season	3.382	2.2	0	0.733
fragmentation + season	4.394	4.9	2.69	0.191
null	-1.145	7.6	5.39	0.05
fragmentation	-0.691	10.4	8.15	0.012
forest type + season	4.779	10.4	8.21	0.012
forest type	-0.529	14.8	12.54	0.001
forest type + season + fragmentation	6.086	16.6	14.39	0.001
forest type + fragmentation	-0.023	20	17.81	0
forest type + season + forest type*season	6.158	29.7	27.45	0
forest type + fragmentation + season + forest type*season	7.856	48.3	46.05	0

480

481 **Table 6.** Competing models, the log-likelihood (LL), the number of parameters in the
 482 model (K), the relative difference in AICc values compared to the top-ranked model
 483 (Δ AICc), and the AIC model weights (W) of the model-selection procedure examining
 484 daily movement rates of lemur groups.

Model	K	LL	AICc	Δ AICc	W
season	1	-27.381	63.3	0.00	0.586
null	0	-29.393	65.1	1.82	0.236
fragmentation + season	2	-28.186	67.1	3.87	0.085
fragmentation	1	-30.082	68.7	5.40	0.039
forest type + season	2	-28.022	69.1	5.87	0.031
forest type	1	-30.101	71.0	7.70	0.012
forest type + season + fragmentation	3	-28.845	73.2	9.89	0.004
forest type + season + forest type*season	4	-27.815	73.6	10.28	0.003
forest type + fragmentation	2	-30.777	74.6	11.38	0.002
Global	5	-28.634	77.7	14.43	0.000



486

487

488 **Fig. 3.** Seasonal movement rates (meters/hour) of golden-crowned sifaka groups using
 489 relocation data collected every 15 minutes. The step length (e.g., the distance between
 490 sequential locations) was divided by the time elapsed between each step to calculate
 491 speed for each lemur group. Data were collected during the dry season (June-August
 492 2019) and the rainy season (February-April 2019). Black lines correspond to 95%
 493 confidence intervals.

494

495 **Habitat Selection**

496

497 We found that lemur habitat selection varied with forest type (Table 7) and within forest
498 type, selection varied by season (Table 8, Tables S1 - S3). Thus, to make inferences
499 about differences in selection across forest type and season, we parsed the data into forest
500 type and then again into season.

501

502 We found that lemur groups in the humid forests selected feeding trees characterized with
503 greater crown volume ($\beta = -5.0$, s.e. ± 1.23 , $p < 0.001$), closer to villages ($\beta = -0.76$, s.e. \pm
504 0.30 , $p = 0.01$), and closer to the forest edge ($\beta = -1.04$, s.e. ± 0.17 , $p < 0.001$), and
505 avoided locations near roads ($\beta = 2.79$, s.e. ± 0.93 , $p = 0.003$) in the dry season. In the
506 rainy season groups in humid forests selected locations with greater tree basal area ($\beta =$
507 0.085 , s.e. ± 0.04 , $p = 0.049$) and greater crown volume ($\beta = 1.34$, s.e. ± 0.06 , $p < 0.001$)
508 that were closer to villages ($\beta = -1.28$, s.e. ± 0.19 , $p < 0.001$), and forest edges ($\beta = -0.24$,
509 s.e. ± 0.05 , $p < 0.001$), and avoided habitats near roads ($\beta = 3.26$, s.e. ± 0.73 , $p < 0.001$).

510 While the effects of crown volume, villages, forest edges and roads were the same across
511 seasons, these effects were stronger in the rainy season (Table 8; Figure 4).

512

513 Lemur groups in moderate evergreen forests selected locations with greater crown
514 volume ($\beta = 0.52$, s.e. ± 0.07 , $p < 0.001$), greater tree basal area ($\beta = 0.35$, s.e. ± 0.17 , $p =$
515 0.03), and locations farther from villages ($\beta = 1.30$, s.e. ± 0.32 , $p < 0.001$) in the dry

516 season. Selection of locations closer to the forest edge approached significance ($\beta =$
517 -1.25 , s.e. ± 0.68 , $p = 0.065$). In the rainy season, troops selected feeding trees with
518 greater tree crown volume ($\beta = 1.24$, s.e. ± 0.07 , $p < 0.001$) and greater tree basal area ($\beta =$
519 0.55 , s.e. ± 0.19 , $p = 0.003$) and avoided habitats closer to villages ($\beta = 1.91$, s.e. ± 0.38 ,
520 $p < 0.001$). Avoidance of the forest edge approached significance ($\beta = -2.76$, s.e. ± 1.5 , p
521 $= 0.069$; Table 8; Figure 4).

