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

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22 Short title: Barbary macaque habitat selection

Abstract:

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

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

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

INTRODUCTION

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

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

Risk perception can significantly influence habitat use. Many species demonstrate great flexibility in adapting their behavior according to the risks (from natural predators or humans) associated with particular areas of their range, and at particular times (Frid & Dill, 2002; Hockings, Anderson, & Matsuzawa, 2012; Coleman & Hill, 2014; Bryson-Morrison et al., 2017; Nowak et al., 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 Commisariat 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

Anthropogenic activity

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

Ecological data

We derived Normalized Difference Vegetation Index (NDVI) values from Landsat 8 satellite 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 km^2 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 $30m^2$) 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

10

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 $30m^2$) 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<AUC≤0.7); 3)

301 moderately accurate (0.7<AUC≤0.9); 4) highly accurate (0.9<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

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

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

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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

REFERENCES

Bates, D. M. (2010). lme4: Mixed-effects modeling with R. Berlin.

Bejder, L., Samuels, A., Whitehead, H., Finn, H., & Allen, S. (2009). Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Mar. Ecol. Prog. Ser.* **395**, 177–185.

Benadi, G., Fichtel, C., & Kappeler, P. (2008). Intergroup relations and home range use in Verreaux's sifaka (*Propithecus verreauxi*). *Am. J. Primatol.* **70**, 956–965.

Beyer, H. L., Haydon, D. T., Morales, J. M., Frair, J. L., Hebblewhite, M., Mitchell, M., & Matthiopoulos, J. (2010). The interpretation of habitat preference metrics under use-availability designs. *Philos. Trans. R. Soc. B Biol. Sci.* **365**, 2245–2254.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**, 127–135.

Bouyer, Y., San Martin, G., Poncin, P., Beudels-Jamar, R. C., Odden, J., & Linnell, J. D. (2015). Eurasian lynx habitat selection in human-modified landscape in Norway: Effects of different human habitat modifications and behavioral states. *Biol. Conserv.* **191**, 291–299.

Boyce, M. S., Vernier, P. R., Nielsen, S. E., & Schmiegelow, F. K. A. (2002). Evaluating resource selection functions. *Ecol. Model.* **157**, 281–300.

Bryson-Morrison, N., Tzanopoulos, J., Matsuzawa, T., & Humle, T. (2017). Activity and Habitat Use of Chimpanzees (Pan troglodytes verus) in the Anthropogenic Landscape of Bossou, Guinea, West Africa. *Int. J. Primatol.* **38**, 282–302.

Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model.* **197**, 1035.

515   Campbell, L. A. D. (2019). Fostering of a wild, injured, juvenile by a neighbouring group:

516   implications for rehabilitation and release of Barbary macaques confiscated from illegal

517   trade. *Primates* **60**, 339–345.

518   Campbell, L. A. D., Tkaczynski, P. J., Lehmann, J., Mouna, M., & Majolo, B. (2018). Social

519   thermoregulation as a potential mechanism linking sociality and fitness: Barbary macaques

520   with more social partners form larger huddles. *Sci. Rep.* **8**, 6074.

521   Campbell, L. A. D., Tkaczynski, P. J., Mouna, M., Derrou, A., Oukannou, L., Majolo, B., & van

522   Lavieren, E. (2018). Behavioural thermoregulation via microhabitat selection of winter

523   sleeping areas in an endangered primate: implications for habitat conservation. *R. Soc. Open*

524   *Sci.* **5**, 181113.

525   Campbell, L. A. D., Tkaczynski, P. J., Mouna, M., Qarro, M., Waterman, J., & Majolo, B. (2016).

526   Behavioral responses to injury and death in wild Barbary macaques (Macaca sylvanus).

527   *Primates* **57**, 309–315.

528   Camperio Ciani, A., & Mouna, M. (2006). Human and environmental causes of the rapid decline of

529   Macaca sylvanus in the Middle Atlas of Morocco. *Barbary Macaque Biol. Manag. Conserv.*

530   *Nottm. Univ. Press Nottm.* 257–275.

