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## **Don't mind the cat: potential for intraguild interactions with lions does not affect spotted hyaena habitat selection**

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1 Don't mind the cat: potential for intraguild interactions with  
2 lions does not affect spotted hyaena habitat selection

3 Running head: Intraguild interactions do not affect large predator habitat selection

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27 † Elias Banda passed away

28

29 **ABSTRACT**

30 Previous work has focused on how prey availability and fear of people affect apex  
31 predators' habitat selection, but few have studied the effects of intraguild interactions.  
32 Patterns of co-occupancy between sympatric carnivores have started to be well  
33 described, but understanding the underlying habitat selection processes is lacking. We  
34 evaluated whether the risk of encountering African lions (*Panthera leo*) influences  
35 habitat selection by spotted hyaenas (*Crocuta crocuta*, hyaena hereafter) using GPS-  
36 collar data and two approaches: 1) resource selection functions considering the static  
37 long-term risk of encountering lions, and 2) step selection functions considering the  
38 dynamic, immediate risk of encountering lions. We explored the interplay between the  
39 risk of encountering lions, vegetation type and moonlight illumination, and examined  
40 individual variation in habitat selection. As expected, hyaenas did not avoid areas  
41 intensively used by lions, and there was even a positive effect of the long-term risk of  
42 encountering lions on habitat selection by hyaenas. As in other study sites, this likely  
43 arises because hyaenas select the same areas as lions. At the finer scale, unexpectedly,  
44 hyaenas did not generally move away from lions. We believe this occurs because  
45 hyaenas can sometimes be attracted to lions because of scavenging opportunities or  
46 because they outnumber lions and are likely to win an aggressive encounter. These two  
47 circumstances can lead to highly contrasting outcomes and highlight the high dynamics  
48 of intraguild interactions. This also illustrates the limits of GPS-based studies that lack  
49 crucial information about the context of interactions. While at the population level, we  
50 detected a selection for open vegetation areas, which are rich in prey in the study  
51 ecosystem and potentially good hunting grounds for cursorial predators, such as  
52 hyaenas; our results show a very high inter-individual heterogeneity underlying this

53 population level result. Our work therefore illustrates the importance of investigating  
54 individual habitat selection.

55

## 56 **KEYWORDS**

57 *Crocuta crocuta*, moon illumination, *Panthera leo*, resource selection function, step  
58 selection function, vegetation cover, Hwange National Park

59

## 60 **LAY SUMMARY**

61 Apex carnivore habitat selection is affected by multiple factors, including prey  
62 availability, fear of humans, and the far less studied intraguild interactions. Here, we  
63 used data from GPS collars to study the effects of lions on hyaenas' habitat selection.  
64 We found that hyaenas did not generally avoid lions and even selected for areas  
65 intensively used by them. We highlight the dynamics of intraguild interactions and the  
66 high intra-individual variability in habitat selection patterns.

67

## 68 INTRODUCTION

69 The abundance and distribution of apex predators are changing rapidly worldwide,  
70 with repercussions on populations of large herbivores and smaller carnivores that can  
71 result in ecosystem-level effects through trophic cascades (Ritchie & Johnson, 2009;  
72 Estes *et al.*, 2011; Chapron *et al.*, 2014; Ripple *et al.*, 2014). Understanding the drivers  
73 of apex predators' space/habitat use (how they distribute their time between  
74 areas/habitats) and the underlying habitat selection process (i.e. the process by which an  
75 animal is using a habitat disproportionately to its availability in the landscape) is a  
76 prerequisite for sound management and conservation of these species and hence the  
77 ecosystems they inhabit.