522

523 Finally, we found that groups in dry deciduous forests selected greater crown volume (β
524 $= 1.22$, s.e. ± 0.45 , $p < 0.001$). During the rainy season, groups in dry forest selected
525 locations with greater crown volume ($\beta = 1.04$, s.e. ± 0.12 , $p < 0.001$) and greater tree
526 basal area ($\beta = 2.89$, s.e. ± 0.73 , $p < 0.001$), and avoided habitat closer to villages ($\beta =$
527 3.06 , s.e. ± 0.74 , $p < 0.001$) and roads ($\beta = 2.42$, s.e. ± 0.50 , $p < 0.001$; Table 8; Figure 4).

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537 **Table 7.** Competitive models AIC table depicting differences in foraging tree selection
 538 among lemurs occupying different forest types. Competitive models, the number of
 539 parameters (K), the relative difference in AIC values compared to the top ranked model
 540 (Δ AIC), the AIC weights (W), and the log-likelihood (LL) of the model-selection
 541 procedure examining foraging tree selection of lemurs based on occupied forest type
 542 (humid, moderate, and dry). CV: Crown Volume, TBA: Tree basal area, V: Distance to
 543 village, R: Distance to roads, F: Distance to forest edge, FT: Forest type. Based on the
 544 models, forest types could not be grouped and were parsed to make assumptions.

	K	AIC	Δ AIC	W	LL
(CV+ TBA + V + R + F)*FT	19	11353.62	0	1	-5657.81
CV+ TBA + V + R + F	7	11425.18	71.56	0	-5705.59

545

546 **Table 8.** Competitive models AIC table of lemur foraging tree selection based on occupied forest type. Competitive models, the
 547 number of parameters (K), the relative difference in AIC values compared to the top ranked model (Δ AIC), the AIC weights (W), and
 548 the log-likelihood (LL) of the model-selection procedure examining foraging tree selection of lemurs based on occupied forest type
 549 (humid, moderate, and dry). CV: Crown Volume, TBA: Tree basal area, V: Distance to village, R: Distance to roads, F: Distance to
 550 forest edge, FT: Forest type.

