

1 **Effect of human activity on habitat selection in the endangered Barbary macaque**

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22 Short title: Barbary macaque habitat selection

23 **Abstract:**

24 The exponential growth of human population and infrastructure is significantly reducing the amount
25 of ecological resources available for wild animals. We analyzed the effect of human activity on
26 Barbary macaques (*Macaca sylvanus*), an endangered species restricted to the fragmented forests of
27 Morocco and Algeria, using location data from five social groups inhabiting Ifrane National Park,
28 Morocco.

29 We used a resource selection function to explore the effects of anthropogenic disturbance on
30 macaque habitat selection, using nine natural, social, and anthropogenic disturbance variables as
31 predictors. Forest cover, home range overlap, herding route proximity, and road proximity were all
32 significant predictors of habitat use. Macaques avoided areas used by local shepherds, to reduce the
33 risk of attack by shepherds' dogs, but approached roads to increase the chances of provisioning by
34 tourists. However, herding route and road use varied seasonally in line with levels of human use,
35 suggesting that macaques may be navigating their environment strategically (in space and time) to
36 balance food acquisition and risk avoidance. The results of this study highlight the importance of
37 assessing human impact on habitat selection in both space and time. Our data on seasonal variations
38 in macaques' use of roads can help prevent road injuries, a major source of mortality for
39 provisioned macaques, by focusing management efforts by national park workers in time and space.
40 Furthermore, understanding when and where macaques seek provisioning from tourists can help
41 combat provisioning, which negatively impacts macaque health, behavior, and susceptibility to
42 poaching.

43

44 **Keywords:** dog-wildlife interactions; ecological niche; home-range use; human disturbance;
45 primate conservation; resource selection.

46 INTRODUCTION

47 Human activities have altered the environmental conditions of every biome on the planet (Ellis &
48 Ramankutty, 2008). As landscapes become increasingly human-dominated, many wildlife species
49 must cope with new ecological pressures (Woodroffe, Thirgood, & Rabinowitz, 2005). The impact
50 of habitat loss/fragmentation, climate change, expanding human infrastructure, hunting, and
51 poaching quickly and dramatically alters habitats, forcing wildlife to adjust, move to more suitable
52 areas (if these are available), or face the threat of extinction (Sih, Ferrari, & Harris, 2011). The
53 species that persist in human dominated landscapes adapt to anthropogenic habitats by modifying
54 their behavior and some invasive and urbanized species (i.e. species that live in habitats that are
55 outside their typical ecological niche, often at high densities) even prosper in dramatically altered
56 habitats (Lowry, Lill, & Wong, 2013).

57 Animals may alter their habitat use to avoid areas of intense human activity (spatial
58 avoidance) (Gill, 2000; Guillemain et al., 2007) and/or use those areas only when human activity is
59 low (temporal avoidance). For example, carnivores avoid areas used intensively by humans or only
60 use/move through those areas when human activity is low (Hebblewhite & Merrill, 2008; Martin et
61 al., 2010; Bouyer et al., 2015; Oriol-Cotterill et al., 2015). A meta-analysis examining diel patterns
62 in 62 mammal species found a strong, positive effect of human activity on nocturnality (Gaynor et
63 al., 2018). A study of the activity patterns in cathemeral *Eulemur* species found that lemurs in more
64 disturbed areas exhibited more nocturnal activity than those in less disturbed areas (Donati et al.,
65 2016).

66 Risk perception can significantly influence habitat use. Many species demonstrate great
67 flexibility in adapting their behavior according to the risks (from natural predators or humans)
68 associated with particular areas of their range, and at particular times (Frid & Dill, 2002; Hockings,
69 Anderson, & Matsuzawa, 2012; Coleman & Hill, 2014; Bryson-Morrison et al., 2017; Nowak et al.,
70 2017). However, risky areas and certain human activities can provide short-term benefits to

71 wildlife, such as predator deterrence and/or feeding opportunities (e.g. refuse sites, roadside
72 provisioning and farming) (Gilchrist & Otali, 2002; McKinney, 2011). Animals may specifically
73 select risky, but profitable, areas when the cost-benefit balance is most strongly in their favor, i.e. at
74 times likely to yield greater rewards at lower potential costs (Hockings, Anderson, & Matsuzawa,
75 2012; Maréchal, MacLarnon, et al., 2016). For example, chimpanzees frequently forage on crops at
76 night to minimize the risk of detection by human guards (Krief et al., 2014). Such flexibility allows
77 animals to adapt to local risk/reward conditions by balancing the potential benefits of provisioning
78 or acquisition of other resources, against the potential risk of predation, capture, or other negative
79 consequences.

80 The capacity of wildlife to be flexible in their habitat selection depending on the timing,
81 intensity, and type of human influence has been under-investigated (Beyer et al., 2010; Wilson,
82 Gilbert-Norton, & Gese, 2012; but see Bryson-Morrison et al., 2017). Such fine-scale assessments
83 are important because they can help to inform land-use planning that minimizes the potential for
84 human-wildlife conflict. Our aim was to assess if and how animals adjust and respond to the new
85 ecological pressures of human-dominated landscapes, using the endangered Barbary macaque
86 (*Macaca sylvanus*) as a model species. The Barbary macaque is threatened by extensive habitat loss
87 and fragmentation, and increased human activity in and around the remaining forests of Morocco
88 and Algeria (Butynski et al., 2018). Our study area is located close to the town of Azrou, and is
89 crossed by numerous herding routes (running primarily North to South) from the relatively low-
90 altitude livestock pens on the outskirts of the town to the higher-altitude pastures above. Pastoralist
91 activity has severely impacted macaque habitat quality by reducing the diversity and abundance of
92 herbaceous and shrub food resources (Ménard & Qarro, 1999; Ciani et al., 2005), and both dogs and
93 shepherds represent serious physical threats to macaques (Waters et al., 2017). There have been six
94 reported incidences of dogs taking Barbary macaque infants (Camperio Ciani & Mouna, 2006) and
95 shepherds and their dogs are reported to have harassed macaques (Mehlman, 1984).

96 Several roads also run through the study site (both North to South, and East to West), one of
97 which is a major transport route towards the Sahara desert in the South (Fig. 1). At two locations
98 along this road, tourist sites were constructed where local vendors sell fossils and other souvenirs to
99 tourists that come to see the macaques. Originally, the vendors fed these macaques to encourage
100 them to remain visible near the roadside and attract tourists. At the time of the study, two groups of
101 macaques (1 of which was included in this study) regularly spent the majority of the day in and
102 around these sites, whether provisioned by vendors or not. The direct and indirect effects of
103 pastoralist activity, in combination with the illegal trade of infant macaques to Europe, have driven
104 a dramatic decline in wild population numbers in recent decades. Although a few studies have
105 investigated the effects of anthropogenic activity on Barbary macaques (Ménard et al., 2014;
106 Maréchal, MacLarnon, et al., 2016; Carne et al., 2017), none has examined the extent to which
107 human activity influences macaque habitat selection. Such information can be used to direct
108 conservation efforts and resources to the issues that warrant the most attention and/or the most
109 immediate action.

