

Environmental Effects on Nocturnal Encounters of Two Sympatric Bushbabies, *Galago moholi* and *Otolemur crassicaudatus* in a High Altitude South African Northern Mistbelt Montane Habitat.

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Conflict of Interest. The authors declare that they have no conflict of interest.

1 **Environmental Effects on Nocturnal Encounters of Two Sympatric Bushbabies, *Galago***
2 ***moholi* and *Otolemur crassicaudatus* in a High Altitude South African Northern Mistbelt**
3 **Montane Habitat.**

4
5 **Abstract**

6
7 Although most primates are tropical mammals, some primate species have been able to adapt to
8 the more stressful ecology of temperate habitats. Such environments are challenging in terms of
9 a combination of climate and weather variability and strong seasonal changes in food
10 availability. As temperate primates are dominated by large-bodied haplorrhine genera, the few
11 nocturnal strepsirrhine primates that also exist in temperate environments may be especially
12 informative in addressing questions such as the role of phylogeny and body size in mediating
13 such environmental stressors. This research focuses on the effect of environmental factors on
14 encounters of two sympatric continental galago species who differ dramatically in body size,
15 *Otolemur crassicaudatus* and *Galago moholi*. Both live in a temperate, high altitude South
16 African Northern Mistbelt forest which has periods of cold temperatures and low food
17 availability (the Lajuma Research Centre). Encounters were used to determine when each species
18 was active or not active. Results indicate that these two species react to environmental stressors
19 differently and indicate that body size and its interplay with physiological and ecological factors
20 is a useful approach for understanding how different species deal with environmental stressors.
21 The smaller *Galago moholi* may have more consistent nutritional needs which requires them to
22 continue to be active at more challenging temperatures, both high and low and to exhibit peaks in
23 activity. At Lajuma, *Galago moholi* must balance both predation and resource stressors. Here
24 they are lunarphilic, indicating a need to emphasize predator detection of a larger number of
25 potential predators such as snakes and smaller felids in addition to insect foraging as they are
26 visually oriented insect predators. Conversely, the much larger *Otolemur crassicaudatus* may be
27 able to buffer themselves during very cold periods and reduce activity at this time but are more

28 sensitive to warmer temperatures where their larger body size may reduce their ability to
29 maintain homeothermy. *Otolemur crassicaudatus* are lunarphobic at Lajuma, which may relate
30 to the activity patterns of potential predators such as the large Verreaux's Eagle Owl and/or
31 African civet. Studying these galagos where they are more environmentally stressed provides a
32 window into the adaptive ranges (the edges of physiological and behavioral adaptations) where
33 natural selection should be most powerful. Adding data on these continental strepsirrhine
34 primates is especially informative in addressing questions such as the role of phylogeny and
35 body size in mediating such environmental stressors. A more complete understanding of
36 temperate primate ecology is also important for clarifying the mechanisms and physiological
37 patterns underlying primate resilience which is key to predicting the sensitivities of species to
38 ongoing climate change.

39 **Keywords:** Thermoregulation; strepsirrhine; sympatry; temperate; seasonality; thermal imaging,
40 environmental ecology, physiology, body size

41
42 **Introduction**

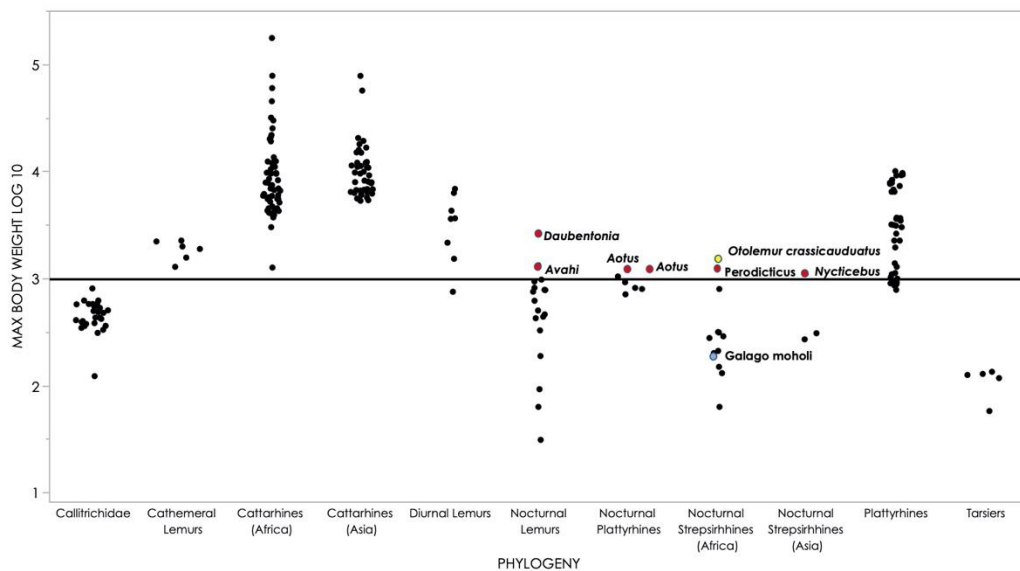
43
44 **Primates in Challenging Environments.** It is perhaps a truism to state that primates are
45 tropical mammals, but of the more than 500+ extant primate species, only a handful inhabit
46 temperate environs (Grueter et al., 2009; Hanya, 2010), with most of these being larger
47 haplorrhine primates (Fleagle, 2013). Temperate habitats are usually defined as those north of
48 the Tropic of Cancer or south of the Tropic of Capricorn, or at higher altitudes within the tropic
49 zones, and are characterized by environmental extremes that include periods with low
50 temperature, low rainfall and/or strong seasonal changes in food availability (Hill & Dunbar,
51 2002; Hanya, 2010). Altitude especially has a significant effect on climate. Indeed, temperature
52 decreases with elevation, making locations at higher altitude colder, with more rainfall than
53 nearby areas at lower altitude. For tropical and subtropical montane ecosystems, temperature,

54 rainfall, and humidity can vary greatly depending on location and altitude. For example, although
55 Mount Kilimanjaro is located near the equator, altitude modifies the climate dramatically such
56 that there are five altitudinal climate zones that include both tropical rainforest and arctic tundra
57 with snow and ice (Hemp, 2002). As such, montane forests occurring within the tropics and
58 subtropics may present environmental challenges similar to more temperate areas, depending on
59 their location and altitude. One such type of habitat is South Africa's Northern Mistbelt Forests,
60 which contain a mixture of Afrotropical and sub-tropical floristics (Mucina & Geldenhuys,
61 2006). Found at an average elevation of 1084m both rainfall and temperature exhibit two clear
62 seasons: warm wet summers and cold dry winters (Mucina & Geldenhuys, 2006). These "sky
63 islands" (White, 1978) are discontinuous, being separated by other lower-lying areas and
64 exhibiting different flora and fauna and high endemism relative to the surrounding areas (White,
65 1978). Although few studies have focused on primates living in these habitats, research indicates
66 that for samango monkeys, (*Cercopithecus albogularis*), water scarcity and thermoregulation
67 affect these mountain living primates, as lower minimum daily temperatures, reduced seed
68 availability and long periods lacking rainfall during the dry season were positively correlated
69 with higher fecal cortisol levels (Allan et al., 2022). Our previous research on thick-tailed greater
70 galagos (*Otolemur crassicaudatus*) in this habitat documented seasonal weather variation effects,
71 including higher rainfall and warmer temperatures in summer months versus winter months, and
72 a reduction in insect and gums (*Vachellia karoo*), during winter months, with lower gum density
73 associated with higher fecal cortisol levels (Long et al., 2021).

74 Given the evidence of physiological responses to environmental variability within Northern
75 Mistbelt habitats, here we assess how environmental variables affect encounters with two
76 nocturnal primates, the thick-tailed greater galago, *Otolemur crassicaudatus* and the much
77 smaller southern lesser galago, *Galago moholi*. Both species have a broad range across tropical

78 and sub-tropical sub-saharan Africa and are the only generally recognized nocturnal primates
79 found in South Africa (Masters et al., 2016). Molecular data indicate that *O. crassicaudatus* and
80 *G. moholi* along with their sister species, form a clearly defined clade among strepsirrhine
81 primates (Delpero et al., 2000) and both likely descended from early Miocene ancestors (Seiffert,
82 2007). They are also ecologically similar as they have morphological adaptations for gum
83 exudate feeding, a specialized feeding niche, and both utilize insects although this is more
84 important for the smaller species. Notably, these galagos vary dramatically in body size (Fig. 1).
85 *O. crassicaudatus* is not only the largest nocturnal continental primate but is larger than any
86 other extant galago (male mean = 1.5 kg, female mean = 1.3 kg: Nekaris & Bearder, 2011). They
87 are also the second largest extant nocturnal primate, only smaller than the highly derived
88 Malagasy lemur, the Aye-aye (*Daubentonia madagascariensis*, mean = 2.62kg, Smith &
89 Jungers, 1997). At 146 g, *G. moholi* is 10x smaller, which is comparable to the body size
90 differences between an *Anubis* baboon and a lowland gorilla. Given that the best single predictor
91 of mammalian biology, physiology and ecology is of course body size (Clutton-Brock & Harvey,
92 1983; Damuth & MacFadden, 1990; Martin, 1990), these two species can provide insight into
93 how body size may facilitate or hinder physiological and behavioral responses to environmental
94 stressors within more seasonal habitats. As first noted by Harcourt (1980), the marked difference
95 in body size should affect not only diet but also how the two species uses time and space. In
96 addition, at 1+kg *O. crassicaudatus* is at the upper body size for extant nocturnal primates. As
97 there is a clear delineation between nocturnal and diurnal forms, with a ~1kg rubicon being the
98 general marker between these activity patterns (Fig. 1) and given that most nocturnal primates
99 are small-bodied, *O. crassicaudatus* may be especially informative in understanding shifts in
100 body size among primates. This includes determining whether larger or smaller bodied species
101 exhibit higher levels of physiological and behavioral flexibility in the face of environmental

102 constraints (e.g., Vuarin et al., 2013). Their close relationship allows better control for
 103 phylogenetic effects. Indeed, through the late 1980s, these two species were both placed within
 104 the genus *Galago* (Nash et al., 1989). Both have similar diets, a combination of insects and gum,
 105 with *Otolemur crassicaudatus* emphasizing gum throughout the year, especially during seasons
 106 of low food availability and *G. moholi* emphasizing insects throughout the year (Harcourt, 1986).
 107 They also both have dietary adaptations for insect and gum feeding (Burrows and Nash, 2010),
 108 but differ in body size. As such, these two species work well to examine how environmental
 109 stressors (rainfall, growing season, food availability, temperature season, ambient temperature,
 110 humidity, moon phase, lunar illumination, night length, and hour), differentially affect
 111 encounters (e.g., active or not active) within a more seasonal Northern Mistbelt forest.