78 For an apex carnivore, habitat selection is driven by prey abundance and/or  
79 catchability (Hopcraft, Sinclair & Packer, 2005; Davidson *et al.*, 2012; Elbroch &  
80 Wittmer, 2012; Kock *et al.*, 2013). In human-dominated landscapes, the fear of people  
81 also influences apex predators' habitat selection (Oriol-Cotterill *et al.*, 2015; Suraci *et*  
82 *al.*, 2019; Mwampeta *et al.*, 2021; Nickel *et al.*, 2021). However, these vertical drivers  
83 of habitat selection (bottom-up with respect to resource availability and top-down with  
84 respect to fear of the superior trophic level) are not the only factors influencing animal  
85 habitat selection, and horizontal drivers (within the same trophic layer), such as  
86 carnivore intraguild interactions, also operate (McLoughlin *et al.*, 2010).

87 Indeed, in areas where several predators are sympatric, competition, aggressive  
88 interactions, and intraguild predation are widespread (Palomares & Caro, 1999; Creel,  
89 Spong & Creel, 2001; Donadio & Buskirk, 2006; Curveira- Santos *et al.*, 2021). These  
90 negative interactions can affect how carnivores use and move in the landscape. This has  
91 been documented for carnivore species characterised by asymmetric competition in

92 which a smaller species avoids a larger dominant one. For example, Arctic foxes  
93 (*Vulpes lagopus*) avoid areas intensively used by red foxes (*Vulpes vulpes*, Hersteinsson  
94 & Macdonald, 1992), wild dogs (*Lycaon pictus*) avoid areas heavily used by African  
95 lions (*Panthera leo*, Mills & Gorman, 1997), and cougars (*Puma concolor*) avoid the  
96 core of wolf (*Canis lupus*) territories (Lendrum *et al.*, 2014). In addition to these  
97 proactive spatial avoidance responses to the risk of encountering a larger carnivore,  
98 avoidance patterns also occur at finer spatiotemporal scales, including reactive  
99 responses allowing the subordinate carnivore to adjust its behaviour to an immediate  
100 and acute risk of encountering the larger dominant carnivore (Creel, 2018). Cheetahs  
101 (*Acinonyx jubatus*), for example, tend to use landscape areas similar to African lions and  
102 spotted hyaenas (*Crocuta crocuta*) but avoid them dynamically when the other  
103 carnivores are nearby (Broekhuis *et al.*, 2013). On the other hand, scavenging  
104 opportunities often arise in carnivores (Pereira, Owen-Smith & Moleón, 2014), resulting  
105 in attraction patterns because some carnivore species facilitate access to carrion to  
106 others (van Dijk *et al.*, 2008b; Prugh & Sivy, 2020).

107 With the development of camera-trapping, knowledge has recently accumulated on  
108 the space use of sympatric carnivores and their co-occurrence patterns (Cusack *et al.*,  
109 2017; Miller *et al.*, 2018; Allen, Elbroch & Wittmer, 2021; Vissia & van Langevelde,  
110 2021). Less is documented on how one carnivore species affects the habitat selection of  
111 other carnivores and on the individual differences in these responses. In Africa, where  
112 the large carnivore guild is one of the most complete, most existing work on the effect  
113 of other large carnivores on habitat selection has focused on wild dogs and cheetahs  
114 (Dröge *et al.*, 2017; Davies *et al.*, 2021), which are both endangered species. Wild dogs  
115 and cheetahs are smaller than African lions (lions hereafter) and spotted hyaenas and, in