531   Carne, C., Semple, S., MacLarnon, A., Majolo, B., & Maréchal, L. (2017). Implications of Tourist–

532   Macaque Interactions for Disease Transmission. *EcoHealth* **14**, 704–717.

533   Ciani, A. C., Palentini, L., Arahou, M., Martinoli, L., Capiluppi, C., & Mouna, M. (2005).

534   Population decline of Macaca sylvanus in the middle atlas of Morocco. *Biol. Conserv.* **121**,

535   635–641.

536   Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. A., & Boyce, M. S. (2012).

537   Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape

538   of fear. *PloS One* **7**, e50611.

Coleman, B. T., & Hill, R. A. (2014). Living in a landscape of fear: the impact of predation, resource availability and habitat structure on primate range use. *Anim. Behav.* **88**, 165–173.

Deag, J. M. (1975). A study of the social behaviour and ecology on the wild Barbary macaque, Macaca sylvanus (PhD Thesis). University of Bristol.

Donati, G., Campera, M., Balestri, M., Serra, V., Barresi, M., Schwitzer, C., Curtis, D. J., & Santini, L. (2016). Ecological and Anthropogenic Correlates of Activity Patterns in Eulemur. *Int. J. Primatol.* **37**, 29–46.

Ellis, E. C., & Ramankutty, N. (2008). Putting people in the map: anthropogenic biomes of the world. *Front. Ecol. Environ.* **6**, 439–447.

Fieberg, J., & Kochanny, C. O. (2005). Quantifying home-range overlap: the importance of the utilization distribution. *J. Wildl. Manag.* **69**, 1346–1359.

Fox, J., & Monette, G. (1992). Generalized Collinearity Diagnostics. *J. Am. Stat. Assoc.* **87**, 178–183.

Frid, A., & Dill, L. M. (2002). Human-caused Disturbance Stimuli as a Form of Predation Risk. *Conserv. Ecol.* **6**.

Ganzhorn, J. U. (2003). Habitat description and phenology. *Field Lab. Methods Primatol.* 40–56.

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science* **360**, 1232–1235.

Gilchrist, J. S., & Otali, E. (2002). The effects of refuse-feeding on home-range use, group size, and intergroup encounters in the banded mongoose. *Can. J. Zool.* **80**, 1795–1802.

Gill, J. A. (2000). Predicting the consequences of human disturbance from behavioral decisions. *Behav. Conserv.* 55–64.

Guillemain, M., Blanc, R., Lucas, C., & Lepley, M. (2007). Ecotourism disturbance to wildfowl in protected areas: historical, empirical and experimental approaches in the Camargue, Southern France. In *Biodivers. Conserv. Eur.* pp. 391–409. Springer.

564 Hanya, G., Ménard, N., Qarro, M., Ibn Tattou, M., Fuse, M., Vallet, D., Yamada, A., Go, M.,

565   Takafumi, H., Tsujino, R., Agetsuma, N., & Wada, K. (2011). Dietary adaptations of

566   temperate primates: comparisons of Japanese and Barbary macaques. *Primates* **52**, 187–198.

567 Hebblewhite, M., & Merrill, E. (2008). Modelling wildlife-human relationships for social species

568   with mixed-effects resource selection models: Mixed-effect resource selection models. *J.*

569   *Appl. Ecol.* **45**, 834–844.

570 Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2006). Road crossing in chimpanzees: A risky

571   business. *Curr. Biol.* **16**, R668–R670.

572 Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2012). Socioecological adaptations by

573   chimpanzees, Pan troglodytes verus, inhabiting an anthropogenically impacted habitat.

574   *Anim. Behav.* **83**, 801–810.

575 Horne, J. S., Garton, E. O., Krone, S. M., & Lewis, J. S. (2007). ANALYZING ANIMAL

576   MOVEMENTS USING BROWNIAN BRIDGES. *Ecology* **88**, 2354–2363.

577 Krief, S., Cibot, M., Bortolamiol, S., Seguya, A., Krief, J.-M., & Masi, S. (2014). Wild

578   chimpanzees on the edge: nocturnal activities in croplands. *PLoS One* **9**, e109925.

579 Laundré, J. W., Hernández, L., & Ripple, W. J. (2010). The landscape of fear: ecological

580   implications of being afraid. *Open Ecol. J.* **3**, 1–7.

581 Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review

582   and prospectus. *Can. J. Zool.* **68**, 619–640.