110 The macaque population in Morocco experiences strong seasonal variations in climate
111 (Majolo et al., 2013), and thus resource availability (Hanya et al., 2011), requiring the Barbary
112 macaque to be an eclectic forager and dietary generalist (Ménard, 2002). These seasonal variations
113 also influence how easily accessible the forest is to local people. For example, during periods of
114 heavy snowfall, shepherds and dogs tend to remain at low elevations with their livestock, and the
115 forest herding routes are relatively quiet. We examined the habitat preferences of five wild groups
116 of Barbary macaques in Morocco across four seasons. The study groups often encountered
117 shepherds and their dogs, and crossed roads. The use of roads by macaques can be both beneficial
118 and risky (Maréchal, MacLarnon, et al., 2016). Roads provide opportunities for macaques to acquire
119 calorie-dense human food from tourists, but also pose a serious threat from vehicle collisions
120 (Campbell et al., 2016; Campbell, 2019). Many large-brained, long-lived animals, like primates,

121 achieve local adaptation to rapidly changing environmental conditions through behavioral
122 flexibility. They are likely to have many opportunities for social learning, through long parent-
123 offspring association, and strong social-learning abilities (Schaik, 2013). This scenario applies to
124 our study species: Barbary macaques display high behavioral flexibility and great ecological
125 plasticity, adapting well across habitat types and seasons (Ménard, 2002). As such, we hypothesized
126 that macaques would display spatial and temporal flexibility in the use of their home ranges, based
127 on a cost/benefit analysis of the different areas used, or available for use. We analyzed how these
128 preferences related to the type and intensity of human activity within their home ranges, habitat
129 productivity, forest cover, slope, and position within the home range. We predicted that macaques
130 (1) would avoid risky areas, that is, herding routes where sheep dogs are abundant and escape
131 possibilities scarce (because of the absence of tree cover) and (2) would do so especially at high-
132 risk times (e.g. when herding routes are most heavily used – spring and summer). We also predicted
133 that macaques (3) would use the most profitable areas within their home ranges (e.g. roads, or
134 highly productive areas) and (4) particularly so when the potential benefits outweigh the risks, i.e.
135 when natural food is scarce.

136

137 **METHODS**

138 **Study area and subjects**

139 Our study was conducted in Ifrane National Park (INP) in the Middle Atlas Mountains of Morocco
140 (33°25'N, 005°10'W), from May 2013 to April 2014 (Fig. 1). The study area is covered by
141 deciduous Atlas cedar and mixed oak (*Quercus ilex* and *Quercus faginea*) forest with patches of
142 open scrubland.

143 We collected data on 54 adult (>4 years old) and 17 subadult monkeys from five groups of
144 Barbary macaques (Supplementary Material S1). The study animals were tolerant of researchers
145 (Bejder et al., 2009) and individually identified. Monkeys in one group received food from tourists

146 and local people at least once per day; the other groups were occasionally provisioned by tourists.
147 Data collection was entirely non-invasive. We complied with the International Primatological
148 Society's ethical guidelines for primate field research and received research permission (number
149 08/2013) from the Haut Commissariat des Eaux et Forêts et à la Lutte Contre la Désertification of
150 Morocco.

151

152 **Data collection**

153 *Home range estimation*

154 We estimated the home ranges of the study groups using Brownian Bridge Movement Models
155 (BBMM). This method accounts for the temporal correlation of locations recorded over brief
156 intervals, and incorporates known estimates of location error to predict trajectories of movement
157 between successive locations (Horne et al., 2007). This quantifies the utilization distribution (UD)
158 parameter of a group/animal based on its path rather than on individual points. Behavioral
159 observations were carried out for five to seven days each week from 06:00 to 19:00 (mean daily
160 observation hours \pm SE = 9.20 \pm 0.19). Each day, different teams of observers followed between
161 one and four (usually three) groups, simultaneously. We took global positioning system (GPS)
162 readings every 60 minutes at the center of the group using a Garmin etrex Summit HC (©Garmin).
163 We estimated the center of the group as the point in the middle of an imagined ellipse around all
164 visible group members. This yielded a total of 1935 GPS locations over 171 working days (total
165 number of GPS locations per group: Blue group = 355, Green group = 499, Purple group = 468,
166 Red group = 230, Yellow group = 383). We analyzed home range data in R version 3.5.3 (R Core
167 Team, 2019) using the BBMM package (Nielson & Sawyer, 2013). Each group's home range
168 overlapped with at least one other group, was crossed by a road, and included at least one type of
169 human structure (i.e., picnic area, water treatment plant, livestock stable and/or a small farm) (Fig.
170 1).

171

172 *Anthropogenic activity*

173 To estimate the changing seasonal intensity of human road and herding route use, we placed fifteen
174 900 m straight-line transects throughout the study area, according to a stratified random sampling
175 design (Ganzhorn, 2003). The original sampling area was based on home range data for two
176 macaque groups identified during previous studies in the area (The Barbary Macaque Project,
177 University of Lincoln, UK). The furthest extent of these groups' home ranges determined the
178 easterly and westerly extent of the study area, and the edge of the forest fragment determined the
179 northerly and southerly extent. We determined the transects spacing and orientation using the
180 software Distance 6.0 release 2 (Thomas et al., 2010). Any transects that were later found to be
181 outside the home ranges of our five study groups were dropped. We walked the transects at
182 different times of day, starting at a different end each time, once every 2 weeks, and recorded all
183 sightings of humans, livestock, dogs, and motor vehicles (hereafter HRS, 'human related sighting').
184 We used identifiable features (e.g. clothes worn by shepherds or dog breeds) of each HRS to
185 distinguish them and avoid repeat recordings within transects. If we encountered the same HRS
186 more than once on the same transect within the same sampling period, we only recorded the first
187 sighting. We walked each transect 24 times (three transects were walked 23 times), for a total of
188 21.6 km and 20.7 km, respectively, per transect. The total transect distance walked was 2222.1 km
189 and the total observation time was 312.15 hours. Where transects crossed a road, we recorded the
190 number of vehicles that passed within five minutes of reaching it. We conducted 307 road counts
191 for a total observation time of 25.6 hours.