116 general, considered subordinate carnivores, illustrating cases of asymmetric  
117 competition. Less is known about how the two largest and most numerous predators in  
118 African savannas, lions and spotted hyaenas (hyaenas hereafter), affect each other's  
119 habitat selection (but see Schuette *et al.*, 2013; Périquet, Fritz & Revilla, 2015 for a  
120 review; Barker *et al.*, 2023). Further, evidence is accumulating on the difference in  
121 individual behavioural responses to risk (Bonnot *et al.*, 2015; Picardi *et al.*, 2021), and  
122 the study of how animal interactions influence habitat selection, which was traditionally  
123 studied at the population level only, needs to account for individual variation as these  
124 responses are individual dependent (see also Muff, Signer & Fieberg, 2020). Lions and  
125 hyaenas clearly have the potential to strongly compete with each other through theft of  
126 carcasses, risk of injury or fatalities during encounters (reviewed in Périquet, Fritz &  
127 Revilla, 2015). Even though lions are generally considered dominant over hyaenas  
128 (Amorós *et al.*, 2020), the outcome of encounters depends on the presence of an adult  
129 male lion and the respective sizes of the predator groups, with hyaenas likely to 'win'  
130 an aggressive interaction when they outnumber lions by a factor of 4 (Cooper, 1991).  
131 The competition between lions and hyaenas can therefore be considered symmetric. It  
132 has been previously shown that hyaenas do not avoid lions at large scale, and hyaenas  
133 also use areas that are intensively used by lions (Cusack *et al.*, 2016; Kittle *et al.*, 2016;  
134 Swanson *et al.*, 2016; Dröge *et al.*, 2017; Barker *et al.*, 2023) Whether these attraction  
135 patterns result from selection for the same habitats by the two species, from an active  
136 attraction mechanism whereby hyaenas actively follow lions in search of scavenging or  
137 kleptoparasitism opportunities (Swanson *et al.*, 2016; Cusack *et al.*, 2017), or both, is  
138 less clear. Previous work on lion habitat selection patterns showed that lions select for  
139 areas where prey are not only abundant (*e.g.* near water sources) but also where they are

140 easier to catch (*e.g.* dense vegetation, river embankments) (Hopcraft *et al.* 2005; Valeix  
141 *et al.*, 2010; Davidson *et al.*, 2012; Oriol-Cotterill *et al.*, 2015; Kittle *et al.*, 2016;  
142 Mwampeta *et al.*, 2021). However, few studies have focused on hyaena habitat  
143 selection. Previous work on hyaenas has concentrated mainly on habitat use, with  
144 hyaenas more abundant in woodlands in Tanzania (Mwampeta *et al.*, 2021) and evenly  
145 distributed across the landscape in the Okavango Delta, Botswana (Cozzi *et al.*, 2013).  
146 To our knowledge, little is known about hyaena habitat selection, and the effects of  
147 lions on this selection are yet to be studied. In addition, all the studies previously cited  
148 (except for Barker *et al.*, 2023) were conducted in the open plains of East Africa, where  
149 prey abundance is very high, and ungulates are often migratory. However, little is  
150 known about hyaena spatial ecology in wooded savannas, which represent a much  
151 larger proportion of this species' geographic range (Bohm & Höner, 2015) and where  
152 the vegetation cover might affect hunting success and prey are often sedentary and  
153 occur at lower densities.

154 In this study, we intended to fill these gaps and provide insights into hyaenas' habitat  
155 selection in a wooded savanna and how sympatric lions affect this process, emphasising  
156 the individual variation of these responses. We used GPS data from simultaneously  
157 radio-collared hyaenas and lions in Hwange National Park, Zimbabwe, to study hyaena  
158 habitat selection and assess whether the risk of encountering lions influences these  
159 patterns. In the study ecosystem, the abundance of large herbivores, *i.e.* prey, is  
160 associated with waterhole areas, which act as spatial anchors for prey and grassland  
161 patches (Davidson *et al.*, 2012) because of their use by large herds of grazers. Further,  
162 hyaenas are cursorial hunters, and their hunting success is likely to be higher in open  
163 areas. Thus, we expected hyaenas to select locations close to waterholes or grassland