583 Lowry, H., Lill, A., & Wong, B. B. M. (2013). Behavioural responses of wildlife to urban

584   environments: Behavioural responses to urban environments. *Biol. Rev.* **88**, 537–549.

585 Luke, S. G. (2017). Evaluating significance in linear mixed-effects models in R. *Behav. Res.*

586   *Methods* **49**, 1494–1502.

587 Majolo, B., McFarland, R., Young, C., & Qarro, M. (2013). The Effect of Climatic Factors on the

588   Activity Budgets of Barbary Macaques (Macaca sylvanus). *Int. J. Primatol.* **34**, 500–514.

25

589   Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2002).

590   Resource selection by animals: statistical analysis and design for field studies. *Nord. Neth.*

591   *Kluwer*.

592   Maréchal, L., MacLarnon, A., Majolo, B., & Semple, S. (2016). Primates' behavioural responses to

593   tourists: evidence for a trade-off between potential risks and benefits. *Sci. Rep.* **6**, 32465.

594   Maréchal, L., Semple, S., Majolo, B., & MacLarnon, A. (2016). Assessing the Effects of Tourist

595   Provisioning on the Health of Wild Barbary Macaques in Morocco. (B.-S. Yue, Ed.)*PLOS*

596   *ONE* **11**, e0155920.

597   Maréchal, L., Semple, S., Majolo, B., Qarro, M., Heistermann, M., & MacLarnon, A. (2011).

598   Impacts of tourism on anxiety and physiological stress levels in wild male Barbary

599   macaques. *Biol. Conserv.* **144**, 2188–2193.

600   Martin, J., Basille, M., Van Moorter, B., Kindberg, J., Allainé, D., & Swenson, J. E. (2010). Coping

601   with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos*).

602   *Can. J. Zool.* **88**, 875–883.

603   McGraw, W. S., Plavcan, J. M., & Adachi-Kanazawa, K. (2002). Adult female Cercopithecus diana

604   employ canine teeth to kill another adult female C. diana. *Int. J. Primatol.* **23**, 1301–1308.

605   McKinney, T. (2011). The effects of provisioning and crop-raiding on the diet and foraging

606   activities of human-commensal white-faced Capuchins (Cebus capucinus). *Am. J. Primatol.*

607   **73**, 439–448.

608   Mehlman, P. T. (1984). Aspects of the ecology and conservation of the Barbary macaque in the fir

609   forest habitat of the Moroccan Rif Mountains. In *Barbary Macaque*. pp. 165–199. Springer.

610   Mehlman, P. T., & Parkhill, R. S. (1988). Intergroup interactions in wild Barbary macaques

611   (Macaca sylvanus), Ghomaran Rif mountains, Morocco. *Am. J. Primatol.* **15**, 31–44.

612   Ménard, N. (2002). Ecological plasticity of Barbary macaques (Macaca sylvanus). *Evol. Anthropol.*

613   *Issues News Rev.* **11**, 95–100.

614 Ménard, N., & Qarro, M. (1999). Bark stripping and water availability: a comparative study

615   between Moroccan and Algerian Barbary macaques (Macaca sylvanus).

616 Ménard, N., Rantier, Y., Foulquier, A., Qarro, M., Chillasse, L., Vallet, D., Pierre, J.-S., & Butet, A.

617   (2014). Impact of human pressure and forest fragmentation on the Endangered Barbary

618   macaque Macaca sylvanus in the Middle Atlas of Morocco. *Oryx* **48**, 276–284.

619 Mun, J. S. C. (2014). Ecology of Long-Tailed Macaques (Macaca fascicularis) and its Implication

620   for the Management of Human-Macaque Interface in Singapore 191.

621 Myneni, R. B., Hall, F. G., Sellers, P. J., & Marshak, A. L. (1995). The interpretation of spectral

622   vegetation indexes. *IEEE Trans. Geosci. Remote Sens.* **33**, 481–486.

623 Nielson, R. M., & Sawyer, H. (2013). Estimating resource selection with count data. *Ecol. Evol.* **3**,

624   2233–2240.