192

193 *Ecological data*

194 We derived Normalized Difference Vegetation Index (NDVI) values from Landsat 8 satellite
195 images of the study area, obtained from the USGS EarthExplorer website (U.S. Geological Survey

196 Earth Resources Observation and Science Center, 2012). These data were used to assess ecological
197 productivity by season (Myneni et al., 1995; Wang et al., 2005). Monthly NDVI rasters were the
198 mean of two satellite images per month, and seasonal NDVI rasters were the mean of three monthly
199 rasters per season. NDVI quantifies the density of plant growth and is calculated by comparing the
200 quantities of visible and near-infrared light reflected by vegetation. Unhealthy or sparse vegetation
201 reflects more visible light and less near-infrared light than thriving or dense vegetation.

202

203 **Data Analysis**

204 We used a resource selection function (RSF) to examine the predicted probability of use (PPU) of
205 an area by a group. A RSF is defined as any function that yields values proportional to the
206 probability of use of a resource unit by an organism (Manly et al., 2002). The units being selected
207 by animals (e.g. pixels of land) are conceived as resources. Predictor variables associated with these
208 resource units may be ‘resource’ variables or covariates of the resources, e.g. elevation or human-
209 disturbance. Logistic regression is commonly used to estimate habitat selection models with used
210 units (e.g. pixels of land in a geographic information system (GIS) model) characterized as
211 1, and unused (or available) units characterized as 0 (Boyce et al., 2002). We measured resource
212 use and availability separately for each group (Thomas & Taylor, 1990). We defined the available
213 area as that within a group’s 95% BBMM home range. To assess the relative influence of
214 anthropogenic, natural, and social landscape characteristics on the probability of a group using an
215 area, we included nine variables (Table 1) and two interaction terms (detailed below) as predictors
216 in the RSF.

217

218 *Anthropogenic features*

219 To analyze whether macaques altered habitat selection in relation to anthropogenic features, we
220 calculated the distance from herding routes and roads to every macaque location (used and

221 available), using the ‘Proximity (Raster Distance)’ tool in the SAGA (2.3.2) toolbox in QGIS 3.6.0
222 (Open Source Geospatial Foundation, 2019). We added the length of herding routes and roads per
223 km² within each group’s home range to the RSF as control variables to account for the differing
224 densities of anthropogenic features and undisturbed areas experienced by each group. Because the
225 intensity of herding route and road use by humans vary throughout the year (largely in line with
226 temperature, snowfall, and thus accessibility), we included interaction terms between distance to
227 herding routes and season, and distance to roads and season to examine whether macaques employ
228 temporal as well as spatial habitat selection in response to anthropogenic features. We used general
229 linear models to compare herding route activity and traffic volume by season, and Post hoc Tukey’s
230 least significance difference (LSD) tests to compare activity/volume between seasons.

231

232 *Natural landscape features*

233 Barbary macaques are known to avoid open areas, due to a lack of opportunities to climb trees when
234 threatened by dogs or other predators (Ménard, 2002; Ciani et al., 2005; Maréchal, Semple, et al.,
235 2016; Waterman, 2016). Therefore, we created a digitized map of forest cover type, collapsed into
236 three classes: dense (50%-100% tree cover), moderate (1%-49% tree cover), and open (no tree
237 cover). We estimated cover type from a satellite map of the study area and ground-truthed using
238 canopy cover, undergrowth density and abundance data, and routine mapping data collected during
239 the study. Next, we analyzed the effect of food distribution on habitat use (Lima & Dill, 1990). For
240 this purpose, we averaged NDVI cell values (cell size 30m²) by season to create productivity raster
241 maps of the study area (one for each of our five study seasons). The NDVI values of all used and
242 available points were drawn from the appropriate raster, i.e. the seasonal raster in which the data
243 were collected. We used a general linear model to compare NDVI values by season, and post-hoc
244 Tukey’s LSD tests to compare NDVI between seasons. Because Barbary macaques live in a
245 mountainous habitat, we derived slope data from Advanced Spaceborne Thermal Emission

246 Reflection Radiometer (ASTER) - Global Digital Elevation Model (GDEM) data (obtained from the
247 USGS Earth Data website; U.S. Geological Survey, 2015), and incorporated it as a 1 arc-second
248 (approximately 30m²) grid (Toutin, 2008). High values correspond to steep gradients, low values to
249 shallow gradients, and zero values to primarily flat terrain.

250

251 *Social features*

252 Barbary macaque home ranges commonly overlap . Therefore, we used the ‘kerneloverlap’
253 command of the ‘adehabitatHR’ (Calenge, 2006) package in R version 3.5.3 to calculate 95%
254 utilization distribution overlap index values (UDOI) for each pair of groups, across the entire study
255 period, and by season (Fieberg & Kochanny, 2005). Values of UDOI < 1 indicate less overlap
256 relative to uniform space use, whereas values of UDOI > 1 indicate higher than normal overlap
257 relative to uniform space use. Because home range overlap can affect the intensity and timing of use
258 of an area (R. W. Wrangham et al., 2007), we included a binary measure (overlapping or not) to the
259 RSF to describe whether each used or available location was within the 95% BBMM home range of
260 more than one group. This was calculated by season for each group (spring 2013 through spring
261 2014), e.g. locations recorded in summer 2013 were only tested for overlap with the home ranges of
262 other groups derived from their summer 2013 home range estimates. We used linear mixed models
263 (LMMs), including random intercepts for group and season, to compare NDVI values, the distance
264 to herding routes, and the distance to roads by overlap status (overlapping or not). No post-hoc tests
265 were required to interpret these results.

266

267 *Statistical models*

268 We constructed a GIS model of the study area using QGIS. We imported GPS locations and
269 generated 10 random locations (within the appropriate home range) per observed location to create
270 an ‘available’ sample. We restricted observed and random locations to within 95% BBBM home

271 ranges because most macaque activity was restricted to these areas and it is difficult to objectively
272 define an ‘available’ area outside a group’s home range (Wilson, Gilbert-Norton, & Gese, 2012).

273 We used logistic regression to estimate a RSF by comparing anthropogenic, natural and
274 social landscape features of used and available locations for each individual. We used a generalized
275 linear mixed model with binary response variable (1 = used, 0 = available but unused), binomial
276 error distribution, and logit link to evaluate habitat selection. We included a random intercept for
277 group to account for correlation of habitat use within group, and uncorrelated random intercepts and
278 slopes for distance to herding routes, and distance to roads within group. These were included to
279 account for the fact that groups had varying baselines of distance from these features, i.e. some
280 groups had little un-disrupted space compared to others. Moreover, we used this method to account
281 for the fact that groups would likely respond to herding route and road proximity differently (in
282 terms of selecting/avoiding areas), e.g. some groups may select roadsides whilst others avoid them.
283 We fitted the RSF using the ‘glmer’ command of the ‘lme4’ package (Bates, 2010) in R version
284 3.5.3 (R Core Team, 2019) and estimated the GLMM parameters using Laplace approximation
285 (Bolker et al., 2009). We used a full model approach throughout. We checked the model for
286 collinearity between predictors using generalized variance inflation factors , which indicated no
287 issues of collinearity (average $GVIF^{1/(2*Df)}$ score = 1.31, maximum $GVIF^{1/(2*Df)}$ score =
288 2.00) (Fox & Monette, 1992). We standardized all distance-based variables.