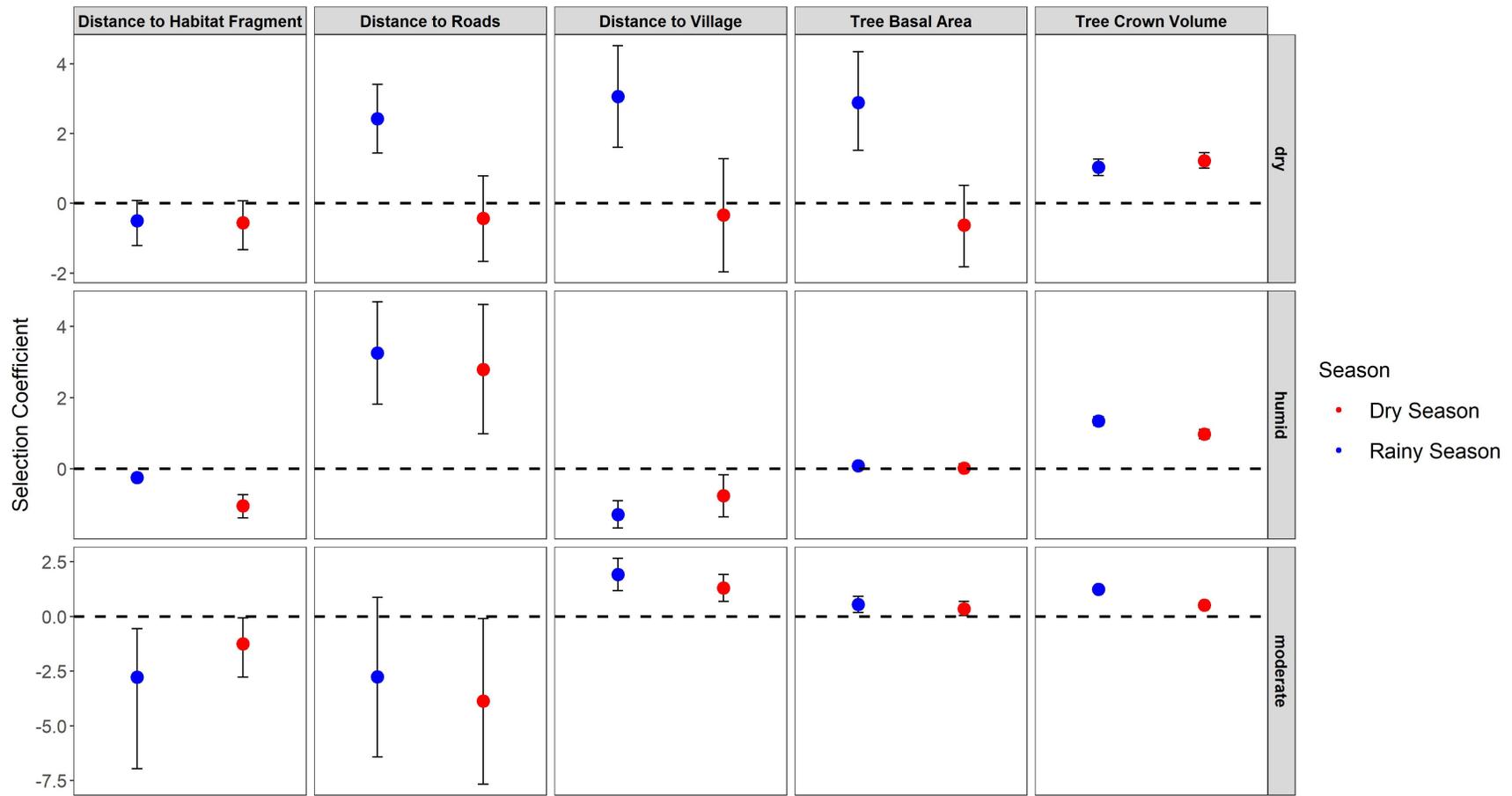
Humid Forest					
	K	AIC	Δ AIC	W	LL
(CV+ TBA + V + R + F)*Season	13	4158.31	0	1	-2066.15
CV+ TBA + V + R + F	7	4206.98	48.68	0	-2096.49
Moderate Forest					
	K	AIC	Δ AIC	W	LL
(CV+ TBA + V + R + F)*Season	13	2944.24	0	1	-1459.12
CV+ TBA + V + R + F	7	3043.27	99.04	0	-1514.64
Dry Forest					
	K	AIC	Δ AIC	W	LL
(CV+ TBA + V + R + F)*Season	13	4085.42	0	1	-2029.71
CV+ TBA + V + R + F	7	4105.11	19.7	0	-2045.56

551

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555

556 **Fig. 4.** Selection coefficient plot for golden-crowned sifakas in the dry and rainy season within the three forest types. This coefficient
 557 plot displays beta estimates for tree basal area and tree crown volume and distance to habitat fragment, roads, and villages. Blue points
 558 represent habitat selection during the rainy season and red points represent habitat selection during the dry season. Solid lines above
 559 and below each point represent the 95% confidence intervals around each beta estimate.

560 **Discussion**

561
562 Our study shows three primary results. First, golden-crowned sifaka movement rates are greater
563 in the rainy season and in the humid forest type. Second, variation in climatic conditions (rainy
564 vs. dry season) influences lemur movement, with core area range sizes being larger in the rainy
565 season. Third, human disturbance influences lemur spatial ecology with lemurs preferentially
566 selecting foraging locations where larger trees are present. We also detected variation in
567 behavioral responses to villages, road networks, and the forest edge. Lemurs in humid and dry
568 deciduous forest fragments specifically avoided locations near road networks in both the dry and
569 rainy seasons, while lemurs in the moderate evergreen forest did not select or avoid locations
570 near road networks. In sum, groups of golden-crowned sifaka show marked variation in
571 behavioral responses to human disturbance, but in all groups, higher-use zones consist of
572 locations closer to large trees. Thus, season, forest type, and forest fragmentation all have effects
573 on lemur space use and ranging behavior.