164 areas. However, waterhole and grassland areas are also strongly selected by lions, which  
165 are crucial hunting grounds for them. Consequently, and as already reported in other  
166 studies (Kittle *et al.*, 2016; Swanson *et al.*, 2016; Cusack *et al.*, 2017; Dröge *et al.*,  
167 2017; Barker *et al.*, 2023), we expected that hyaenas would not globally avoid areas  
168 intensively used by lions (static long-term risk). At this scale, we did not expect a high  
169 individual variation. However, we hypothesised that hyaenas would modify their spatial  
170 behaviour when lions are nearby because of the risk of aggressive encounters between  
171 the two species, with a high individual variation at this finer scale, because we expect  
172 the habitat selection response at this scale to be individual-dependent (based on the age  
173 and experience of the animal, and its personality) and context-dependent (*e.g.*, relative  
174 size of the lion and hyaena groups). We considered that the overall hyaena perception of  
175 risk associated with lions may arise from (1) the probability of encountering a lion at a  
176 given location; (2) the visibility condition at night that results from a combination of  
177 moon illumination and the density of the canopy cover, and influences the capacity of  
178 lions and hyaenas to see one another; and (3) the capacity for lions to be hidden and  
179 undetected, often linked to the vegetation structure (Fig. 1). Indeed, several studies  
180 demonstrated the importance on vegetation cover and moon illumination in shaping  
181 large carnivore interactions (*e.g.* Cozzi *et al.*, 2012; Barker *et al.*, 2023), with lions  
182 being more active and more successfully ambushers/hunters during dark nights and in  
183 habitats providing cover for ambushing prey (Funston, Mills & Biggs, 2001; Preston *et*  
184 *al.*, 2019; Barker *et al.*, 2023). We therefore predicted that when in proximity to lions  
185 (dynamic, immediate risk), hyaenas would select for locations in densely wooded  
186 vegetation that provided hiding opportunities, especially during bright nights (*i.e.* high  
187 moon illumination). Finally, because hyaenas are cursorial hunters whose hunting

188 success depends on the body condition of prey, which decreases as the dry season  
189 progresses, we tested the effect of seasonality to explore whether hyaenas have different  
190 habitat selection strategies in seasons contrasted in terms of prey body condition (for  
191 instance, they could rely more on scavenging opportunities from lions in the wet season  
192 when prey are all in very good body condition).

193

## 194 **METHODS**

### 195 *Study area*

196 Hwange National Park (Hwange) is located in western Zimbabwe (19°00'S, 26°30'E)  
197 and covers an area of approximately 14,600 km<sup>2</sup>. The study area ( $\approx$  1 500 km<sup>2</sup>, see  
198 Supplementary material S1.1) in the northern part of Hwange is characterised by  
199 Kalahari sandy soils. The vegetation is typical of primarily bushed woodland and  
200 bushland, with patches of grassland (Chamaillé-Jammes, Fritz & Murindagomo, 2006).  
201 Hwange is semi-arid (long-term mean annual precipitation is 600 mm, coefficient of  
202 variation=25%) with a wet season from November to April, an early dry season from  
203 May to July and a late dry season from August to October (Chamaillé-Jammes *et al.*,  
204 2006). In this work, we analysed data from the two most contrasting seasons, the wet  
205 and late dry seasons ("dry season" hereafter). Water availability to animals is primarily  
206 from rainwater collected in natural depressions. However, most of them do not hold  
207 water during the dry season, when water is artificially supplied in about 50 waterholes  
208 (pumped waterholes hereafter) spread throughout the northeastern sector of Hwange.  
209 The estimated large carnivore densities in the study area are 11 hyaenas/100 km<sup>2</sup>  
210 (Périquet, 2014), 4.3 lions/100 km<sup>2</sup> (Loveridge *et al.*, 2016), 2 leopards/100km<sup>2</sup>  
211 (Loveridge *et al.*, 2022). Wild dogs and cheethas also occurs in the study area, albeit at

212 very low density (van der Meer, Rasmussen & Fritz, 2015) (van der Meer, 2015).