289 Because of the difficulty in defining the denominator degrees of freedom in mixed models
290 (Luke, 2017) (i.e. does one count the number of observations, or the number of subjects and/or
291 items, or the number of random effects, or some combination of these?), we determined the
292 significance of the fixed effects using likelihood-ratio tests (“mixed” function in the package “afex”
293 (Singmann et al., 2017)). We fitted full and restricted models (models in which the parameter of
294 interest, the fixed effect, are withheld, i.e. fixed to 0) and based test statistics on comparisons of the
295 full model with the restricted models. The significance of the likelihood ratio test statistic is

296 calculated using a χ^2 distribution with the appropriate degrees of freedom. All statistical tests were
297 two-tailed with α set to 0.05. We examined the residuals of all relevant models for normality and
298 homoscedasticity and detected no problems. We carried out model validation using k -fold ($k=10$)
299 cross-validation, testing predictive performance using area under the curve (AUC) (Boyce et al.,
300 2002). We classified models as: 1) non-informative (AUC=0.5); 2) less accurate ($0.5 < \text{AUC} \leq 0.7$); 3)
301 moderately accurate ($0.7 < \text{AUC} \leq 0.9$); 4) highly accurate ($0.9 < \text{AUC} < 1$); and 5) perfect (AUC=1)
302 (Swets, 1988). For further model validation we also calculated the GLMM dispersion parameter
303 when relevant. For a step-by-step summary of the data analysis procedure see Supplementary
304 Material S2.

305

306 **RESULTS**

307 Barbary macaques showed temporal and spatial habitat selection in relation to anthropogenic
308 features (Tables 2-4): They avoided herding routes and selected/avoided areas close to roads, but
309 this behavior varied seasonally. They also preferred overlapping areas of their home ranges, and
310 avoided open areas. AUC values indicated that the RSF model was ‘less accurate’ and close to
311 being classified as ‘moderately accurate’ (AUC=0.66). The GLMM dispersion parameter value was
312 1.05.

313 Mean NDVI, herding route activity, and traffic volume differed significantly between
314 seasons (NDVI general linear model: $F(3,20720)=7611.9$, $p < 0.001$, marginal $R^2=0.52$. Herding
315 route activity general linear model: $F(3,20720)=762.1$, $p < 0.001$, marginal $R^2=0.10$. Traffic volume
316 general linear model: $F(3,20720)=210.7$, $p < 0.001$, marginal $R^2=0.03$). Post hoc LSD tests showed
317 that mean NDVI, herding route activity, and traffic volume differed significantly between all four
318 seasons (all $p < 0.001$). Most notably, in autumn and winter, NDVI and herding route activity were
319 lowest whilst road traffic volume peaked (Fig. 2a, b, c).

320 Median NDVI, distance from herding routes, and distance from roads also differed
321 significantly between areas of exclusive and overlapping home range use (overlaps derived using
322 seasonal home range estimates, see above; NDVI linear mixed model: $F(1,1930.2)=4.0181, p=0.04$;
323 distance to herding routes linear mixed model: $F(1,1928.8)=11.978, p<0.001$; distance to roads
324 linear mixed model: $F(1,1931.9)=34.921, <0.0001$; Fig. 3a, b, c).

325 The UDOI of macaque 95% home ranges indicated that all pairs of groups showed less
326 overlap than would be expected from wholly overlapping distributions at 95% contour levels (Table
327 5). In autumn and winter only the green-purple group pair showed any overlap. The winter UDOI
328 was the highest recorded throughout the study.

329 Overall, macaques selected dense and moderately forested areas, and avoided open areas.
330 They preferred areas that overlapped the home ranges of neighboring groups. They avoided herding
331 routes in summer and avoided areas close to roads in spring. The predicted probability of use (PPU)
332 of areas close to herding routes in summer was almost half that of the other seasons. However, they
333 used areas close to roads more extensively in autumn and winter months. The PPU of areas close to
334 roads in autumn and winter was approximately double that of spring, and a third greater than in
335 summer (Fig 4a and 4b).

336

337 **DISCUSSION**

338 Our study showed that Barbary macaques navigate their environment strategically in relation to
339 human activity, to balance food acquisition and risk avoidance. As predicted, macaques consistently
340 avoided open areas. This is likely a response to the limited escape possibilities, given that macaques
341 usually climb trees to avoid dogs, which are their primary predators at this study site (Waterman,
342 2016). This may explain why macaque density is lowest in open grassland areas, even though this
343 species feeds extensively on grass (Ménard, 2002; Ciani et al., 2005). The distribution of dogs
344 affects the use of space of pudu deer (*Pudu puda*) via both predation and avoidance mechanisms

345 (Silva-Rodríguez & Sieving, 2012); the space use patterns of Barbary macaques may be affected in
346 a similar way. Animals can assess the levels of predation risk in different parts of their habitat and
347 respond to them by modifying their spatial and temporal use of their home range and/or by
348 modifying behavior (e.g. increasing vigilance in high-risk areas). The spatial distribution of
349 predation risk perceived by a population of animals can be described as a “landscape of fear”
350 (Laundré, Hernández, & Ripple, 2010). In such a “landscape of fear,” animals should avoid areas
351 where the risk of encountering predators (i.e. the “degree of fear”) is highest, unless using those
352 areas yield high rewards. For example, areas with high densities of predators may contain a large
353 amount of food if potential preys rarely feed in those areas. In human-dominated landscapes, human
354 disturbance may have a larger effect on the behavior of wild animals than their natural predators
355 (Ciuti et al., 2012). In the case of Barbary macaques, the direct effect of human disturbance is
356 amplified by the disturbance resulting from the presence of domestic dogs. Thus, for Barbary
357 macaques the “landscape of fear” can be determined by both the presence of predators (dogs) and of
358 human activities.

359 Macaques preferentially used areas of home range overlap. It seems unlikely that macaques
360 purposely select overlapping areas in general, but rather that they choose the most productive areas
361 available to them. Given that these areas are on the periphery of groups’ home-ranges, multiple
362 groups may try to make use of them. This usually takes place at different times, although numerous
363 intergroup encounters were observed in direct relation to contested food sources within overlapping
364 areas. This was particularly true during winter, when areas that contained hawthorn bushes and
365 berries (*Crataegus* spp.) were contested by two of the study groups almost daily for several
366 consecutive weeks. Considered together, the preference for overlapping areas indicated by the RSF,
367 and the relatively low UDOI values (Table 5) support the idea that macaques may attempt to use
368 overlapping areas at different times. The UDOI takes into account the intensity of use of an area (by
369 both groups) when assessing the extent of home-range overlap. This may be why the RSF indicates

370 a preference for overlapping areas, despite the fact that the UDOI values indicate only limited
371 overlap. Although there may be few areas of actual overlap (low UDOI values, but see winter 2013-
372 2014), groups showed a strong preference for these, and seemed willing to share them, and/or
373 compete over them. Neighboring groups of Barbary macaques are known to use the same sleeping
374 sites located in areas of home range overlap and compete for these sleeping sites (Campbell,
375 Tkaczynski, Mouna, et al., 2018). It is also possible that the preference for overlapping areas was
376 driven by the large amount of time that some of the study groups spent waiting for provisioning by
377 the road within the shared portion of their home ranges. This is supported by the results of the
378 analysis comparing distance from roads by overlap status (see above): overlapping areas were, on
379 average, closer to roads than non-overlapping areas (Fig 3c).