574
575 Using Dynamic Brownian Bridge Movement Models, home range sizes of golden-crowned
576 sifaka groups varied between 3-32 hectares, indicating an incredible amount of home range size
577 variation within the species. These home range sizes are smaller than those of diademed sifaka
578 (*Propithecus diadema*), a species inhabiting Madagascar's eastern humid forests, which range
579 from 19-79 ha (95% kernel; Irwin, 2008), but larger than those of Verreaux's sifaka (*Propithecus*
580 *verreauxi*), a species inhabiting Madagascar's southern dry forests, which have home range sizes
581 ranging from 5-10 ha [78]. Similar to this trend, mouse lemurs (*Microcebus* spp) inhabiting
582 western dry forests were able to maintain higher population densities than mouse lemur species

583 inhabiting eastern humid forests [79]. Contrary to these previous findings and our predictions,
584 we found that golden-crowned sifaka groups in humid forest fragments do not occupy
585 significantly larger home range or core area sizes compared to groups living in moderate
586 evergreen or dry deciduous forest fragments. This finding was unexpected because Malagasy
587 humid evergreen forests are often described as being lower quality habitats compared to drier
588 forests due to decreased food availability, requiring wildlife to occupy larger ranges to meet
589 nutritional demands [80]. In sum, our study is the first determining that the same species of
590 sifaka can inhabit drastically different forest types and display great variation in home range size.

591
592 Our prediction that lemur home range sizes would vary between the rainy season and the dry
593 season was partially supported. While home range sizes (95% isopleth) were not significantly
594 different between seasons, core area range size (50% isopleth) was statistically larger for lemur
595 groups in the rainy season compared to the same groups' core area range sizes in the dry season.
596 Similar to findings of Milne-Edwards' sifaka, we found that golden-crowned sifaka maintained
597 similar home range (95% isopleth) locations in both seasons, but displayed considerable seasonal
598 shifts in core area (50% isopleth) locations [42]. This result demonstrates that golden-crowned
599 sifaka have significant site fidelity for their home ranges, but a lower degree of fidelity for core
600 area ranges. This difference is likely due to the non-uniform and seasonal variation in
601 distribution of resources which influenced how golden-crowned sifaka distributed their space use
602 to efficiently forage [81]. Surprisingly, the degree of core area overlap observed did not vary
603 based on the forest type or forest fragmentation level occupied.

604

605 Unlike our prediction that sifaka groups in more degraded habitats would occupy larger home
606 ranges, we found limited evidence that forest fragmentation (edge vs. interior) influenced home
607 range or core area size in golden-crowned sifaka. Previous studies have demonstrated varying
608 effects of disturbance on home range size of eastern sifaka species in rainforest habitats. For
609 instance, diademed sifaka (*Propithecus diadema*) living in edge forests occupied significantly
610 smaller home range sizes than conspecifics in contiguous forests [41] while Milne-Edwards'
611 sifaka (*Propithecus edwardsi*) in fragmented (logged) forests maintained larger home range sizes
612 [42]. While these studies indicate contrasting effects of forest fragmentation on lemur home
613 range size, fragmentation and other anthropogenic habitat changes are known to produce
614 negative impacts on lemurs [82]. Unfortunately, the majority of lemur studies (87%) examining
615 the influence of anthropogenic habitat changes on lemur health, genetics, biodiversity, and
616 behavior were conducted in the humid forests of eastern Madagascar [82]. Further, lemur
617 responses to habitat edges in dry forest are often highly variable, with groups avoiding, selecting,
618 or demonstrating no response in regards to feeding along forest edges. As a result, further
619 investigation of home ranges of golden-crowned sifaka and other dry forest lemurs are needed to
620 understand how increasing anthropogenic changes are influencing lemur ecology and
621 conservation.

622

623 Across seasons, regardless of forest type or forest fragmentation, golden-crowned sifaka groups
624 daily movement rates shifted, with groups moving farther per unit time in the rainy season.

625 Contrary to this finding in golden-crowned sifaka, previous studies indicate that Milne-Edward's
626 sifaka do not increase or decrease their distance moved per day (i.e., daily path length) between
627 seasons [42]. Thus, there exists some degree of variability among sifaka species. Movement rates

628 in golden-crowned sifaka groups were also closely linked to home range size in that as home
629 range increased in the rainy season, so did the average distance moved per hour. This finding is
630 consistent elsewhere in highly mobile mammals as movement rates and resource availability
631 determined home range size of white-tailed deer (*Odocoileus virginianus*) and Iberian ibex
632 (*Capra pyrenaica*) [83,84].