213

#### 214 ***Predator GPS data***

215 From July 2009 to October 2013, nine adult hyaenas (8 females and 1 male)  
216 belonging to four different clans were equipped with GPS collars. Collars were  
217 programmed to take hourly fixes between 6 pm and 6 am. During the same period, 41  
218 lions (26 males and 15 females) were also equipped in the study area with GPS collars  
219 taking locations every hour or two hours from 7 pm to 5 am (see Benhamou *et al.*, 2014  
220 for details). At least one male per coalition and one female per pride were collared.  
221 Fission-fusion occurs at different levels in Hwange prides (Mbizah *et al.*, 2020), but  
222 lionesses from the same pride spent most of their time together in the study area (Valeix  
223 *et al.*, 2009). Hence, we assumed that individual locations generally represent those of  
224 their pride and coalition. Carnivores were immobilised by a professional team and  
225 relevant animal care protocols were followed during their capture and collaring  
226 (Wildlife Drugs Sub-committee of the Drugs Control Council of Zimbabwe and  
227 Zimbabwe Veterinary Association, Wildlife Group, and licenses to acquire, possess and  
228 administer game capture drugs/dangerous drugs). Permissions were provided by the  
229 appropriate agencies (Zimbabwe Parks and Wildlife Management Authority). Full  
230 recovery of immobilised carnivores was ensured by staying with the animals until they  
231 moved away normally.

232

#### 233 ***Environmental data***

234 A vegetation map was designed based on three Landsat-7 ETM+ satellite images  
235 from August 2002, November 2002 and April 2003 with a resolution of 30 m (see

236 Courbin *et al.*, 2016 for details). We defined three vegetation types: open, bushed and  
237 wooded vegetation (used as the reference class in the following analyses, see Suppl.  
238 Mat S1.2). Using three vegetation types is relevant for carnivore habitat selection, as  
239 vegetation structure, in particular the contrast between open vegetation and the other  
240 types of vegetation, is tightly linked to their foraging strategy (*e.g.* Davidson *et al.*,  
241 2012), and the existence of trees in wooded vegetation is important for canopy cover,  
242 and hence visibility conditions at night. We characterised each hyaena GPS location by a  
243 vegetation type and the distance to the closest pumped waterhole (distance to water  
244 hereafter, see Suppl. Mat. S1.3 for the spatial distribution of pumped waterholes). There  
245 is no other surface water available in our study area apart from these pumped waterholes  
246 during the dry season. In the study area, these pumped waterholes are attractors of large  
247 herbivores in the dry season (Valeix *et al.*, 2009), but also in the wet seasons when  
248 herds of grazers concentrate on the nutrient-rich grassland areas (due to dung  
249 accumulation in the dry season) associated to these waterholes. As a consequence, they  
250 can be considered as prey hotspots for large carnivores throughout the year; lions  
251 clearly use these pumped waterhole areas as their hunting grounds and select them in all  
252 seasons (Valeix *et al.*, 2010). We also estimated night brightness for each location by  
253 extracting the Moon Illumination Index (MII) as the fraction of the moon illuminated  
254 (ranging from 0 -new moon- to 1 -full moon-). MII was obtained from the R package  
255 *suncalc* (Agafonkin & Thieurmél, 2018) and set to 0 if the moon was below the horizon  
256 at the time of the location. Unfortunately, we do not have data on cloud cover, which  
257 could affect night brightness. Clouds are almost inexistent in the dry season in the study  
258 area but could have affected night brightness in the wet season and potentially bias our  
259 results on moon illumination that season.

260

261 ***Static long-term risk of encountering lions***

262 Hyena GPS locations were also characterised by the static long-term risk of  
263 encountering lions. We estimated this static long-term risk as the value of the  
264 Utilization Distribution (UD) estimated for lion GPS locations for the season-year  
265 corresponding to the hyena location using movement-based kernel density estimation,  
266 i.e., biased random bridge (Benhamou & Cornélis, 2010; Benhamou, 2011) with a time  
267 threshold of 5h and length threshold and smoothing of 50. Pixel values were  
268 standardised within each UD. When several standardised lion UDs overlapped on a  
269 given pixel, we used the maximum value over all overlapping individuals (see Suppl.  
270 Mat. S1.4 for the spatial distribution of this variable during the wet and dry seasons).