112
 113
 114 Figure 1. Primate body size by phylogeny. Horizontal line denotes 1kg. Body masses are from
 115 Smith & Jungers, 1997. Red circles are 1kg+ nocturnal primates. Yellow is *Otolemur*
 116 *crassicaudatus*; Blue is *Galago moholi*.

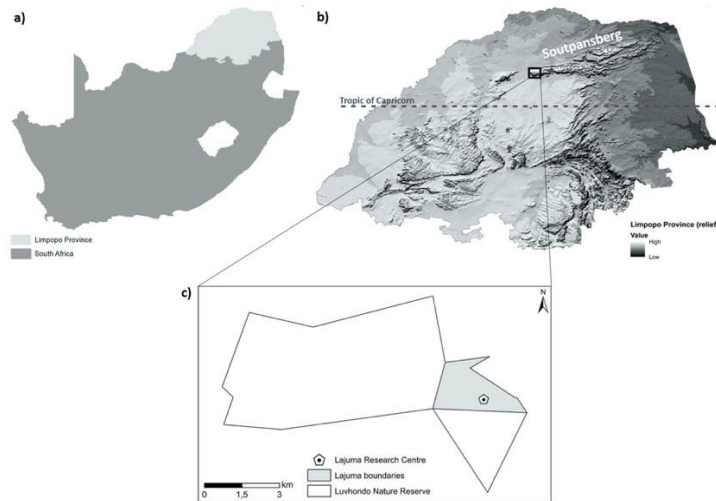
117 **METHODS**

118

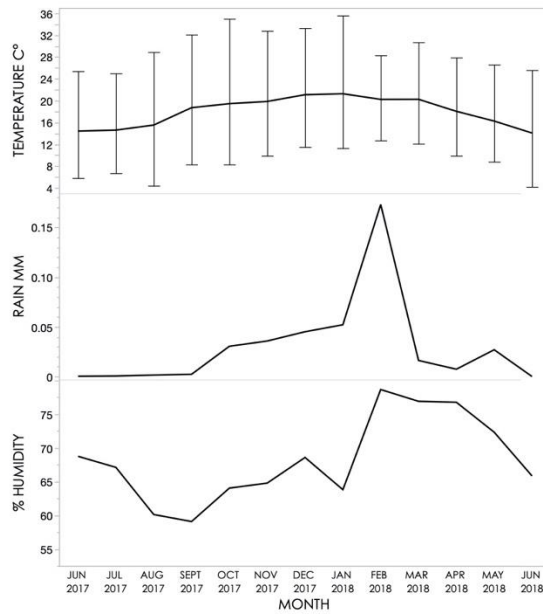
119 **Research Site.**

120

121 The research site of Lajuma is located 44km north of the Tropic of Capricorn (Fig. 2) within the
122 10,000-hectare Luvhondo Nature Reserve of the UNESCO Vhembe Biosphere Reserve in
123 Limpopo Province, South Africa. It is part of the Afromontane archipelago (Huntley, 1978,
124 White 1978) and has an altitudinal range of 1100m to 1747m (Baker & Brown, 2010). Lajuma is
125 a combination of Northern Mist Belt Forest and Soutpansberg Mountain Bushveld and exhibits
126 high floristic and faunal endemism (Hahn, 2017). In terms of floristics, the prominence of
127 temperate species has resulted in botanists including it in the temperate forest category, even
128 though it is just above the Tropic of Capricorn (Acocks, 1953; Mostert et al., 2009). Located on
129 the south-facing wetter side of the Soutpansberg mountains and exhibiting considerable
130 orographic effect, Lajuma's climate varies seasonally and can be classified as
131 temperate/mesothermal, with cool to cold dry winters during which temperatures can sometimes
132 reach freezing (April-September) and warm to hot wet summers (October-March, Willems,
133 2007). During the months sampled, monthly temperature averaged $17.89 \pm 5.13^{\circ}\text{C}$ (4.2°C to 35.6
134 $^{\circ}\text{C}$), total rainfall was 533mm with monthly averages of 0.03 ± 0.37 mm ($0.0 - 232\text{mm}$), and
135 humidity averaged $68 \pm 20\%$ (range:7–97 %; data from the Lajuma Research Centre South
136 African Environmental Observation Network, SAEON, Ndlovu Node; Fig. 3). Rainfall
137 seasonality directly affects availability of food resources, with the growing season occurring
138 from October to April and a non-growing season from May to September, leading to reduced
139 food resources during the colder winter (Willems et al., 2009; Long et al., 2021). Seasonality
140 also affects the availability of the major foods for the study species with both gum and insects
141 being more available during the summer months (Long et al., 2021). As such summer and winter
142 can be seen as periods of relatively low and high ecological and thermal stress.



143
 144 Figure 2. Map of the Lajuma Research Centre. Map by Berthe Linden.
 145



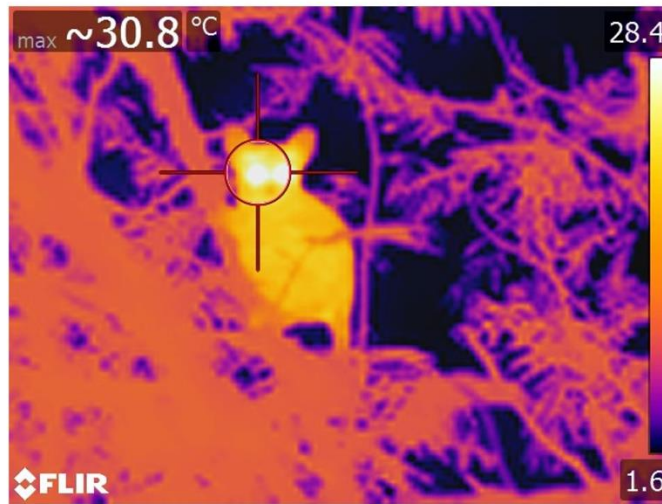
146
 147 Figure 3. Lajuma Research Centre Mean Temperature, Range in Celsius, Rainfall in MM and
 148 Percentage Humidity. Data provided from the Lajuma Research Centre South African
 149 Environmental Observation Network (SAEON) Ndlovu Node, Jabu Linden.

150 All five generally recognized primate species endemic to South Africa are present at Lajuma: the
 151 two galago species, *Galago moholi* and *Otolemur crassicaudatus*, chacma baboons (*Papio*
 152 *ursinus*), samango monkeys (*Cercopithecus albogularis*) and vervet monkeys

153 (*Chlorocebus aethiops*) (Willems, 2007). An array of smaller mammalian predators and snakes
154 that may prey on galagos also occur at Lajuma including civets (*Civvettictis civetta*), genets
155 (*Genetta tigrine*), serval (*Leptailurus serva*), caracal (*Caracal caracal*), a variety of mongoose
156 species (dwarf mongoose, *Helogale parvula*, slender mongoose, *Galerella sanguinea*, banded
157 mongoose, *Mungo, mungo*), African wild cats (*Felis silvestris*), pythons (*Python natalensis*), and
158 poisonous snakes (Willems, 2007). Verreaux's eagle owl, *Bubo lacteus*, Verreaux's eagle, *Aquila*
159 *verreauxi*, and the crowned eagle (*Stephanoetus coronatus*), also inhabit the reserve (Willems,
160 2007). These two galago species are not endangered, being currently listed as "Least Concern"
161 by the IUCN Red List of Threatened Species (Masters & Genin, 2016; Masters et al., 2016). This
162 unique habitat provides a rare opportunity to study for the first time thick-tailed greater and
163 southern lesser galagos living sympatrically within a diverse and ecologically intact community.
164 This is especially key, as previous studies of the two species were allopatric and carried out on
165 South African farms without an intact faunal -- especially predator -- community (Bearder, 1974;
166 Harcourt, 1980; Crompton, 1984).

167 **Data Collection.** Given the difficulty in studying nocturnal primates, we used professional grade
168 thermal imaging cameras (Model T600, Teledyne FLIR® LLC, Wilsonville, OR USA) to locate
169 and record galago encounters by species during nightly encounter walks (75 encounter walks
170 across 12 months (July 2017 to June 2018) with total species encounters being *Otolemur*
171 *crassicaudatus* N=245, *Galago moholi* N=207. For the methods and results section, *Otolemur*
172 *crassicaudatus* is referred to as "otolemur" and *Galago moholi* is referred to as "galago". Our
173 prior decade of research at the site has documented that both species use all the areas surveyed for
174 this study. We used these encounters to determine when species were active or not active relative
175 to survey location, growing season, ambient temperature, temperature season, rainfall, humidity,
176 night length, hour, moon phase and fraction of moon illumination. To date, a similar approach has

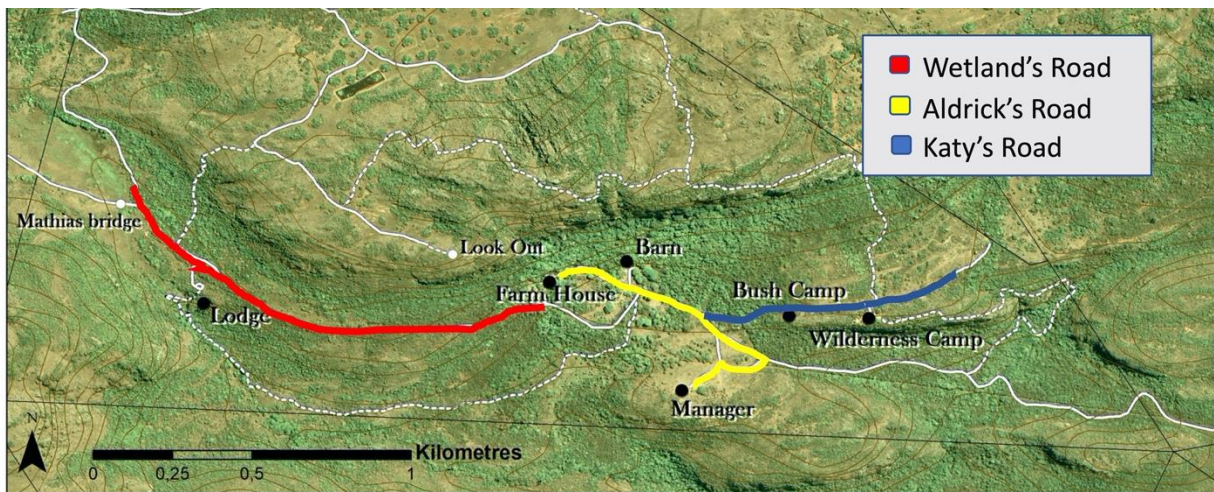
177 been used via camera-trap data at other sites to determine how biotic and abiotic factors may
178 impact mammal activity (Frey et al., 2017), but this depends on animals triggering such traps and
179 thus may not be accurate in detecting different species. Our technology facilitated encounters as
180 they provide a heat signature of individuals along the survey route making it easier to quickly
181 locate and identify each species (Fig. 4). For each encounter the date, species, time, distance,
182 general location, and GPS location data were recorded. Survey walks were along three existing
183 roads within a 3 km² area (Aldrick's Road, Katy's Road, Wetlands Road; Fig. 5). Aldrick's road
184 was a mosaic of open acacia and low to tall forest. Katy's Road was low to tall forest and
185 Wetlands Road was primarily short to low forest between two cliff bases, one above and one
186 below, which included an elevation gain of 165m and an open marsh area. Each encounter walk
187 sampled each area approximately equally (Aldrick's Road N=57, Katy's Road N=46, Wetlands
188 Road N=46). Not all roads were sampled on each survey night, and in some cases more than one
189 survey road might be sampled per night. Sampling for any specific night was done only once for
190 each road and only in one direction to avoid sampling the same individuals. Encounter walks
191 were carried out either from sundown to midnight or midnight to sunrise. There were no
192 temperature differences by sampling area.