625 Nowak, K., Wimberger, K., Richards, S. A., Hill, R. A., & le Roux, A. (2017). Samango Monkeys

626   (Cercopithecus albogularis labiatus) Manage Risk in a Highly Seasonal, Human-Modified

627   Landscape in Amathole Mountains, South Africa. *Int. J. Primatol.* **38**, 194–206.

628 Oriol-Cotterill, A., Macdonald, D. W., Valeix, M., Ekwanga, S., & Frank, L. G. (2015).

629   Spatiotemporal patterns of lion space use in a human-dominated landscape. *Anim. Behav.*

630   **101**, 27–39.

631 Payne, H. F. P., Lawes, M. J., & Henzi, S. P. (2003). Fatal Attack on an Adult Female

632   Cercopithecus mitis erythrarchus: Implications for Female Dispersal in Female-Bonded

633   Societies. *Int. J. Primatol.* **24**, 1245–1250.

634 R Core Team. (2019). R: A Language and Environment for Statistical Computing. Vienna, Austria:

635   R Foundation for Statistical Computing.

636 Rare and The Behavioural Insights Team. (2019). Behaviour Change For Nature: A Behavioural

637   Science Toolkit For Practitioners. p. 84. Arlington, VA: Rare.

638 Russon, A. E., & Wallis, J. (2014). Primate Tourism. Cambridge University Press.

639 Schaik, C. P. van. (2013). The costs and benefits of flexibility as an expression of behavioural

640   plasticity: a primate perspective. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **368**, 20120339.

641 Scheffrahn, W., Ménard, N., Vallet, D., & Gaci, B. (1993). Ecology, demography, and population

642   genetics of Barbary macaques in Algeria. *Primates* **34**, 381–394.

643 Sih, A., Ferrari, M. C., & Harris, D. J. (2011). Evolution and behavioural responses to human-

644   induced rapid environmental change. *Evol. Appl.* **4**, 367–387.

645 Silva-Rodríguez, E. A., & Sieving, K. E. (2012). Domestic dogs shape the landscape-scale

646   distribution of a threatened forest ungulate. *Biol. Conserv.* **150**, 103–110.

647 Singmann, H., Bolker, B., Westfall, J., & Aust, F. (2017). afex: Analysis of Factorial Experiments.

648   R Package Version.

649 St. John, F. A. V., Keane, A. M., Jones, J. P. G., & Milner-Gulland, E. J. (2014). FORUM: Robust

650   study design is as important on the social as it is on the ecological side of applied ecological

651   research. (M. Cadotte, Ed.)*J. Appl. Ecol.* **51**, 1479–1485.

652 Steg, L. (2016). Values, Norms, and Intrinsic Motivation to Act Proenvironmentally. *Annu. Rev.*

653   *Environ. Resour.* **41**, 277–292.

654 Swets, J. A. (1988). Measuring the accuracy of diagnostic systems. *Science* **240**, 1285–1293.

655 Thomas, D. L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop,

656   J. R. B., Marques, T. A., & Burnham, K. P. (2010). Distance software: design and analysis

657   of distance sampling surveys for estimating population size. *J. Appl. Ecol.* **47**, 5–14.

658 Thomas, D. L., & Taylor, E. J. (1990). Study Designs and Tests for Comparing Resource Use and

659   Availability. *J. Wildl. Manag.* **54**, 322–330.

660 Toutin, T. (2008). ASTER DEMs for geomatic and geoscientific applications: a review. *Int. J.*

661   *Remote Sens.* **29**, 1855–1875.

662 Wang, Q., Adiku, S., Tenhunen, J., & Granier, A. (2005). On the relationship of NDVI with leaf

663   area index in a deciduous forest site. *Remote Sens. Environ.* **94**, 244–255.

664 Waterman, J. (2016). Human-macaque encounters in Ifrane National Park, Morocco. Behavioural,

665   spatial, and temporal coping strategies of the Barbary macaque (Macaca sylvanus)

666   (Unpublished MSc Thesis). University of Lincoln, Lincoln.

667 Waters, S., Harrad, A. E., Chetuan, M., Bell, S., & Setchell, J. M. (2017). Dogs Disrupting Wildlife:

668   Domestic Dogs Harass and Kill Barbary Macaques in Bouhachem Forest, Northern

669   Morocco 5.

670 Wilson, R. R., Gilbert-Norton, L., & Gese, E. M. (2012). Beyond use versus availability: behaviour-

671   explicit resource selection. *Wildl. Biol.* **18**, 424–430.