271

272 ***Statistical analyses***

273 The aim was to assess how vegetation type, distance to water, moon illumination, the  
274 risk of encountering lions (considering both the static long-term risk and the dynamic  
275 immediate risk), and their interactions influence hyena habitat selection (see Fig. 1).

276 In a first analytical step, we focused on the role of the static long-term risk of  
277 encountering lions, and we used the Selection Ratio (SR) as defined in Manly et al.  
278 (2002) to estimate hyena habitat selection at night depending on vegetation type,  
279 distance to water, the static risk of encountering lions, and their three-way interaction.  
280 Here, the response to the static risk of encounter is equivalent to a proactive response.  
281 Following Chamaillé-Jammes (2019), the SR was computed using Resource Selection  
282 Functions (RSFs, Manly *et al.*, 2002). RSFs compare spatial attributes at GPS locations  
283 with those at available locations. For each individual and each season-year, we sampled

284 available locations by drawing 15 times the number of used locations randomly within  
285 individual home ranges delineated by the 95% isopleth of individual utilisation  
286 distribution computed using a kernel method (with a bandwidth  $h = h_{ref}$ ). The SR was  
287 calculated as  $SR_i = \beta_i \times N_{available}/N_{used}$  with  $\beta_i$  being the RSF coefficient for  
288 variable  $i$  and  $N_{available}/N_{used}$  representing the ratio available to used location  
289 ( $N_{available}/N_{used} = 15$  in our case). We used a two-step approach, first fitting RSFs  
290 separately for each individual, then building a population model as suggested by  
291 Murtaugh (2007). We chose the two-steps approach for simplicity, acknowledging that  
292 complex mixed-effect models can have convergence issues and be difficult to interpret.  
293 The individual RSF models were fitted using Generalized Linear Models (GLMs) with  
294 a logit link and a binomial distribution of errors. We used vegetation type, distance to  
295 water, the static risk of encountering lions, and their three-way interaction as predictors.  
296 We evaluated the predictive power of the individual RSF models using the Spearman  
297 rank correlation based on k-fold cross-validation proposed by Boyce *et al.* (2002) with 5  
298 folds, 10 bins and 100 repetitions. For each season, the population RSF was computed  
299 using intercept-only Linear Models (LMs) using betas from all the individual RSFs as  
300 response variables weighted by the inverse of their squared standard error (Murtaugh,  
301 2007; Dickie *et al.*, 2020). The population model was fitted separately for each predictor  
302 (including main effects and interactions, see Suppl. Mat. S2 for more details and model  
303 coefficients). Regarding the effects of moonlight, we focused on habitat use instead of  
304 selection. While habitat selection takes into account habitat availability, habitat use  
305 simply describes how animals use the habitat. First, we tested if the MII influenced  
306 hyaena habitat use in terms of vegetation types by comparing the distribution of hyaena  
307 GPS locations in each vegetation type between full and new moon nights. Full moon

308 nights were defined as nights with a MII  $\geq 80\%$  and new moon nights as nights with a  
309 MII  $\leq 20\%$ . These MII thresholds led to the selection of 4-5 nights around the full and  
310 new moons each month. For each individual, we computed the difference in the  
311 proportions of each vegetation type used between full and new moon nights. We used  
312 these differences as response variable in Linear Mixed Models (LMMs), including  
313 vegetation type as a predictor and hyaena identity as a random intercept. Second, we  
314 used LMMs to test the effects of the interaction between vegetation type and MII (full  
315 vs new moon night) on long-term lion risk and distance to waterhole at locations used  
316 by hyaenas. Hyaena's identity was included as a random intercept.