380 These results suggest that macaques choose the most profitable areas available to them, even
381 if they overlap the home ranges of other groups. Few studies have focused on the effects of
382 neighboring groups on the behavior of primates, but in those that have, overlapping zones are
383 routinely reported to be under-used (R. W. Wrangham et al., 2007). A limited number of studies
384 have recorded primates making use of overlapping home range areas, but no consistent pattern of
385 use emerges. Verreaux's sifaka (*Propithecus verreauxi*) use overlapping zones, but their
386 behavioral patterns do not differ significantly from those observed in core areas (Benadi, Fichtel, &
387 Kappeler, 2008). Aggressive intergroup encounters in some other species such as chimpanzees,
388 Diana monkeys (*Cercopithecus diana*), and Stuhlmann's blue monkeys (*Cercopithecus mitis*) can
389 result in the extensive wounding and even death of individuals (McGraw, Plavcan, & Adachi-
390 Kanazawa, 2002; Payne, Lawes, & Henzi, 2003; R. W. Wrangham, Wilson, & Muller, 2006).
391 However, such lethal aggression between groups is rare in Barbary macaques (Deag, 1975). Thus,
392 Barbary macaques may perceive overlap zones as both high reward and low risk areas. This
393 hypothesis should be tested by examining, for example, duration of stay in overlap areas, selection
394 of food resources and of sleeping sites.

395 The probability of macaques using areas close to herding routes varied seasonally. The PPU
396 in summer was approximately half that of spring, autumn, and winter (Fig 4a). This seasonal
397 reduction may be explained by the increased probability of encountering predators, particularly
398 dogs, in these areas during the busiest herding periods, i.e. the summer months. The probability of
399 macaques using areas close to roads also varied seasonally. The PPU in autumn and winter was
400 approximately double that of spring, and a third greater than that of summer (Fig 4b). In spring,
401 natural food (herbs, grasses, seeds etc.) is relatively abundant; however, the availability of natural
402 food in the study area declines steadily throughout the year as temperatures drop and winter
403 snowfall makes foraging difficult and energetically costly (Majolo et al., 2013). Winter is a time of
404 energetic deficit for Barbary macaques (Campbell, Tkaczynski, Lehmann, et al., 2018; Campbell,
405 Tkaczynski, Mouna, et al., 2018). This may shift the cost/benefit balance by making access to
406 energy-rich foods from tourists more valuable in autumn and winter: 38% of human-macaque
407 provisioning encounters in our study occurred within 20 m of a road (Waterman, 2016). This
408 consideration of energy balance affects selection of sleeping sites by Barbary macaques (Campbell,
409 Tkaczynski, Mouna, et al., 2018), and also their social behavior (Campbell, Tkaczynski, Lehmann,
410 et al., 2018), so diurnal habitat use (use of roads) may be another strategy to maximize energy
411 balance.

412 The benefit of accessing calorie-dense human food during food shortages may exceed the
413 cost associated with the risk of being injured/killed by road traffic (Campbell et al., 2016;
414 Campbell, 2019). Similar trade-offs in the use of roads have been observed in other primate species:
415 Long-tailed macaques (*M. fascicularis*) habitually consume human food near roads, and both the
416 number of groups and group size increase with proximity to roads and human settlements, despite
417 35 road-accident deaths (2.4% of the population) in one year (Mun, 2014). The combination of
418 roads and human provisioning is particularly deleterious for wild animals, since the risk of

419 injuries/death, infectious human diseases, and diseases linked to a hyper-caloric diet is high, and its
420 reduction/avoidance should be a top priority for any conservation efforts.

421 Chimpanzees adjust their behavior according to variations in the perceived risk of road
422 injuries, as they wait longer to cross wide roads than narrow ones, and wait longer on wide roads as
423 traffic volume increases (Hockings, Anderson, & Matsuzawa, 2006). Barbary macaques appear to
424 follow a similar strategy: when roads are busy (and natural food is scarce) the potential rewards of
425 provisioning may outweigh the perceived risks; when roads are less busy (and/or natural food is
426 abundant) the potential rewards may be low enough that even a reduced risk is no longer worth the
427 reward. The fact that road traffic was highest in autumn (followed closely by winter) (Fig 2b), and
428 that 40% of our recorded human provisioning events occurred during winter (Waterman, 2016),
429 supports the idea that macaques engage in fine-scale behavioral adjustment in response to varying
430 levels of perceived risk and reward.

431 The impact of human activity on the behavior of the Barbary macaque varies on a spatio-
432 temporal scale. The few remaining populations of this species occur in areas of relatively low
433 human density but high human impact, due to logging, farming and grazing (Scheffrahn et al.,
434 1993; Ciani et al., 2005). As such, macaques are increasingly unable to avoid contact with humans
435 and must cope with greater constraints on their habitat choices. Macaques appear to deal with these
436 challenges in a very flexible way. They minimize risk by avoiding herding routes when they are
437 most trafficked (presumably to minimize the possibility of encountering dogs and humans), and
438 maximally exploit the potential of being provisioned near roads as a high-calorie food source. They
439 also preferentially use overlapping areas of their home ranges. However, this apparent preference
440 could be interpreted both as a response to the declining availability of suitable habitat/forage,
441 forcing macaque groups closer together, and/or a result of direct competition over particularly
442 profitable areas, e.g. roadside provisioning spots, patchy winter food sources, sleeping sites. Thus,

443 even groups that only occasionally receive food from humans show a considerable degree of
444 habituation to human presence in the Middle Atlas Mountains of Morocco.

445 The opportunity exists to ‘use’ such habituation to develop eco-tourism programs that could
446 benefit both the survival of this population and the local economy. However, our data also show
447 that human activity in the area can significantly affect macaque behavior and habitat choices, with
448 potentially dramatic consequences for their survival. Our conclusions are limited by the absence of
449 a fine-scale, on-the-ground measure of macaque food availability that spans the entire study area.
450 Although the NDVI values matched our ground productivity samples well, macaques are highly
451 flexible foragers and many of their preferred food items may not be well represented by NDVI, e.g.
452 acorns, fungi, and arthropods. Despite the significant logistical challenge of sampling ground-
453 productivity, at a fine scale, across such a large study area, future work could benefit from a full-
454 coverage ecological ground-sampling grid. This would allow us to more accurately assess the
455 influence of anthropogenic activity on macaque habitat selection, taking in to account the local
456 availability of preferred macaque food items, and water sources.