672 Woodroffe, R., Thirgood, S., & Rabinowitz, A. (2005). People and wildlife, conflict or co-

673   existence? Cambridge University Press.

674 Wrangham, R. W., Crofoot, M., Lundy, R., & Gilby, I. (2007). Use of Overlap Zones among

675   Group-Living Primates: A Test of the Risk Hypothesis. *Behaviour* **144**, 1599–1619.

676 Wrangham, R. W., Wilson, M. L., & Muller, M. N. (2006). Comparative rates of violence in

677   chimpanzees and humans. *Primates* **47**, 14–26.

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
	Slope	Continuous	0.74 – 41.47
Social	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 (α=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	

683

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

685 Statistically significant (α=0.05) *p*-values are underlined.

Variable	Parameters		
	df	Chisq	*P*
Cover	2	168.58	**<0.0001**
Home range overlap	1	16.98	**<0.0001**
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	**<0.0001**
Distance-from-road * Season	3	77.08	**<0.0001**

686

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.

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

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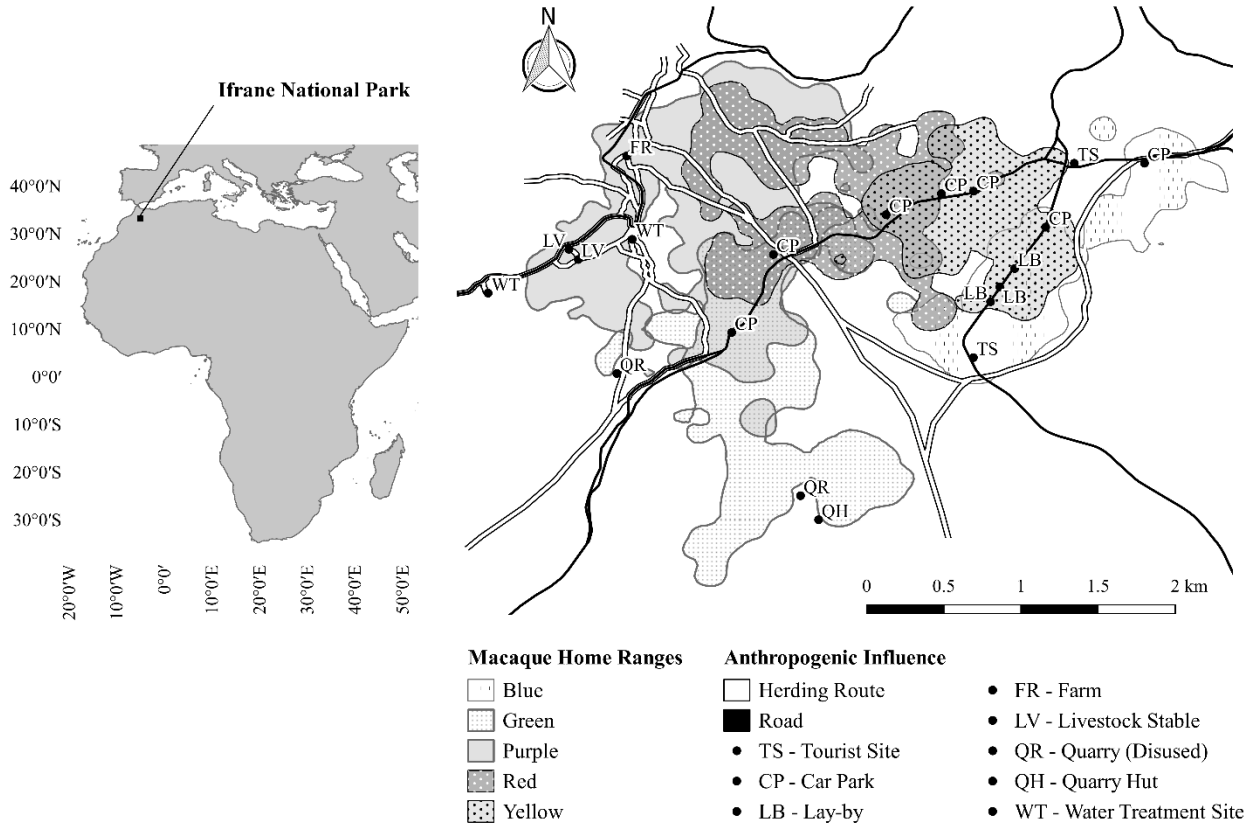
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718   Figure 1. Map showing the geographic location of the field site, the home range of the study groups