317 In a second analytical step, we focused on the role of the dynamic immediate risk of  
318 encountering lions and used Step Selection Functions (SSFs, Fortin *et al.*, 2005;  
319 Forester, Im & Rathouz, 2009; Avgar *et al.*, 2016; Dickie *et al.*, 2020). We investigated  
320 the effect of the distance to the closest lion (distance to lion hereafter) depending on  
321 vegetation types and distance to water and if these effects were mediated by night  
322 brightness. We refrain from calling the response to the proximity of lion a reactive  
323 response as we cannot ensure that hyaena actually encountered lions and/or perceived  
324 their presence, and their response might be a combination of both reactive and fine-scale  
325 proactive responses to the presence of lions. Distance to lion was computed as the  
326 minimum distance between a hyaena location (used or random; see below for the  
327 definition of random locations) and any lion for which a simultaneous location (within  
328 30 minutes of the given hyaena location) was available. For lions sampled every 2h  
329 (n=10), we generated the “missing” 1h location using the midpoint between the two  
330 locations taken at 2h intervals. We used the same method to generate actual missing  
331 locations (i.e. not recorded when they should have been) in the dataset of lion sampled

332 every hour. When successive GPS locations were actually missing, we did not generate  
333 the intermediate positions and discarded the steps. SSFs compare the environmental  
334 attributes at the ending locations of observed steps (i.e., straight-line segments linking  
335 successive 1h locations) to the environmental attributes at the end of paired random  
336 steps. For each observed step, we generated a set of 15 random steps starting at the  
337 same location as the observed one but with step length and turning angle randomly  
338 drawn from the empirical distribution of step lengths and turning angles for all the other  
339 individuals, as recommended by Fortin *et al.* (2005) and Forester *et al.* (2009). One  
340 used location and its associated 15 random locations constituted a stratum. SSFs were  
341 fitted with a conditional logistic regression. In addition to the tested predictors  
342 (vegetation type, distance to water and lion, MII), SSF included step length, log(step  
343 length) and cos(turning angle) to remove bias in other model parameters and relax the  
344 independence assumption between habitat selection and movement (Forester *et al.*,  
345 2009; Avgar *et al.*, 2016). Again, we first fitted a SSF for each individual and then  
346 calculated an averaged SSF at the population level using the same method as explained  
347 above (Murtaugh, 2007). The individual SSF models were fitted using conditional  
348 logistic regression with a binomial distribution of errors. We used the interaction terms  
349 between the distance to lion and vegetation type, distance to lion and MII, vegetation  
350 type and MII and between these three variables as predictors. The population model was  
351 fitted with an intercept-only linear model including the betas coefficients, a response  
352 variable from the individual models, and using the squared inverse of the respective  
353 standard errors as weights.

354 One female hyaena was discarded from the analyses during the dry season due to  
355 very low sample size. Since we expected a nonlinear response to the distance to lion, we

356 tested several transformations of this variable (logarithm, inverse and square root  
357 transformation). We ran individual models with each transformation and computed their  
358 AIC. We chose to use the log transformation as it was the one that led to models with  
359 the lowest AIC in both seasons (Suppl. Mat. S2, Table S2.1). We ran SSF for each  
360 season separately. We used used- habitat calibration (UHC) plots for validating the  
361 SSFs models as recommended by Fieberg *et al.* (2018). We used 80% of the data of  
362 each individual as a training set and the remaining 20% as a testing set and ran 20  
363 simulations.

364 Data wrangling and analyses were conducted in the R software version 4.0.3 (R Core  
365 Team, 2024) using the packages *suncalc* (Agafonkin & Thieurmel, 2018) for moon  
366 illumination index extraction, *adehabitatHR* and *adehabitatHS* (Calenge, 2006) for UD  
367 estimation and compositional analysis respectively, *amt* to generate random steps and  
368 run the SSFs and create the UHC plots (Signer, Fieberg & Avgar, 2019). Results are  
369 given with their 95% confidence interval unless mentioned otherwise. We used visual  
370 graphic inspection to assess correlation among continuous variables, and none was  
371 detected.