457 Our study has identified two key spatio-temporal parameters that macaques ‘prioritize’
458 when selecting areas within their home ranges. This knowledge should be used to implement
459 guidelines that sustain both a viable population of macaques and the local economy (Russon &
460 Wallis, 2014). Due to the varying land uses, motivations, and social norms of people in contact with
461 the macaques, mitigating human-wildlife conflict in the region will require a holistic approach by
462 multiple stakeholders, including law enforcement, government, communities, and pastoralists. We
463 therefore recommend a baseline socio-demographic study of these stakeholders to identify their
464 attitudes, values, and behaviours. Rigorous social scientific survey design is essential in guiding,
465 monitoring and evaluating any social interventions effectively (St. John et al., 2014; Steg, 2016;
466 Rare and The Behavioural Insights Team, 2019).

467 Tourist sites could be developed into sustainable ecotourism programmes to minimise their
468 effect on macaque stress levels (Maréchal et al., 2011). Education stands in the area could provide
469 an opportunity to empower locals to become ambassadors for macaque conservation, with the
470 support of NGO's and government. A team of local Community Scouts currently works in Ifrane
471 National Park to prevent poaching, feeding, and road deaths of Barbary macaques (Campbell et al,
472 in review). Understanding the spatio-temporal variation in the approach vs. avoidance of humans
473 and roads by macaques can help the management of human-macaque interactions by prioritizing the
474 time and locations to focus these efforts. Our results indicate that efforts to combat feeding and road
475 deaths could be prioritized during autumn/winter. Identifying priorities where efforts are likely to be
476 most effective, especially if resources and funding for conservation management are limited, can
477 benefit conservation efforts. In conclusion, our findings highlight the importance of protecting
478 natural foraging areas for wildlife, particularly in areas where they come into contact with humans,
479 and regulating areas where wildlife has access to human food.

480

481 **ACKNOWLEDGEMENTS**

482 We thank the Moroccan Haut Commissariat aux Eaux et Forêts et à la Lutte Contre le
483 Désertification for research permission (Authorisation Number 08/2013), and Professor Mohamed
484 Qarro for his help and support in the field. We are grateful to Ifrane National Park and the local
485 community for their support. We thank the following parks for a grant that funded this study: La
486 Montagne des Singes and La Foret des Singes (France), Affenberg Salem (Germany) and Trentham
487 Monkey Forest (Great Britain). We are grateful to Elina Rantanen, Brenda McGowan and two
488 anonymous reviewers for comments on an earlier draft of the manuscript. We thank Olivier
489 Mouchette, Barbora Kuběnová, Alice Marks, Vamsi Rani, Selma el Fassi Fihri, Camille Deman,
490 Callum Martin, Laura McHenry, Kevin Remeuf, Melanie LaCava, and Patrick Tkaczynski for their
491 help in data collection, and Corinne Bailey for advice on conservation strategies.

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- 678

679 Table 1. Predictors included in resource selection functions.

Characteristic	Variable description	Variable type	Range
Anthropogenic	Distance from herding route	Continuous	0 – 1595 m
	Distance from road	Continuous	0 – 1788 m
Natural	Forest cover	Discrete	open, moderate, dense
	Ecological productivity (NDVI)	Continuous	0.012 – 0.42
Social	Slope	Continuous	0.74 – 41.47
	Home range overlap	Discrete	not overlapping, overlapping
Temporal	Season	Discrete	spring, summer, autumn, winter
Control	Length of herding routes (per km ² of home range)	Continuous	0.23 – 2.84 km
	length of roads (per km ² of home range)	Continuous	0.63 – 1.65 km

680

681 Table 2. Results of the generalized linear mixed model. Statistically significant ($\alpha=0.05$) p -values are
 682 in bold and underlined.

Variable	Parameter			
	β	SE	Z	P
Intercept	-3.101	0.175	-17.757	<0.001
Cover-Dense	0.290	0.112	2.586	0.010
Cover-Open	-0.995	0.142	-6.998	<0.001
Home Range Overlap (1)	0.252	0.061	4.147	<0.001
Slope	-0.016	0.029	-0.547	0.584
Herding route density	0.056	0.148	0.379	0.704
Road density	-0.235	0.126	-1.86	0.0632
Productivity (NDVI)	0.081	0.058	1.393	0.163
Distance-from-herding route	-0.584	0.135	-4.33	<0.001
Season (Summer)	-0.110	0.070	-1.562	0.118
Season (Autumn)	0.027	0.090	0.295	0.768
Season (Winter)	0.078	0.119	0.659	0.510
Distance-from-road	-0.392	0.318	-1.233	0.218
Distance-from-herding route (Summer)	0.412	0.066	6.213	<0.001
Distance-from-herding route (Autumn)	0.022	0.092	0.235	0.814
Distance-from-herding route (Winter)	0.006	0.095	0.061	0.951
Distance-from-road (Summer)	-0.374	0.062	-6.008	<0.001
Distance-from-road (Autumn)	-0.620	0.091	-6.802	<0.001
Distance-from-road (Winter)	-0.435	0.088	-4.935	<0.001
Random effects	Variance		Std. deviation	
Group	0.076		0.275	
Group (Distance-from-herding route)	0.070		0.264	
Group (Distance-from-road)	0.486		0.697	

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684 Table 3: Results of the likelihood ratio test (type 3 tests) for the generalized linear mixed model.

685 Statistically significant ($\alpha=0.05$) p -values are underlined.

Variable	Parameters		
	df	Chisq	<i>P</i>
Cover	2	168.58	<u><0.0001</u>
Home range overlap	1	16.98	<u><0.0001</u>
Slope	1	0.30	0.580
Herding route density	1	0.14	0.710
Road density	1	2.64	0.100
Productivity (NDVI)	1	1.94	0.160
Distance-from-herding route	1	6.72	0.010
Season	3	2.69	0.440
Distance-from-road	1	3.80	0.050
Distance-from-herding route * Season	3	47.92	<u><0.0001</u>
Distance-from-road * Season	3	77.08	<u><0.0001</u>

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687 Table 4. Descriptive summary of statistically significant habitat selection preferences.