193

194 Figure 4. Example of imagery from thermal imaging camera used in survey to document

195 encounters.



196

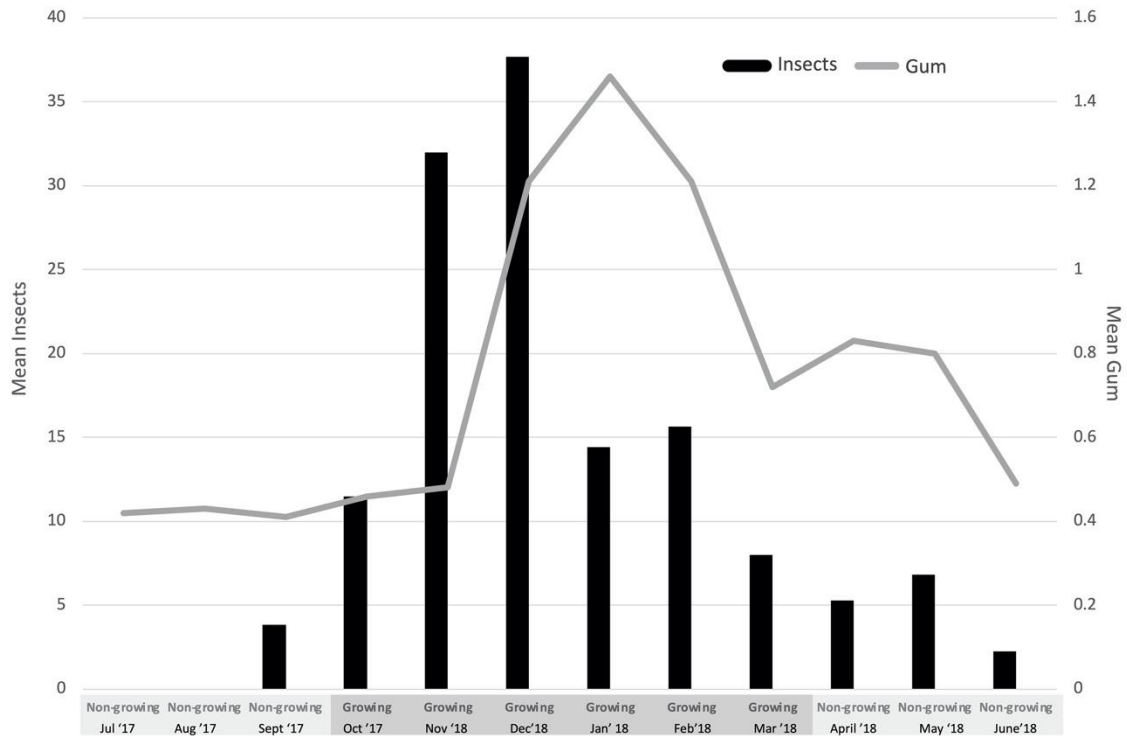
197 Figure 5. Map showing encounter survey walks.

198 To understand the effects of growing versus non growing seasons, we used Willems et al., (2009)

199 results, who used NDVI time-series over a home range of vervet monkeys at Lajuma and the

200 phenophase of species used by both species to determine growing and non-growing seasons by

201 month. We then determined food availability of insects and gums using methods described in
 202 Long et al., (2021). Briefly, insects were captured and counted monthly using light traps. Gum
 203 availability was based on collecting a total of 257 samples across 12 months from 50 gum trees
 204 known to be used by the galagos and located throughout the research area. Insect and gum
 205 availability relative to the growth season are shown in Fig. 6.



206
 207 Fig. 6. Mean insect (number of insects captured in daily insect traps), and gum availability
 208 (average weight in grams) by growth season during sample period. Insects were sampled
 209 beginning in September 2017.

210 Temperature (°C) and relative humidity (%) were recorded every 30 minutes throughout the
 211 study, using the 15 Kestrel Drop D2 wireless temperature and humidity data loggers (accuracy of
 212 ± 0.5°C), positioned throughout the study area (Kestrel® Instruments, Nielsen-Kellerman Co, PA,
 213 USA). Data from monitors closest to galago observations were used to provide real time
 214 temperature and humidity data within 30 minutes of the encounter. Moon phases were calculated

215 using geographical coordinates for the research site using mooncalc.org
216 (<https://www.mooncalc.org/>). Fraction of moon illumination was determined using the mphase
217 program in astrolibR package in CRAN (<https://rdrr.io/cran/astrolibR/man/mphase.html>). Night
218 length in hours and minutes were calculated using sunset and sunrise data from suncalc.org
219 (<https://www.suncalc.org/>).

220 **Statistical Analyses.**

221
222 We used JMP® Pro 16.0 program for most statistical analyses with $p \leq .05$. Given that extensive
223 research among many mammalian species indicate body size is an essential predictive factor, and
224 given we are focusing on understanding how body size affects species encounters relative to
225 different environmental factors, we used species as a categorical, dependent variable (galago or
226 otolemur). Pearson Chi-square tests were used for these analyses when both dependent and
227 independent variables were categorical. A Student's T-test or Anova was used when independent
228 numerical data was normally distributed, and we used the Tukey's HSD test for multiple
229 comparisons. We used the Wilcoxon Rank Sums test for non-normal distributions. A Kernel
230 density plot was used to visualize the effect of ambient temperature with temperature seasons on
231 species encounters. To determine overlap in encounters by time we first modified time
232 observations data in *radians* (*i.e* from $[0-2\pi]$) to use the nonparametric circular Kernel density
233 estimation (KDE) to model the activity patterns of otolemurs and galagos. According to this
234 statistical method, each individual animal detection is treated as a random sample of an
235 underlying continuous distribution (Ridout and Linkie, 2009; Frey et al., 2017). Therefore,
236 Kernel density estimation calculates the probabilities that a species will be found at any time
237 within a 24-hour period, and the resulting Kernel density estimates reflects the species' activity
238 pattern (Linkie and Ridout, 2011). We used Ridout and Linkie's (2009) coefficient of overlap Δ_4 ,

239 ranging from 0 (no overlap) to 1 (identical activity patterns) to estimate the overlap between the
240 activity patterns of the species for large sample sizes ($n_{\min} > 75$):

$$241 \quad \Delta_4 = \frac{1}{2} \left(\frac{1}{n} \sum_{i=1}^n \min \left\{ 1, \frac{\hat{g}(x_i)}{\hat{f}(x_i)} \right\} + \frac{1}{m} \sum_{j=1}^m \min \left\{ 1, \frac{\hat{f}(y_j)}{\hat{g}(y_j)} \right\} \right)$$

242 where $(x_1 \dots x_n)$ and $(y_1 \dots y_m)$ denote two sets of sample times, $f(x)$ and $g(x)$ correspond to the fitted
243 Kernel density functions of the two species of interest, and where i takes values (t_1, t_2, \dots, t_T)
244 spaced between 0 and 2π , with $t_i = 2\pi i / T$. The overlap between two species is considered high
245 for $\Delta_4 > 0.75$, intermediate for $0.75 > \Delta_4 > 0.50$, and low for $\Delta_4 < 0.50$ (Frey *et al.* 2017). As
246 recommended by Ridout and Linkie, (2009), we conducted 10,000 bootstraps on our sample to
247 estimate the precision of the coefficient of overlap. To determine the accuracy of the estimator
248 Δ_4 , we then calculated the 95% confidence intervals (CI) of the bootstrap sample (Frey *et al.*,
249 2017). We finally conducted the Watson's two-sample tests of homogeneity to test the
250 significance of the activity patterns between *O. crassicaudatus* and *G. moholi* as recommended
251 by Frey *et al.*, 2017 and Landler *et al.*, 2021. Watson's two-sample tests of homogeneity
252 provides the range of p values for the data. For this analysis we employed R software (version
253 4.2.2, R Core Team 2018) using packages 'Overlap' (Meredith and Ridout 2016) and 'Circular'
254 (Lund *et al.* 2022) to conduct all our activity analysis. As our response variables are categorical
255 (e.g., galago or ootlemur), we used a generalized linear model using binomial logistic regression
256 and a Logit Probability Model Link to assess continuous data and nominal logistic fit for
257 categorical data. We selected our best fit model using the corrected Akaike's Information
258 Criterion (AICc). As some of the predictive factors were nominal, we could not use model
259 leveraging to determine the best model. For some comparisons we used the Kaplan-Meier
260 survival analysis to directly compare encounters with each species to assess if these were
261 different.

262 **Ethical Statement.**

263

264 For this research we had ethical clearance to conduct research as described herein from the
265 Research and Ethical Sciences Committee at the South African National Biodiversity Institutes'
266 (SANBI) National Zoological Gardens (NZG; Project 18/26), the Animal Ethics Committee of
267 the University of Pretoria (Project V037-17, REC078-20) and Animal Protocol Approval
268 Assurance D16-00388 from the IACUC office of the University of Colorado, which reviewed
269 our research protocols.

270

271 **RESULTS**

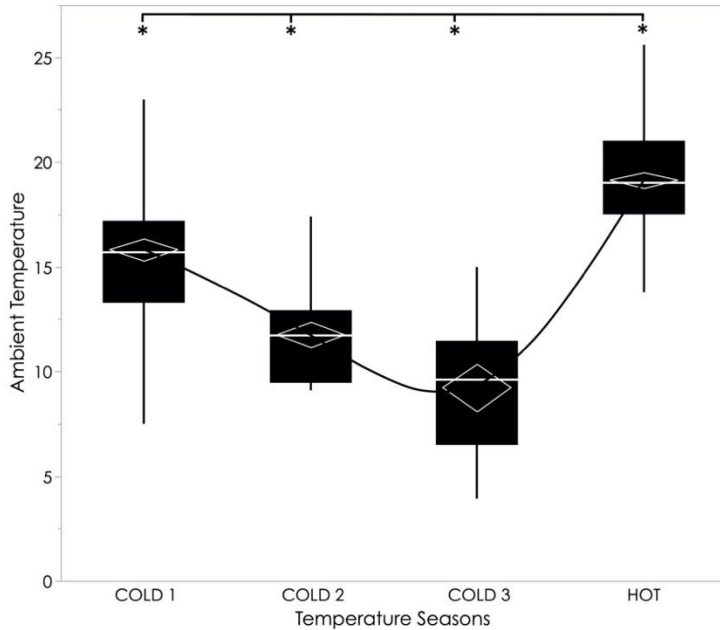
272

273 **Monthly Rainfall and Sampling Location and Plant Growth Season Effects.** We found no
274 statistical effect of rainfall [$t(438)=0.14, p=0.89$], survey location [$X^2(2, 452)=5.35, p=0.07$], or
275 plant growth season [$X^2(1, 452)=3.78, p=0.06$] on species' encounters.