719   and the location of major anthropogenic features within the study site. Basemap source: Natural

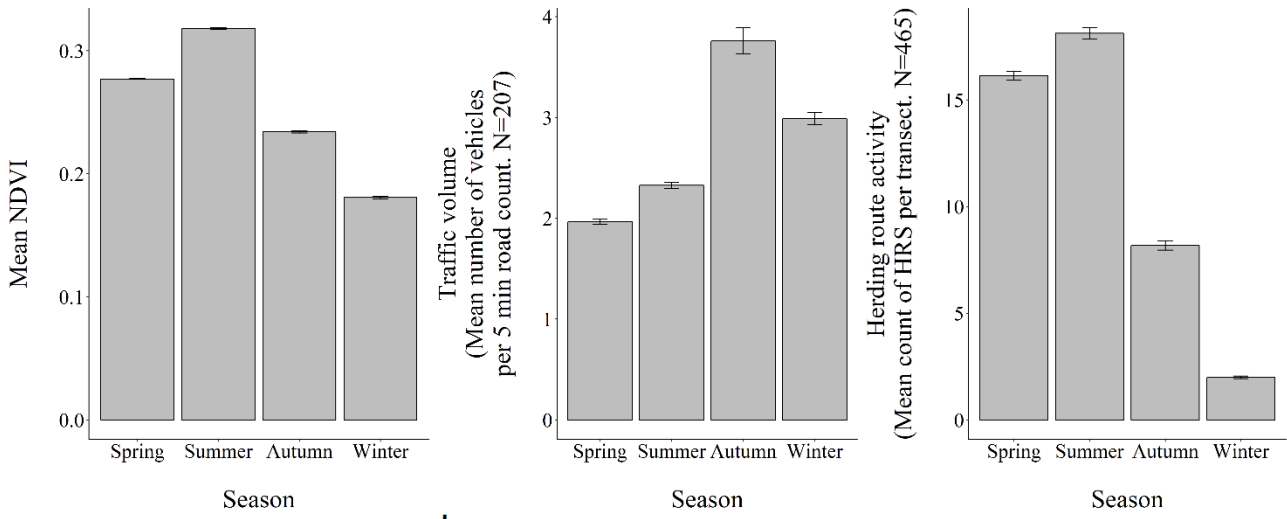720   Earth Data (2017)

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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.

725　　**a**　　　　　　　　　　　　　　**b**　　　　　　　　　　　　　　**c**

726

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

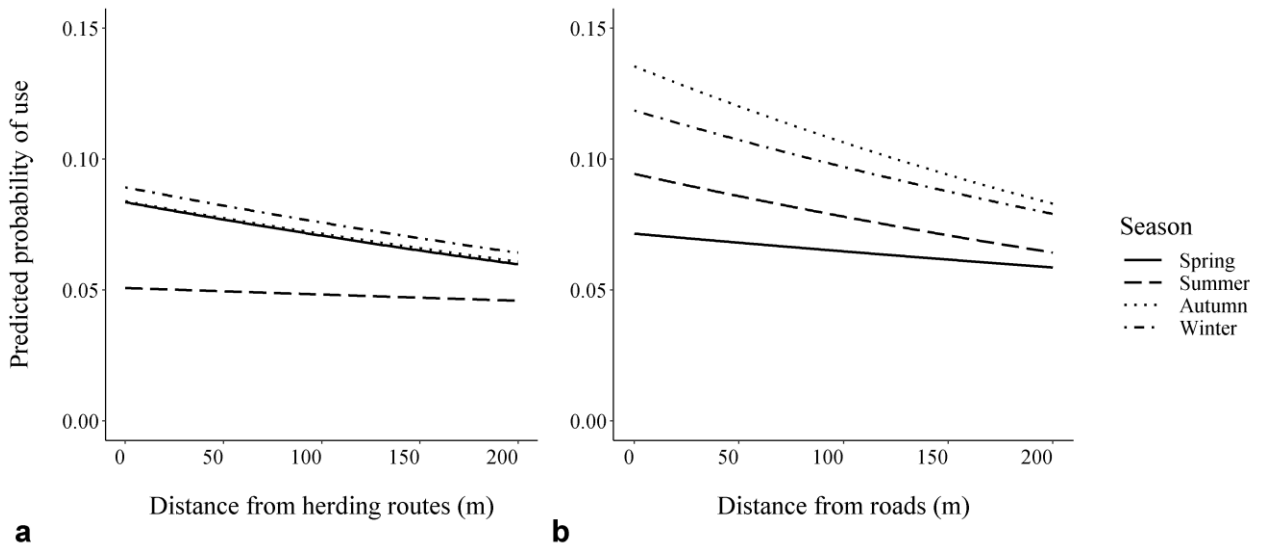731   outliers. If the notches do not overlap, this is evidence that the medians are different.