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Landscape feature	Response	Interpretation
Cover	Select areas of dense and moderate cover. Avoid open areas	Open areas lack cover; this limits escape possibilities, given that macaques usually climb trees to avoid dogs; their primary predators in this study site.
Home Range Overlap	Greater use of areas of home range overlap	Macaque home ranges overlap in key locations: areas of high natural productivity, and areas close to roads. Multiple groups inhabit a shrinking home range fragment and must share/compete for use of these profitable areas.
Herding Routes	Avoid in Summer	Macaques avoid areas used by local shepherds, to reduce the risk of being attacked by their dogs.
Roads	Avoid in Spring. Select in Autumn, and to a lesser extent in Winter	Macaques avoid roads in Spring when natural food is abundant, and approach roads in Autumn and Winter (as natural food availability declines and road traffic peaks) to increase the chances of being provisioned by tourists.

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692 Table 5. Values of the utilization distribution overlap index (UDOI) for Barbary macaque groups
 693 comparing home-range overlap between different groups and seasons.

Group Pairs	All Seasons	Spring 2013	Summer 2013	Autumn 2013	Winter 2013-2014	Spring 2014	694 695
Blue-Green	0	0	0.045	0	0	0	696
Blue-Purple	0	0	0	0	0	0	
Blue-Red	0.006	0.001	0.050	-	-	-	697
Blue-Yellow	0.095	0.201	0.208	0	0	0.186	
Green-Purple	0.153	0	0.057	0.012	0.655	0	698
Green-Red	0.042	0	0.072	-	-	-	
Green-Yellow	0	0	0.002	0	0	0	699
Purple-Red	0.366	0.552	0.118	-	-	-	700
Purple-Yellow	0	0.010	0	0	0	0	701
Red-Yellow	0.067	0.247	0.061	-	-	-	

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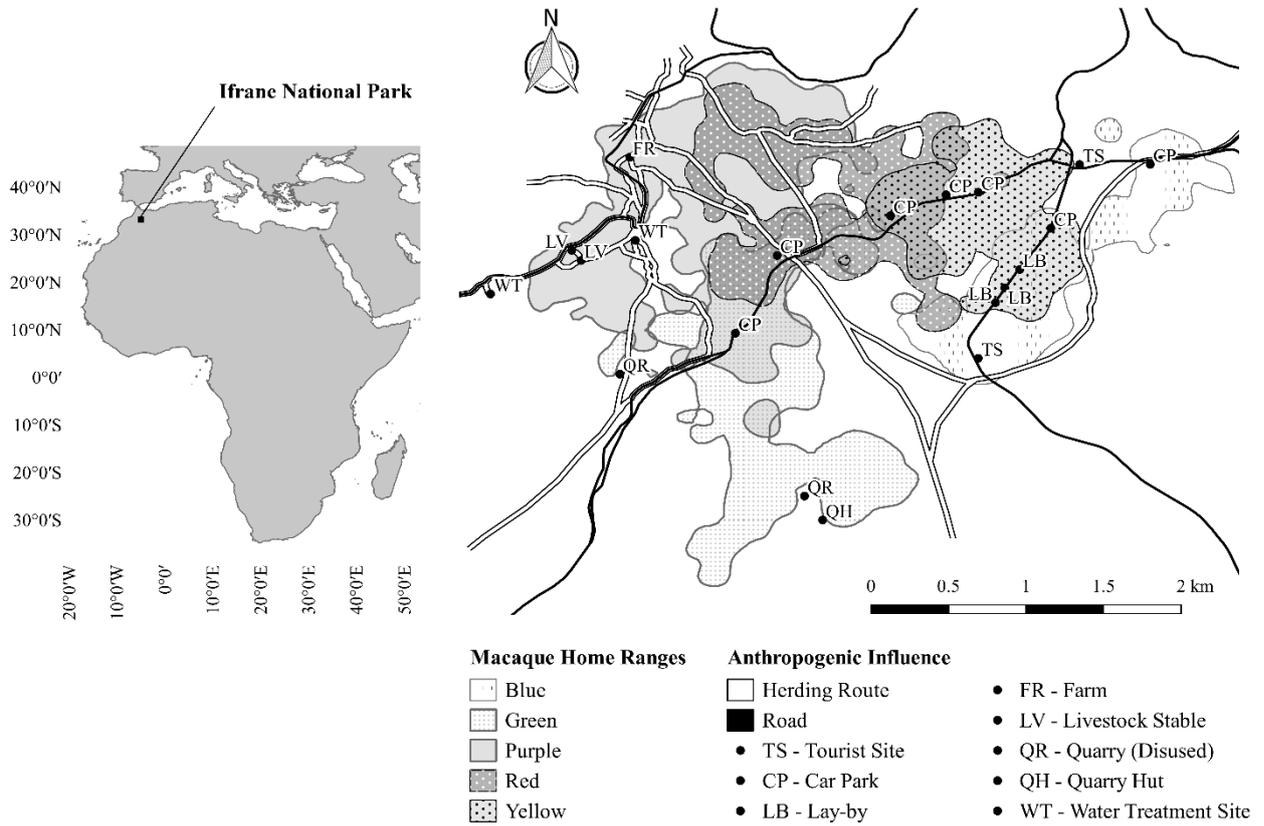
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717 Figures

718 Figure 1. Map showing the geographic location of the field site, the home range of the study groups
719 and the location of major anthropogenic features within the study site. Basemap source: Natural
720 Earth Data (2017)

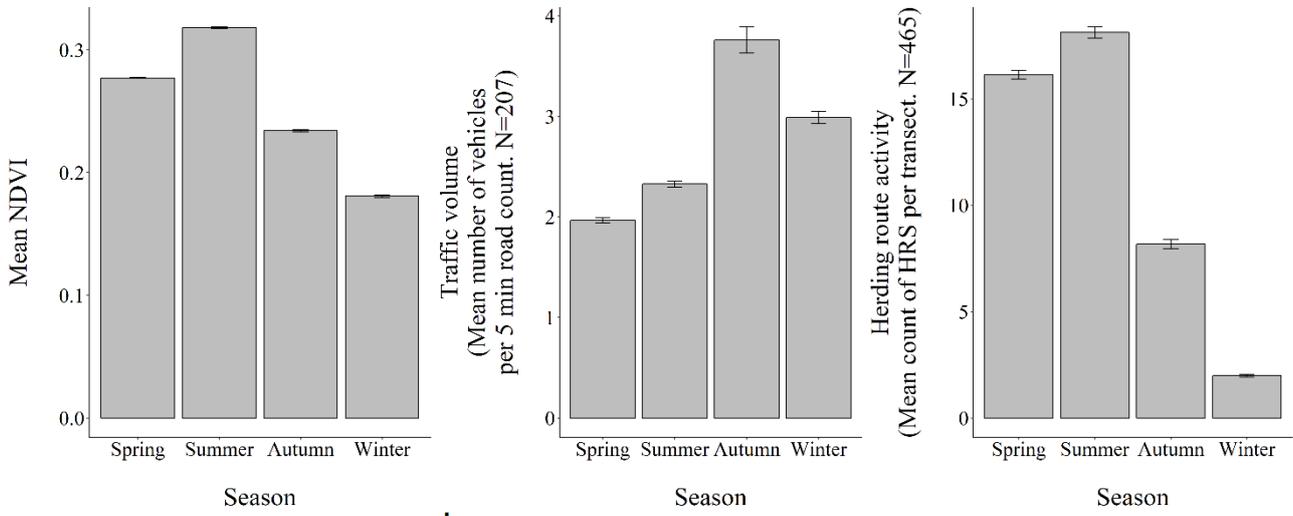


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723 Figure 2. Seasonal variation in (a) mean NDVI, (b) traffic volume, and (c) herding route activity.