276

277 **Temperature Season.** Comparing species by ambient temperatures overall revealed no
278 significant effects [$t(399)=0.66, p=0.51$]. Given the high variability in ambient temperatures in
279 this seasonal habitat, we thus compartmentalized temperatures during encounters into different
280 seasons. As there were no significant differences between December 2017–March 2018 mean
281 monthly temperatures during galago encounters [$F(3)=1.78, p=0.16$], we combined this data
282 into one hot season. There were no monthly differences between July 2017–November 2017 and
283 April 2018 [$F(4)=1.43, p=0.23$], and these were combined into Cold1. Ambient Temperatures
284 in both May 2018 and June 2018 differed from each other and all other months [$F(3)=144,$
285 $p=2.85e-65$], and were noted as Cold2 (May 2018) and Cold3 (June 2018). Survey walks relative
286 to temperature season were: Cold 1=35 walks, Cold 2=8 walks, Cold 3=3 walks, Hot=29 walks.
287 Encounter temperatures at Lajuma varied by each temperature season [$F(3)=143.95, p=2.83e-$
288 65]. Tukey's HSD test for multiple comparisons found mean temperatures during encounters

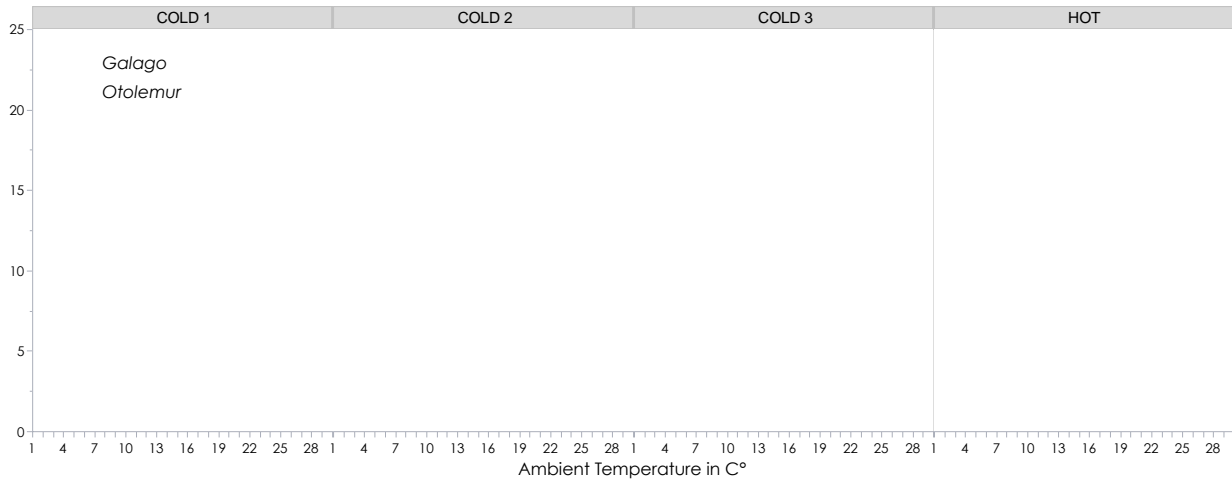
289 were significantly different between each temperature season (Cold1 mean= 15.82 ± 3.62 C°,
 290 range= $7.5-25.90$ C°; Cold2 mean= 11.76 ± 2.18 C°, range= $9.1-17.4$ C° Cold3 mean= 9.25 ± 2.74
 291 C°, range= $3.9-15.00$ C° Hot mean= 19.13 ± 2.49 C°, range= $13.8-25.60$ C°, Fig 7).



292
 293 Fig. 7. Ambient Temperatures at Lajuma in C° by Temperature Season during species
 294 encounters. Line shows mean, diamond shows 95% confidence intervals, * = significant result
 295 among all temperature seasons.

296 Ambient temperatures during each species' encounters varied by season and are visually
 297 represented by a kernel density plot (Fig. 8). For most cold seasons the two species show a very
 298 similar pattern in terms of being active relative to ambient temperatures. During Cold1 season,
 299 encounters for both species peaked between $15-7.5$ C° (galago range = $8-25.9$ C°, otolemur
 300 range = $7.5-25.8$ C° and during Cold2 both species' encounters peaked between $9-12$ C° (galago
 301 range = $9.1-16$ C°, otolemur range = $9.1-17.4$ C°, Fig. 8). However, during Cold3 galago
 302 encounters peaked between $6-10$ C° with a broader range of ambient temperature ($3.9-15$ C°)
 303 while otolemur encounters peaked between $10.5-11$ C° with a narrower range of ambient

304 temperatures (6.7–11.3 C°). In the Hot season galago encounters peaked between 21–22 C°
 305 (range = 13.9–25.6) while otolemur encounters peaked at lower temperatures, between 18–19 C°
 306 and had a smaller range of ambient temperature during encounters (13.8–23.8 C°).

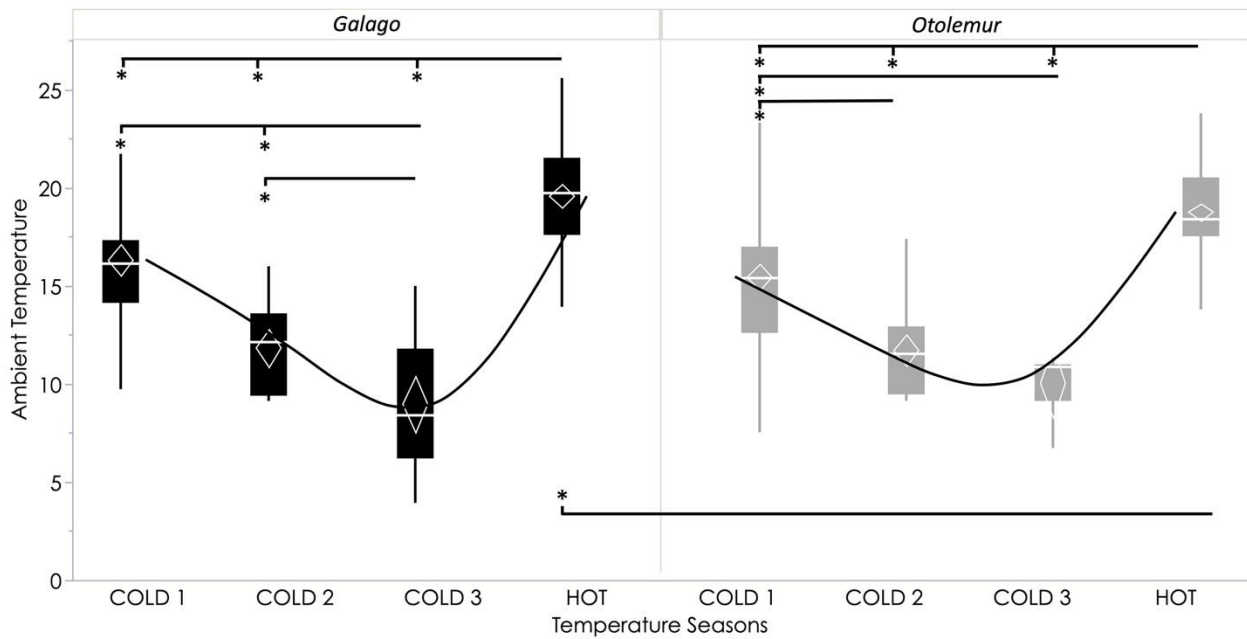


307
 308 Figure 8. Kernel Density plot of encounters by species relative to ambient temperature by
 309 season. Survey walks relative to temperature season were: Cold 1 = 35 walks, Cold 2 = 8 walks,
 310 Cold 3 = 3 walks, Hot = 29 walks.

311
 312 There were species differences for mean temperatures of encounters within the four temperature
 313 seasons. Galago encounters were significantly affected by temperature season [$F(3)=81.32$,
 314 $p=1.36e-34$, Fig. 9], and Tukey’s HSD test for multiple comparisons found mean temperatures at
 315 encounters were significantly different between each temperature season. Encounters during the
 316 hot season were greater than each cold season (Cold1 mean= 16.32 ± 3.66 C°, range=8.8–.90 C°;
 317 Cold2 mean= 11.83 ± 2.25 C°, range = 9.1–16.0 C° Cold3 mean= 8.99 ± 2.97 C°, range = 3.9–15.00
 318 C° Hot mean= 19.57 ± 2.81 C°, range=13.9-25.60 C°).

319
 320 Mean temperatures during otolemur encounters were also significantly affected by temperature

321 season [$F(3) = 63.47, p = 3e-30$, Fig. 9]. Tukey's HSD test for multiple comparisons found mean
 322 temperatures at encounters were significantly higher during the Hot season compared to all Cold
 323 seasons, but only the Cold1 season differed from the other two Cold seasons (Cold1 mean =
 324 15.45 ± 3.58 C°, range = 7.5-25.80 C°; Cold2 mean = 11.70 ± 2.15 C°, range = 9.1-17.4 C°
 325 Cold3 mean = 10.08 ± 1.72 C°, range = 6.7-11.30 C° Hot mean = 18.76 ± 2.13 C°, range = 13.8-
 326 23.80 C°).

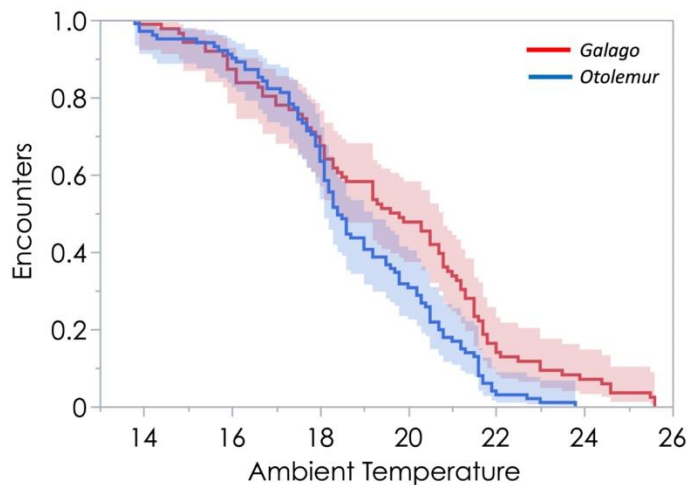


327
 328 Figure 9. Encounters by Species by Ambient Mean Temperature in C° within Temperature
 329 Seasons. Line shows mean, diamond shows 95% confidence intervals, * = significant result.