732   **a**   **b**   **c**
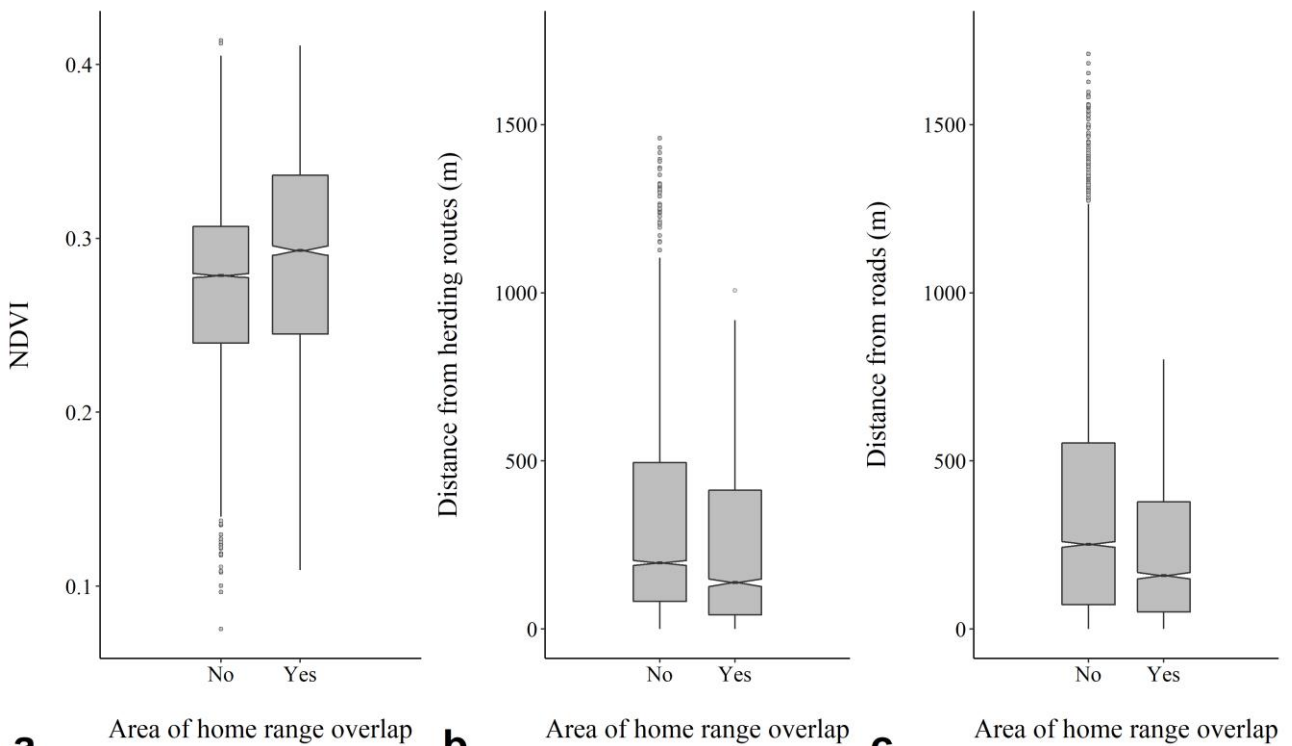
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735   Figure 4. Predicted probability of a location being 'used' in relation to (a) herding route and (b)

736   road proximity.

737   **a**   **b**