724 All seasons differed significantly from each other. Error bars represent standard errors.



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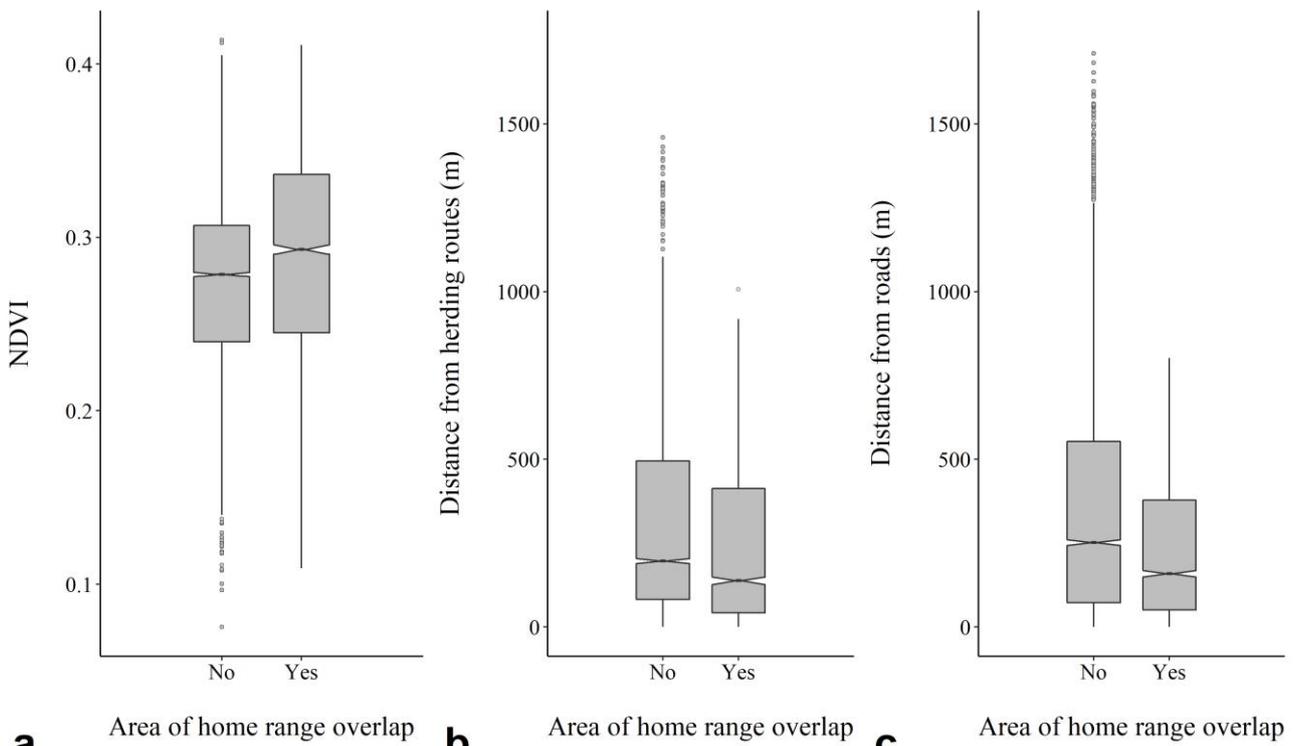
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727 Figure 3. Variation in median (a) NDVI, (b) distance from herding routes, and (c) distance from
728 roads by home range overlap. All variables differed significantly by home range overlap status.
729 Boxplots represent 25th and 75th percentiles, the inter-quartile range (IQR), center line indicates the
730 median, whiskers extend to the furthest data point that is within 1.5 times the IQR, and dots are
731 outliers. If the notches do not overlap, this is evidence that the medians are different.

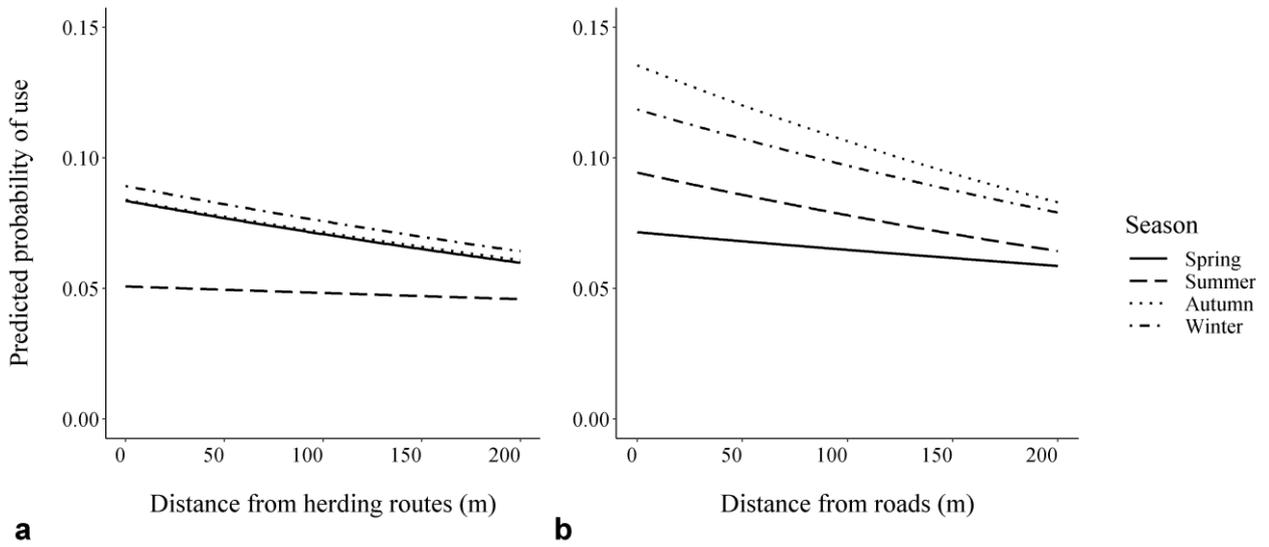


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735 Figure 4. Predicted probability of a location being 'used' in relation to (a) herding route and (b)
736 road proximity.



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