330
 331 There were differences in species' encounters by temperature seasons [$X^2(3, 452) = 10.14, p =$
 332 0.02]. For the Cold3 season only, galagos were encountered more often than expected while
 333 otolemurs were encountered less than expected [galago expected/observed = 19/12 encounters,
 334 otolemur expected/observed = 6/14 encounters: $X^2(1, 25) = 5.34, p = 0.002$].

335 Mean ambient temperature within each temperature season during encounters also differed
 336 between species; we found no cold season effects, but encounters did differ during the Hot

337 season with otolemurs encountered at lower mean temperatures compared to galago encounters
 338 [otolemur = 18.76 ± 2.13 , galago = 19.57 ± 2.81 ; $t(187) = 2.21$, $p = 0.03$, Fig. 9]. A Kaplan-
 339 Meier Survival Analysis for the Hot season showed little difference in encounters by species
 340 below 18 C° but above this, galagos were encountered more often [galago median = 19.70 C° ,
 341 95% CI $18.4 - 20.7$, otolemur median = 18.40 C° , 95% CI $18.1-19.0$, Wilcoxon $X^2 = 9.31$, $df =$
 342 1 , $p = 0.05$, Fig. 10].



343
 344 Figure 10. Kaplan-Meier Survival Analysis Plot for species encounters by Ambient Temperature
 345 in C° during the Hot Season. Shaded area indicates 95% confidence intervals.

346 **Availability of Insects and Gums.** Both insect and gum availability were greater at higher
 347 temperatures [insects: $F(1) = 46.59$, $p = 3.57\text{e-}11$; gum: $F(1) = 74.24$, $p = 1.45\text{e-}16$]. Relative
 348 to temperature seasons, insect availability was greater during the Hot season compared to other
 349 seasons [$F(3) = 10.55$, $p = 1.123\text{e-}6$; Hot mean = 34.83 ± 50.58 , Cold1 mean = 15.81 ± 15.75 ,
 350 Cold2 mean = 16.91 ± 11.56 , Cold3 mean = 5.44 ± 1.80]. Gum availability was also greater
 351 during the Hot season than other seasons and greater during the Cold1 season compared to Cold2
 352 and Cold3 season [$F(3) = 202.21$, $p = 7.18\text{e-}81$, Hot mean = 1.13 ± 0.31 , Cold1 mean = $0.57 \pm$
 353 0.18 , Cold2 mean = $0.80 \pm 1.009\text{e-}15$, Cold3 mean = $0.49 \pm 1.7\text{e}16$]. Neither insect or gum

354 availability were affected by moon phase or illumination. Encounters relative to insect
355 availability by temperature season did not vary by species for any of the cold seasons (Cold1
356 mean insect availability during encounters: galago= 16.27 ± 12.01 , otolemur = 16.38 ± 18.61 ,
357 $t=0.33$, $p=0.74$; Cold2 mean insect availability during encounters: galago= 13.53 ± 10.44 ,
358 otolemur= 17.65 ± 12.21 , $t=1.22$, $p=0.23$; Cold3 mean insect availability during encounters:
359 galago= 5.42 ± 1.87 , otolemur= 5.50 ± 1.77 , $t=0.09$, $p=0.93$). However, during the hot season, insect
360 availability was greater during galago encounters compared to otolemur encounters (Hot mean
361 insect availability during encounters: galago= 47.73 ± 67.34 , otolemur= 24.85 ± 28.83 , $t=2.75$,
362 $p=0.007$). Encounters relative to gum availability by temperature season also did not vary by
363 species for any of the cold seasons (Cold1 mean gum availability (in grams) during encounters:
364 galago= 0.61 ± 0.60 , otolemur = 0.49 ± 0.58 , $t=1.19$, $p=0.89$; Cold2 mean gum availability during
365 encounters: galago= 0.89 ± 0.62 , otolemur= 0.73 ± 0.62 , $t=0.67$, $p=0.54$; Cold3 mean gum
366 availability during encounters: galago= 0.47 ± 0.13 , otolemur= 0.56 ± 0.15). However, during the
367 hot season, gum availability was greater during otolemur encounters compared to galago
368 encounters (Hot mean gum availability during encounters: galago= 0.81 ± 0.92 ,
369 otolemur= 1.86 ± 2.09 , $t=2.39$, $p=0.02$).

370

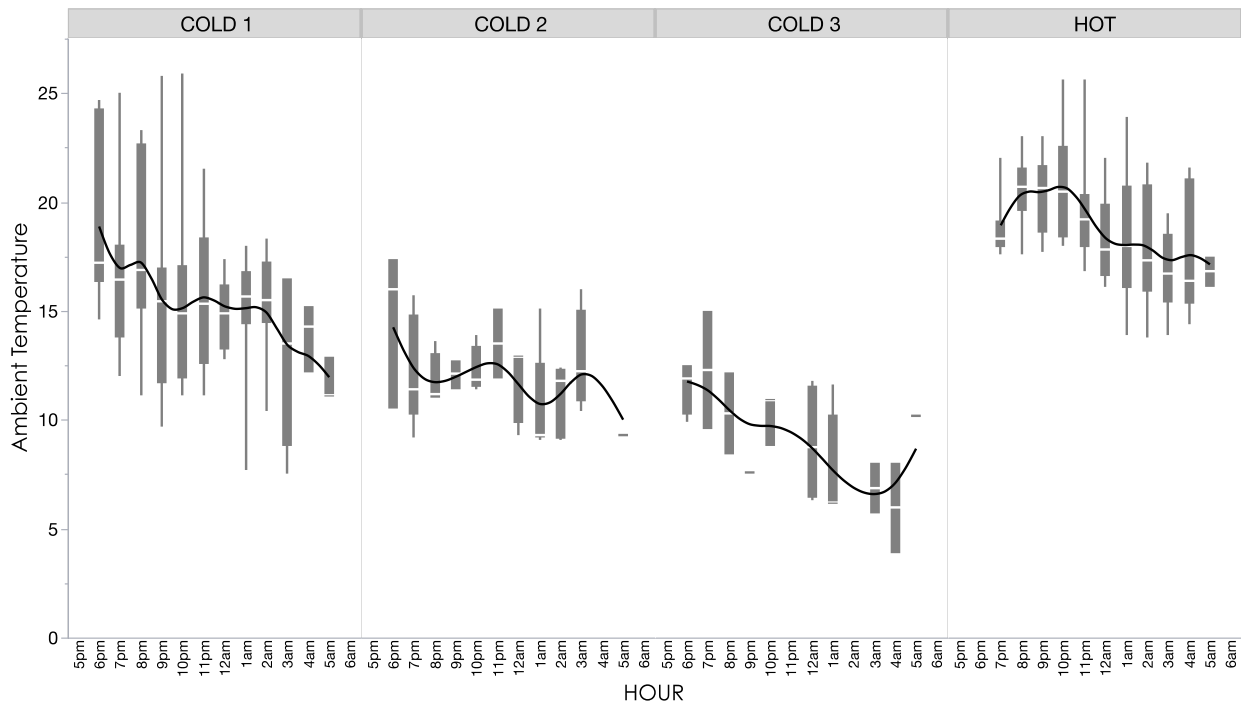
371 **Humidity.** In the seasonal environment of Lajuma, temperatures were negatively correlated with
372 percentage humidity, with higher percentage humidity at lower ambient temperature [$F(1) =$
373 172.36 , $p = 1.49e-33$]. Overall, species encounters relative to humidity was not significantly
374 different [$t(1) = 1.06$, $p = 0.29$].

375

376 **Night Length.** In this study, December was associated with the shortest mean night length (mean

377 = 7.39 hours) and July had the longest photoperiod (mean = 10.32 hours). Mean night length
 378 during encounter walks ranged from 10.1 hours to 13.55 hours with a mean of 11.88 ± 0.99
 379 hours across the research period. Night length varied by each season [$F(3) = 236.47, p = 6.13e-$
 380 92 , Cold1 mean = 12.12 ± 0.79 hours, Cold2 mean = 13.05 ± 0.36 hours, Cold3 mean = $13.54 \pm$
 381 0.007 hours, Hot mean = 11.09 ± 0.51 hours]. However, species encounters did not differ either
 382 overall or by temperature seasons relative to night length [$X^2 = 0.05, df = 1, p = 0.82$].

383
 384 **Temporal Effects.** Ambient temperature varied by time, becoming cooler as the night
 385 progressed for all temperature seasons (Figure 11). Mean ambient temperature during encounters
 386 were warmer before midnight and cooler after midnight (before midnight mean = 17.25 ± 4.14
 387 C° , after midnight mean = $15.09 \pm 3.93 C^\circ$; Wilcoxon $X^2 = 27.85, df = 1, p = 1.308e7$).

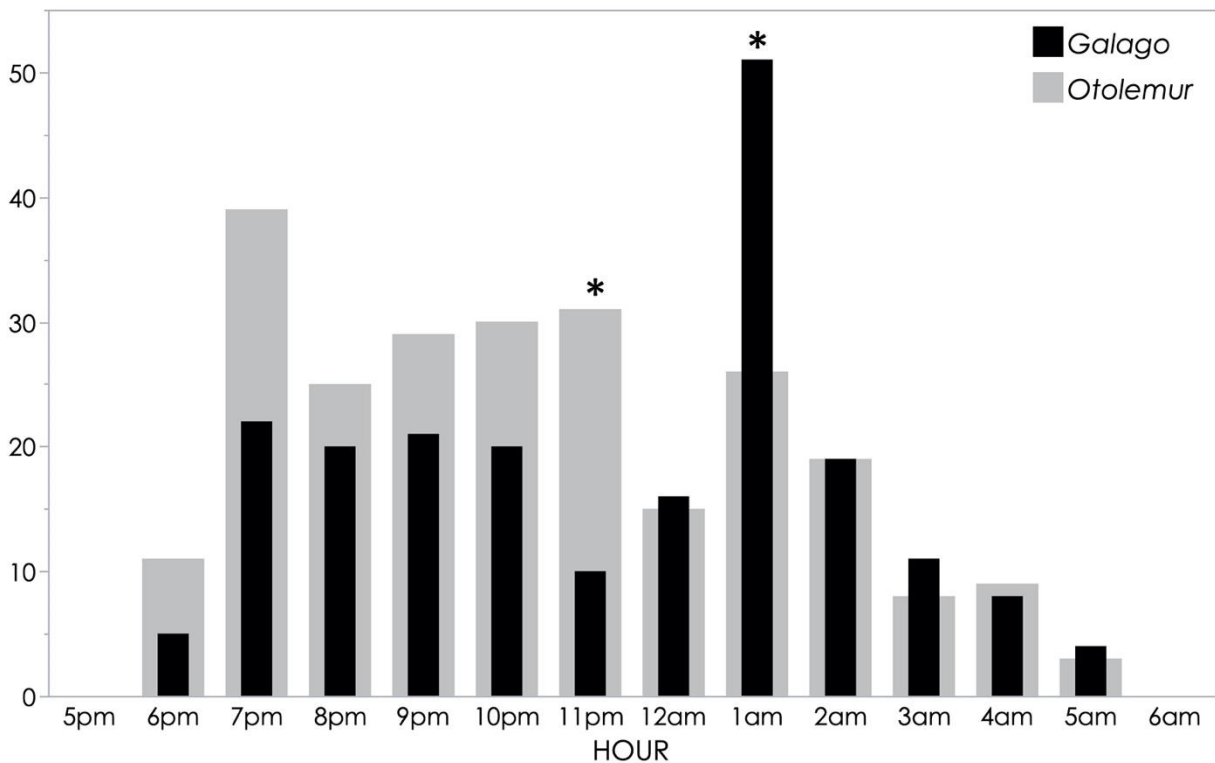


388
 389 Figure 11. Box plots Showing Median Temperature in C° by Survey Hour. Line shows median.