633
634 Aligning with our predictions, sifaka habitat selection was influenced by proximity to human
635 settlements and permanent manmade structures, with golden-crowned sifaka groups
636 preferentially avoiding these areas. Studies examining the influence of road networks on other
637 mammalian species have similarly found that elk (*Cervus canadensis*) and caribou (*Rangifer*
638 *tarandus*) tend to avoid road crossings and seek cover when in close proximity to road networks
639 [85]. Road expansion and paving is known to increase the prevalence of vehicle collisions with
640 wildlife (e.g., Asiatic cheetah (*Acinonyx jubatus venaticus*; Mohammadi et al., 2018) and Florida
641 panther (*Puma concolor coryi*; Criffield et al., 2018). The national road that bisects the global
642 range of golden-crowned sifaka is currently being improved to enhance access to mineral
643 reserves and transportation through the region. The combination of road expansion and human
644 population growth is expected to intensify the already harmful degree of resource extraction
645 within the region (e.g., selective logging of hardwoods and gold mining) [39]. Thus, given the
646 current level of avoidance golden-crowned sifaka display towards roads, the continued road
647 paving initiatives within their global range, and evidence gained from other mammalian studies,
648 increased avoidance on golden-crowned sifaka are likely. Our results indicating sifaka avoidance
649 of human villages have been documented in other mammalian taxa; for example, caracal
650 (*Caracal caracal*) avoided areas visited by and adjacent to human settlements [88]. Lastly, even

651 low vehicle traffic (0-30 vehicles/12hrs) can lead to animal avoidance as demonstrated in
652 wolverines (*Gulo gulo*), where space use in regard to road networks led to avoidance and altered
653 movement patterns [89]. Consequently, increasing human activity and road prevalence has the
654 potential to impact foraging and space use behavior of wildlife species, and in the case of
655 golden-crowned sifaka, could result in an impact large enough to threaten their population.

656

657 **Conclusions**

658

659 **Conservation implications**

660

661 Our study illustrates the complex anthropogenic and ecological processes that influence
662 movement behavior of golden-crowned sifaka groups. We found clear evidence that human
663 settlements and road networks play an important role in shaping golden-crowned sifaka foraging
664 and ranging behavior. Additionally, ecological factors such as season are drivers of home range
665 size and space use in this species. In terms of conservation implications, our study illustrates the
666 importance of studying primate groups in both the rainy and dry seasons to gain an accurate
667 snapshot of their ecology and resources needs. More specifically, by understanding how forest
668 type influences golden-crowned sifaka movement and foraging behavior, we can make
669 conservation management plans specific to the individual forest types throughout the Loky-
670 Manambato Protected Area (humid, moderate evergreen, dry deciduous, littoral, etc.), rather than
671 the region as a whole. Our findings will also inform Malagasy infrastructure and road
672 development plans by working with local conservation NGOs, government officials, and
673 construction teams to limit construction nearby lemur home ranges that are most impacted by

674 human activity. We would advise that the national road not be re-routed towards Binara, the
675 humid forest fragment, due to the strong avoidance lemurs display towards existing road
676 networks and the increased movement of lemurs within this forest fragment. We detected the
677 least avoidance of anthropogenic activity for lemurs in the moderate evergreen forest type,
678 suggesting they are more resilient to the negative effects of human infrastructure. Overall, as
679 anthropogenic disturbance continues to alter habitat structure throughout Madagascar, a deeper
680 knowledge of how fragmentation, habitat loss, and infrastructure development influence golden-
681 crowned sifaka space use, density, and population health will be essential for wildlife managers
682 to make well informed decisions that improve conservation plans for at-risk species.

683

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693

694 **Authors Contributions**

695 MS and IM designed the study. MS, BS, and TR conducted the fieldwork. MS, HA, and MC
696 conducted the coding and data analyses. MS wrote the first draft of the manuscript and all
697 authors contributed substantially to revisions.

698

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703

704 **Availability of data and materials**

705 The datasets used and/or analyzed during the current study are available from the corresponding
706 author on reasonable request.

707

708 **Declarations**

709 **Ethics approval and consent to participate**

710 This research was conducted with permission from the Ministry of Foreign Affairs of
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715 Institutional Animal Care and Use Committee (IACUC) office (permit #17-127).

716

717 **Consent for publication**

718 Not applicable.

719

720 **Competing interests**

721 The authors declare that they have no competing interests.

722

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