390
 391 Species encounters also varied significantly before and after midnight [$X^2(1, 452) = 18.45, p =$

392 1.741e-5]. Within species, galago encounters were lower before midnight compared to after
 393 midnight [$X^2(1, 207) = 10.00, p = 0.002$], while otolemur encounters were greater before
 394 midnight than after midnight [$X^2(1, 245)=8.45, p = 0.004$]. Between species, otolemur
 395 encounters were greater than galago encounters before midnight [$X^2(1, 263)=7.72, p=0.006$],
 396 while galago encounters were greater than otolemur encounters after midnight [$X^2(1, 189) =$
 397 $10.74, p=0.001$].

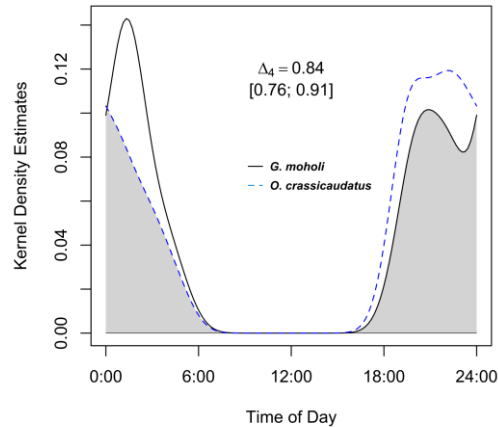
398 Overall species encounters also varied by hour [$X^2(11, 452)=28.34, p=0.029$], which is shown in
 399 the bullet density plot in Fig. 12. Hourly comparisons revealed that during hour 11 (11pm to 12
 400 am), galago encounters were significantly reduced compared to otolemur encounters [galago N =
 401 9 encounters, otolemur N = 31 encounters: $X^2(1, 51)=8.75, p=0.003$]. Galago encounters were
 402 greater than otolemur encounters during hour 1 (1 am to 2 am) [galago N = 51 encounters,
 403 otolemur N = 27 encounters: $X^2(1, 77) = 12.96, p=0.0003$, Fig. 12].



405

406 Figure 12. Bullet plot of encounters by species relative to hour; * = significant result between
407 species.

408
409 Temporal analysis using the Kernel density estimation indicate otolemurs and galagos were
410 primarily active from 5:45 p.m. and 6:30 a.m. during the study period (N=452 observations;
411 N=207 for galagos and N=245 for otolemurs Fig. 13). Both of their temporal activity patterns
412 differed significantly over a 24-hour period (Watson's two-sample test of homogeneity: $U^2=$
413 0.33, $p = 0.001$ to 0.01). Within-species time comparisons showed that among this period, the
414 activity for galagos were the highest between 1 a.m. and 2 a.m. (Kernel density estimates=1.4,
415 Fig. 13) and lowest between 11 p.m. and 12 a.m. (Kernel density estimates=0.6, Fig. 13). In
416 contrast, otolemurs showed a high activity peak from 10 p.m. to 11 p.m. (Kernel density
417 estimates=0.11, Fig. 13) and low activity peak from 5 a.m. to 6 a.m. (Kernel density
418 estimates=0.01, Fig. 13). The maximum level of otolemur activity corresponds to a decrease of
419 galago activity (from 10:00 p.m. to 11p.m., Fig. 1) whereas the maximum level of galago activity
420 corresponds to a decrease of otolemur activity (from 12 a.m. to 3 a.m., Fig. 1). Despite these
421 differences in activity patterns, the two species showed an overall high degree of overlap
422 ($\Delta 4=0.84$, 95% CI: [0.76; 0.91], Fig. 13).



423

424

425 Figure 13. Kernel density functions of daily activity patterns and temporal overlap of *Otolemur*
 426 *crassicaudatus* ($N=245$) and *Galago moholi* ($N=207$) at Lajuma estimated from direct observations
 427 from June 2017-July 2018. Temporal activity is plotted over a 24-hour period (x-axis), with higher
 428 density values (y-axis) representing increased activity. The coefficient of overlap Δ_4 (denoted in
 429 grey) with 95% CI (bracketed values) is the area under the two-density and was estimated from
 430 10,000 bootstraps.

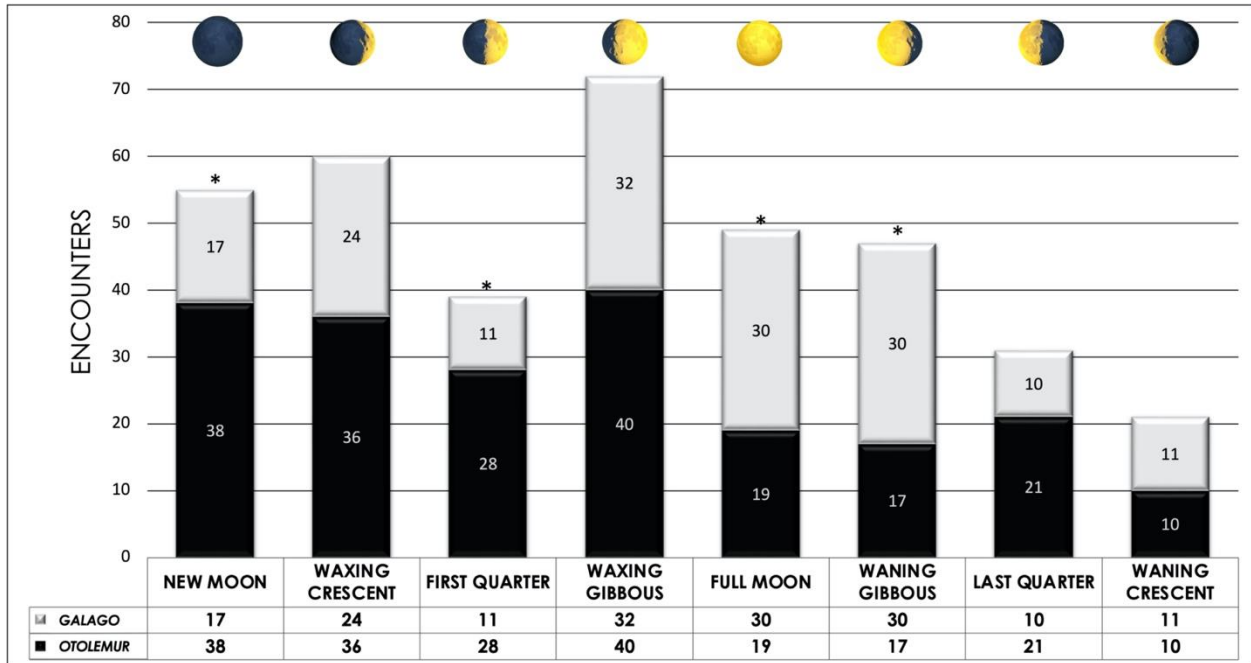
431

432 Lunar Effects

433

434 *Moon Phase*. Otolemurs were encountered more than expected during the new moon compared
 435 to galago encounters [$X^2(1, 72)=3.57, p=0.05$, otolemur encounters $N=38$, galago encounters N
 436 $= 17$] while galagos were encountered more than expected during the full moon compared to
 437 otolemurs [$X^2(1, 49)=5.81, p=0.015$, galago encounters $N=30$, otolemur encounters $N=19$, Fig.
 438 14]. Otolemur encounters during the first quarter moon were greater than expected compared to
 439 galago encounters [$X^2(1, 39)=4.00, p=0.045$, otolemur encounters $N=28$, galago encounters
 440 $N=11$], and during the waning gibbous moon, galago encounters were greater than expected
 441 compared to otolemurs [$X^2(1, 47)=7.46, p=0.006$, galago encounters $N=30$, otolemur encounters

442 N=17; Figure 14]. Within species, galago encounters were lower than expected during the new
 443 moon compared to the full moon [$X^2(1, 47)=4.48$ $p=0.03$, new moon encounters N=17, full
 444 moon encounters N=30;] while for ootlemurs, encounters were greater during the new moon than
 445 the full moon [$X^2(1, 57)=3.78$, $p=0.05$, new moon encounters N=38, full moon encounters
 446 N=19].



447
 448
 449 Fig 14. Encounters by Moon Phase Comparing *Ootlemur crassicaudatus* with *Galago moholi*, *
 450 = significant result between the two species.

451
 452 *Fraction of Moon Illumination.* Encounters were also compared by the fraction of moon
 453 illumination. Overall, mean galago encounters were at 0.52 moon illumination, while ootlemur
 454 encounters were at 0.44 moon illumination [Wilcoxon Rank Sums Test, N=452 encounters,
 455 $Z=2.23$ $p = 0.03$].

456
 457 **Overall Model.** We used a Generalized Linear Model using a Binomial distribution and a logit
 458 link function to assess which factors best predicted species encounters. We tested the following

459 parameters: Ambient Temperature, Moon Phase, Moon Luminosity, Insect Availability, Hour,
 460 Before/After Midnight. The best fit model is shown in Table 1 which shows Temperature
 461 Season, Moon Phase, Hour, Insect Availability and Ambient Temperature best predicted species
 462 encounters.

463 **Table 1.** Result of Generalized Linear Model.
 464

	df	AICc	ChiSq	P
Whole Model Test: Temperature Season +Moon Phase+ Hour +Insect Availability+Ambient Temperature	23	490.87	77.98	6.729e-8
Effects Likelihood Ratio Test	DF	L-R ChiSq	Prob>Chi Sq	
Temperature Season	3	21.14	0.00009	
Moon Phase	7	25.26	0.0007	
Hour	11	31.34	0.0010	
Insect Availability	1	5.07	0.024	
Ambient Temperature	1	4.87	0.03	

465
 466 **DISCUSSION**

467
 468 **Encounters and Environmental Factors.** Most animals demonstrate bias in terms of their
 469 activity patterns. Primates primarily exhibit diurnal or nocturnal activity patterns, although some
 470 are cathemeral or crepuscular (Hill, 2006a; Fernández- Duque & Erkert, 2006; Fleagle, 2013;
 471 Santini et al., 2015; Bray et al., 2017; Svensson et al., 2018; Campera et al., 2019). These
 472 patterns are driven in part by predictable ecological factors known as Zeitgebers, but such
 473 patterns can be affected by less predictable changes called masking factors which can alter a
 474 species physiology and behavior and thus provide some flexibility (Kavanau & Peters, 1976;
 475 Marques & Waterhouse, 1994). For primates, key masking factors include moon illumination
 476 and seasonal variation in temperature, humidity and rainfall (*Aotus azarai*: Fernández- Duque,
 477 2003; Fernández- Duque et al., 2010; *Nycticebus javanicus*: Starr et al., 2012; Rode-Margono &
 478 Nekaris, 2014; Campera et al., 2022; *Nasalis larvatus*: Kooros et al., 2021). Thermal challenges

479 can alter activity budgets and even foraging times, and these are exacerbated in more seasonal
480 environments (e.g., Hill, 2006b; Donati et al., 2007; Donati et al., 2011; Majolo et al., 2013;
481 Gestich et al., 2014; Donati et al., 2013; LaFleur et al., 2014; Li et al., 2020). In nocturnal
482 primates, temperature can affect patterns of non-activity such as sleep (Reinhardt et al., 2019;
483 Pozzi et al., 2022) and overall activity (Fernández-Duque et al., 2010; Starr et al., 2012; Nowack
484 et al., 2013a; Rode-Margono & Nekaris, 2014). In this study we focused on how such
485 environmental variables affected encounters with two nocturnal primates of differing body size
486 within a seasonal temperate habitat, building off Harcourt's seminal study of body size effects in
487 these two species (Harcourt, 1980).

488
489 **Food Availability.** Previous research suggest *G. moholi* focuses on insects throughout the year
490 and supplements this with gums in the winter, when insects are less available (Harcourt, 1980,
491 1986; Nash, 1986; Nowack et al. 2013b). Former research reports that *O. crassicaudatus*
492 emphasize insects during the warm summer months and switch more to gum during the winter
493 (Harcourt, 1980, 1986). As noted by Harcourt (1980), this makes sense in terms of body size
494 effects. With a higher metabolic rate and greater protein requirements relative to body size, *G.*
495 *moholi* must continue to forage throughout the year for high quality resources such as insects,
496 while the larger *O. crassicaudatus*, with lower requirements for energy and nutrients per unit
497 body weight, can switch to lower quality foods (Clauss et al., 2013), such as gum (Power, 2010).
498 *O. crassicaudatus* may also switch from insects to fruit resources, especially figs, when available
499 (Bearder, 1974; Nash et al., 1989) and even seeds (Doyle & Bearder, 1977). *G. moholi* does not
500 eat fruit on a regular basis (Harcourt, 1986; Harcourt & Bearder, 1989) and emphasizes fruit only
501 within highly fragmented anthropogenically altered environments where *Vachellia karoo* gum is
502 rare (Scheun et al., 2014). *Vachellia* gums are important for both species as these are available

503 all year long (Bearder & Martin, 1980; Nash, 1986; Nowack et al. 2013a), but *O. crassicaudatus*
504 may exhibit less seasonal variation in gum use than *G. moholi* (Nash, 1986) and has been
505 characterized as an “intensive exudativore” (Burrows & Nash, 2013). Our results support these
506 general species differences. The lack of differences during the cold seasons indicates both
507 species are using what gum and insect resources are available. However, even though insect
508 availability was higher during the Hot season overall, insect availability was still greater during
509 *G. moholi* encounters compared to *O. crassicaudatus*. In comparison, while gum availability was
510 greater during the Hot season, gum availability was greater during *O. crassicaudatus* encounters
511 compared to *G. moholi*. Thus *G. moholi* may emphasize insects when they become more
512 available while *O. crassicaudatus* continues to emphasize gum throughout the year.

513
514 **Temperature Effects.** Low temperatures place a greater relative demand on small homeotherms
515 as compared to large ones, while the opposite is true of high temperatures (Peters, 1983), It is
516 thus expected that the two galago species exhibit different biological and/or behavioral reactions
517 to seasonal temperature fluctuations and this was documented in this study. For both species,
518 encounters were greater during the Hot Season compared to other temperature seasons, which
519 likely reflects the greater availability of food resources such as insects and gum (Fig. 6). For the
520 Cold1 and Cold2 seasons, the two species mirrored each other in terms of overall pattern as well
521 as the temperatures for peaks of being active (Fig. 8). The Cold3 temperature season was the one
522 exception. Here temperatures were considerably colder than other seasons, with temperatures
523 dropping below 4 C° and not rising to more than 15 C° during encounters (Fig. 8). During this
524 period, *G. moholi* were encountered across a wider range of ambient temperatures, with peaks in
525 encounters at lower temperatures compared to *O. crassicaudatus*, whose encounters showed a

526 narrower range of ambient temperatures and whose peak of encounters were at higher
527 temperatures.

528
529 During the Hot season *O. crassicaudatus* encounters peaked at lower temperatures than *G.*
530 *moholi* and they were not observed above 23.8 C° while *G. moholi* remained active to 25.60 C °
531 (Fig. 8, 9). These differences can be interpreted relative to the physiological responses to
532 temperature by animals of differing body size. As noted, the two species' body weights are
533 dramatically different, with *G. moholi* being roughly 10 times smaller than *O. crassicaudatus*.
534 Relative to body size, cooler ambient temperature is a critical concern for small mammals as they
535 lose heat quickly (Millar & Hickling, 1990; Halle, 2000; Merritt & Vessey, 2000; Zielinski,
536 2000; Langer, 2002), and, as demonstrated by Bergmann's Rule (Meiri & Dayan, 2003), larger
537 animals usually have reduced heat loss and better thermoregulation at lower temperatures
538 (Clutton-Brock & Harvey, 1983; Peters, 1983). In addition, because surface area to volume
539 reduces with increasing size, larger animals have less relative surface area for heat exchange and
540 consequently have higher vasomotor indices (VMI) compared to smaller animals; this gives
541 larger animals more control over surface temperature (Phillips & Heath, 1995). For small
542 animals, who have greater surface area to volume they have lower VMI and depend on changing
543 their metabolic rate to regulate their body temperature. However, because larger animals have
544 less relative surface area, maintaining homeothermy at higher temperatures may present a greater
545 challenge (Peters, 1983).

546
547 The limited data on thermal neutral zone, where heat production is equal to heat loss, is 25 –
548 31 °C in captive *O. crassicaudatus* (Müller & Jaksche, 1979) and 28 - 35° C in captive *G. moholi*
549 (Knox and Wright, 1989) indicating that the smaller *G. moholi* can maintain homeothermy
550 within higher temperatures ranges than the larger *O. crassicaudatus*. Nevertheless, both species

551 can be vulnerable to high temperatures as they have thermoregulatory sweat glands only on their
552 pes and manus (Montagna & Yun, 1962; Hiley, 1975) and thus may need to rely primarily on
553 behavioral adjustments at high temperatures (Müller & Jaksche, 1979). Unlike Malagasy mouse
554 lemurs of similar body size which commonly use torpor, *G. moholi* uses this adaptation only
555 under severe conditions (extremely low temperatures and/or reduced food) with torpor only
556 employed when other behavioral responses fail, as they have extreme difficulty rewarming
557 (Nowack et al., 2010; 2013a). Torpor in *G. moholi* is associated with poor body condition and is
558 expressed primarily by young (non-reproductive) individuals (Nowack et al., 2013b). There is no
559 evidence of torpor in *O. crassicaudatus* (Müller & Jaksche, 1979). Captive data has
560 demonstrated that the smaller *G. moholi* are able to endure much higher temperatures than *O.*
561 *crassicaudatus* before losing homeothermy (loss of homeothermy: *G. moholi* above 35 °C, *O.*
562 *crassicaudatus* above 28° C, Müller & Jaksche, 1979). Captive data also indicate that *G. moholi*,
563 possess brown adipose tissue and the capacity for non-shivering thermogenesis throughout the
564 year (Nowack et al., 2013b). We could find no comparable data regarding this for *O.*
565 *crassicaudatus* so it is unclear whether they have this ability. Our results do suggest that it is
566 only at the coldest or hottest temperatures that we see species differences. At the coldest
567 temperatures, insect and gum availability are reduced. The much smaller bodied *G. moholi*, with
568 their greater need to change their metabolic rate to regulate their body temperature, and their
569 greater energetic and protein requirements, may not be able to reduce being active and foraging
570 to meet their needs. However, at colder temperatures *O. crassicaudatus* may be more buffered by
571 their larger body size and potentially greater energy stores, and thus reduce being active at
572 extremely low temperatures, (Ramen et al., 2005; Higginson et al., 2012), which also potentially
573 reduces predation risk during such times. Winter months in northern South Africa are associated
574 with reduced insect and gum availability, especially fresh *Vachellia* gum which has a higher

575 energy content in the winter compared to the summer (Nowack et al., 2013a). This may relate to
576 reports of *G. moholi* even searching for food during the day in cold periods when insect
577 availability is low and/or gum feeding sites are frozen (Bearder et al., 2006; Nowack et al.,
578 2013a). Alternatively, or in tandem, *G. moholi* may be able to effectively use non-shivering
579 thermogenesis and thus continue to forage (Nowack et al., 2013b). Conversely, during the Hot
580 season, *O. crassicaudatus* may have to reduce being active given their larger body size and
581 reduced ability to maintain homeothermy and their lower thermal neutral zone compared to *G.*
582 *moholi* as suggested by captive studies, but they can do so given they may have more fat
583 reserves. Overall, our results indicate that body size differentially affects when galagos are active
584 and may limit *G. moholi* behavioral adjustments during extremely cold seasons, while *O.*
585 *crassicaudatus* can use behavioral adjustments, e.g., reduce when they are active, as reflected in
586 lower encounter rates during both extremely cold and hotter periods.

587 **Temporal Effects.** We also found differences relative to time. Comparing encounters before and
588 after midnight revealed that *O. crassicaudatus* were encountered more than expected during the
589 first half of the night while *G. moholi* were encountered more after midnight. This was also tied
590 to temperature, as temperatures tended to be warmer during the first half of the night. Breaking
591 down encounters by hour, *G. moholi* encounters reduced around 11pm and then increased
592 dramatically around 1am. The coefficient of overlap analysis also indicates significant species
593 differences by hour. Our data suggest that the larger *O. crassicaudatus* is primarily active early
594 on, when ambient temperature is greater while *G. moholi* are active primarily during the latter
595 half of the night when temperatures are cooler. Temporal effects have been noted for the pygmy
596 loris (*Nycticebus pygmaeus*) with greater activity after 3 am (Starr et al., 2012). The specific
597 pattern shown by *G. moholi* may relate to a need to rest and then increase being active and thus
598 increase foraging effort about halfway through the night. The differences seen may reflect body

599 size effects, with the smaller *G. moholi* needing to forage more extensively later in the night to
600 attain enough food to support them throughout the following day, whereas the larger *Otolemur*
601 may be more buffered overall, focusing their foraging early on when temperatures are warmer,
602 and when gum is less hard (Harcourt, 1980). Alternatively, or in tandem with physiological
603 effects of body size, these results may also reflect temporal partitioning between the two species
604 of galago as both species forage on similar foods (e.g., gum and insects). Emphasizing activity at
605 different times of the night could reduce direct feeding competition. Behavioral observations
606 indicate that in direct encounters over baited traps, *O. crassicaudatus* chase the smaller *G.*
607 *moholi* away (Sauther, pers. obs.). Temporal landscape partitioning has been observed in baboon
608 social groups (Markham et al., 2014) and even ecologically similar Malagasy nocturnal primates
609 (Campera et al., 2019). Here ecologically similar sympatric lemurs, *Avahi meridionalis* and
610 *Lepilemur fleuretae* showed different activities that may be related to reducing feeding
611 competition as well as predation.

612
613 **Moon Phase and Illumination.** Moon phase and the amount of moon illumination can be seen
614 as important environmental factors that may affect insect availability and predation. In our study
615 moon phase and illumination affected galago encounters. *G. moholi* is lunarphilic at Lajuma
616 while *O. crassicaudatus* is lunarphobic. In other studies, male *G. moholi* also move farther on
617 moon-lit nights than during periods without moon light (Bearder et al., 2002). Activity relative to
618 moon phase and/or luminosity can be driven by both foraging and predation (Gursky, 2003). The
619 predation risk hypothesis (Huck et al., 2017; Pratas-Santiago et al., 2017), predicts nocturnal
620 prey will reduce activity during the full moon (e.g., be lunarphobic) as predators can see their
621 prey more effectively. However, the visual acuity hypothesis (Huck et al., 2017, Prugh &
622 Golden, 2014), argues bright moonlight also allows prey to both see their own predators and

623 their own prey, such as insects, more effectively and predicts visually oriented prey species can
624 both forage better and detect predators under brighter moonlight.

625
626 In the cathemeral night monkey, *Aotus azarai*, nocturnal activity was positively correlated with
627 moonlight, especially following a day of relatively hot temperatures (Fernández-Duque, 2003)
628 and also increasing luminosity (Fernández-Duque et al., 2010). The Javan slow loris, *Nycticebus*
629 *javanicus*, however appears lunarphobic, increasing activity during dark nights, which may relate
630 to preferred prey being more available during the new moon as well as predator effects (Campera
631 et al., 2022). Spectral tarsiers (*Tarsius spectrum*), are lunarphilic, being most active during full
632 moons (Gursky, 2003). In sympatric ecologically similar lemurs, *Avahi meridionalis* is
633 lunarphilic while *Lepilemur fleuretae* is lunarphobic (Campera et al., 2019).

634
635 In terms of predation effects, there is considerable variability in terms of lunarphobia versus
636 lunarphilia with most studies focusing on mammalian carnivores. Felids that are sit and wait
637 ambush predators are affected by lunar luminosity, reducing activities on lighter nights (Sunquist
638 & Sunquist, 1989; Martins & Harris, 2013). For example, in leopards (*Panthera leo*) living in the
639 Cederberg Mountains, South Africa, successful kills were greater during lower light periods,
640 between new and half-moon phases (Martins & Harris, 2013; but see Bidner et al., 2018 who
641 found no moon phase effects in leopards visiting baboon resting sites). Many predators are not
642 affected by the lunar cycle at all (Botts et al., 2020), including pumas, *Puma concolor*, (Pratas-
643 Santiago et al., 2017) and north China leopards, *Panthera pardus japonensis*, (Zaman et al.,
644 2022). Predation by snakes is also a factor, with most snakes and their prey reducing activity
645 during bright moonlight (Clarke et al., 1996; Lillywhite & Brischoux, 2011). Owl predation is
646 also of interest. In eagle owls, *Bubo bubo*, activity was higher around the full moon than the new
647 moon (Penteriani et al., 2011) and rates of predation were higher in barn owls *Tyto alba* during

648 the full moon (Kotler et al., 1988).

649
650 While the relationship between encounters and moon phase and lunar illumination might be a
651 factor of when insects are active, we found no lunar effects. Instead, insect availability tracked
652 ambient temperature, being higher at warmer temperatures. At Lajuma, the large and small
653 galago species may need to avoid different types of predators. *O. crassicaudatus* at Lajuma are
654 prey for the large Verreaux's Eagle Owl, *Bubo lacteus* which is the largest owl in South Africa
655 (66 cm in length and weighing up to 2 kg, Biggs et al., 1979), as predated remains have been
656 found (Sauther pers. obs). They are documented predators of the larger *O. crassicaudatus* at
657 other sites, such as in Kenya (Brown, 1965). As these owls are more active during the full moon,
658 the larger *O. crassicaudatus* may reduce potential predation by being more active at lower levels
659 of ambient light. The medium sized African civet (*Civettictis civetta*) is also present at Lajuma.
660 Little information is available regarding overall lunar effects on African civet activity, but in a
661 study in Botswana density of observations were greatest during the full moon (Satterfield,
662 2014). At 12 kg. (Kingdom, 1977), this species is much larger than *O. crassicaudatus* and given
663 their behavior towards African civets at Lajuma (e.g., moving to higher areas in trees, alarm
664 calling in the presence of African civets; Sauther, pers. obs), *O. crassicaudatus* clearly views this
665 species as a potential predator. While *O. crassicaudatus* do feed on insects, they emphasize gum
666 year-round and utilize fruits, flower secretions and seeds more than insects (Bearder, 1974). As
667 such, lunarphobia in this species may relate primarily to predator avoidance, which fits the
668 predation risk hypothesis (Huck et al., 2017; Pratas-Santiago et al., 2017).

669
670 At their small body size *G. moholi* faces two constraints, the need to maintain a higher quality
671 diet of insects and being potential prey for many predators. Snakes in general may reduce their
672 activity during bright moonlight and are especially a factor for the smaller bodied *G. moholi*

673 (Sauther, pers. obs). Genets are also predators at Lajuma. The large spotted genet (*Genetta*
674 *tigrina*), a small, semi-arboreal carnivore, is a known predator of *G. moholi*, often caching bodies
675 of half-eaten individuals at other sites (Burnham et al., 2013). *G. moholi* also appear to be
676 captured more often by large spotted genets under new moon rather than full moon nights,
677 indicating genets may hunt more often at times of lower ambient light, and of the 14 encounters
678 between *G. moholi* and predators at another research site, ten of these were with genets, and
679 elicited frantic calling and even communal mobbing (Bearder et al., 2002). In general, small
680 carnivores, including Indian and palm civets, show significantly higher activity on darker nights
681 (Bhatt et al., 2021). At a body size of 1.5g kg (Larivière & Calzada, 2001), large spotted genets
682 are similar in body size to adult Lajuma *O. crassicaudatus* which may limit their ability to
683 predate on this larger galago species but are potential predators on *G. moholi*. Although insect
684 availability did not track moon phase or illumination, *G. moholi* are visually oriented insect
685 predators and being lunarphilic may facilitate both predator detection and enhance successful
686 insect predation, and this species may support the visual acuity hypothesis (Huck et al., 2017,
687 Prugh & Golden, 2014), Thus, both body size, food and predator behavior may drive differences
688 seen here in terms of lunar effects on galago encounters.

689
690 **Whole Model.** Our results indicate that while no single environmental factor explains galago
691 species' encounters, a combination of environmental factors may drive encounters as a measure
692 of being active or not active. These factors differentially affect the two species, and this is likely
693 primarily due to body size effects. In the temperate habitat of Lajuma small and large bodied
694 galagos react differently to temperature seasons, moon phase, hour, insect availability and
695 ambient temperature. Thus, overall *G. moholi* are expected to be more active than *O.*
696 *crassicaudatus* during both very cold and hot temperatures, with a full moon after midnight

697 during higher insect availability, while *O. crassicaudatus* are expected to be more active during
698 less challenging temperatures, with a new moon, before midnight.

699
700 **Limitations.** Environmental effects on mammals are complex but are important for
701 understanding how climate change will differentially affect mammals of variable body size.
702 Limits of this study is the lack of galago physiological data. For example, the causal relationship
703 between ambient temperature and metabolic rate (the Arrhenius effect), can inform vulnerability
704 to heat stress (Lovegrove et al., 2013). Understanding the effect of ambient temperature on
705 thermal neutral zone is also important and can vary across temperatures in seasonal habitats
706 (Liao et al., 2023). Ecological and behavioral data on predators at this site would also better
707 contextualize galago activity patterns. In addition, reproductive status likely affects species'
708 encounters especially during lactation when females must reduce foraging to nurse infants
709 throughout the night, or during the mating season when both species are likely more active, as
710 seen in Javan loris (Campera et al., 2022).

711
712 **Conclusions.** Studying nocturnal primates is challenging but essential to understanding primate
713 diversity. This study used thermal imaging cameras to facilitate nocturnal galago encounters as a
714 measure of each species being active or not active and demonstrates the usefulness of this
715 technology in facilitating our goal, which was to assess behavioral responses of two sympatric,
716 homeothermic strepsirrhine primates of dramatically different body sizes to the same
717 environmental stressors within a temperate habitat. Comparing these two closely related species
718 elucidates the effects of body size in mediating temperate environmental stressors and indicate
719 that body size and its interplay with physiological and ecological factors is a useful approach for
720 understanding how different species deal with environmental stressors. The smaller *G. moholi*
721 has more consistent nutritional needs which requires them to be active at more challenging

722 temperatures, both high and low and thus limits these behavioral adjustments. At Lajuma, where
723 they are lunarphilic, they must balance both nutritional needs and predation, which supports the
724 visual acuity hypothesis. Conversely, the large *O. crassicaudatus* may be able to buffer
725 themselves by being less active during both very cold and very hot periods but are especially
726 more sensitive to warmer temperatures where their larger body size reduces their ability to
727 maintain homeothermy without reducing activity levels. They are also lunarphobic, which may
728 relate primarily to predator avoidance of large predators such as the Verreaux's Eagle Owl and
729 which fits the predation risk hypothesis. Importantly, studying these galagos where they are more
730 stressed provides a window into the adaptive ranges (the edges of physiological and behavioral
731 adaptations) where natural selection should be most powerful. As primates at these temperate
732 "edges" may be encountering stronger selective factors in terms of non-human primate
733 adaptation and ecology, adding data on these continental strepsirrhine primates may be
734 especially informative in addressing questions such as the role of phylogeny and body size in
735 mediating such environmental stressors. Such comparative data may also be relevant for
736 understanding how ancestral primates mediated past climatic change during key environmental
737 periods such as the dramatic cooling marking the Plio-Pleistocene transition. A more complete
738 understanding of temperate primate ecology is also important for clarifying the mechanisms and
739 physiological patterns underlying primate resilience which is key to predicting the sensitivities of
740 species to ongoing climate change (Canale & Henry, 2010).

741
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