372

## 373 **RESULTS**

374 *Effect of vegetation, distance to water and the static risk of encountering lions on*  
375 *hyaena habitat selection*

376 *Population-level results* - At the population level, the triple interaction between  
377 vegetation, distance to water and the static risk of encountering lions had a significant  
378 effect on hyaena habitat selection in both seasons (Table 1). Overall, at the population  
379 level, the static risk of encountering lions had either a neutral or a positive effect on

380 habitat selection by hyaenas (Fig. 2 but note the high inter-individual variability, Fig. 3).  
381 Besides, hyaenas selected for open vegetation compared to any other vegetation type in  
382 both seasons (Fig. 2, but note the high inter-individual variability, Fig. 3). In the dry  
383 season, when close to a waterhole, hyaenas increased their selection for open and  
384 wooded vegetations with increasing static risk of encountering lions (Fig. 2a). However,  
385 far from water, hyaenas selected for bushed vegetation in the riskiest places (Fig. 2a). In  
386 the wet season, the static risk of encountering lions only had an effect in open  
387 vegetation far from water, and hyaenas showed selection for these locations (Fig. 2b).

388 *Individual level results* - In both seasons, we found that individual model  
389 coefficients, and sometimes the signs of these coefficients, were very variable, with  
390 coefficients of individuals belonging to the same clan being more similar than those of  
391 individuals from different clans (Fig. 3). For instance, if we focus on dry season, some  
392 individuals selected for open vegetation (AS1, AS2, Fig. 3a) while others avoided it  
393 (Mak1, Mak3, Fig. 3a), and some individuals selected for sites with a high static risk of  
394 encountering lions (Guv1, Fig. 3a) while others avoided such sites (Ken2, Fig. 3a). The  
395 predictive power of the individual RSF models was moderate in both seasons (cross-  
396 validation scores: dry season  $\bar{r}_s = 0.60 \pm 0.03$ , range = 0.30-0.78; wet season  $\bar{r}_s = 0.70 \pm$   
397 0.02, range = 0.46-0.87).

398 *Moon effect* - Although there were significant effects of moon on overall habitat use  
399 by hyaenas and on habitat use in varying conditions of static risk of encountering lions,  
400 these effects were minimal (~1% in use change) and therefore not biologically  
401 meaningful (Suppl. Mat. S3).

402

403 *Effect of the distance to a lion and night brightness on hyaena step selection*

404 *Population-level results* - We did not find any significant effect of the distance to the  
405 closest lion (i.e., dynamic immediate risk of encountering lions), alone or in interaction  
406 with night brightness on hyaena habitat selection patterns at the step selection scale  
407 (Table 2, Fig. 4). Night brightness alone did not have an effect either (Table 2, Fig. 4).

408 *Individual level results* - None of the variables or interactions investigated in this  
409 study explains the step decisions in hyaenas (Fig. 4). The UHC plots showed that our  
410 models were well-calibrated for both seasons with some variation between individuals  
411 (Suppl. Mat. S4).

412

## 413 **DISCUSSION**

414 Our study, based on the analysis of 1h-interval GPS data from radio-collared hyaenas  
415 and lions, leads to two main conclusions: (1) the potential for intraguild aggressive  
416 interactions with lions does not affect hyaena habitat selection, as we failed to detect  
417 avoidance concerning either the static long-term risk or the dynamic immediate risk of  
418 encountering lions, and (2) hyaena habitat selection patterns are highly variable between  
419 individuals and thus weak at the population level.

420

### 421 *Response to lion risk*

422 In accordance with our expectations, the results showed that hyaenas show no overall  
423 spatial avoidance of lions to reduce the risk of aggressive encounters with them or limit  
424 competition for live prey and carrion. In the first approach (RSF with the static long-  
425 term risk), hyaenas even selected locations that were intensively used by lions. This can  
426 be explained by three non-mutually exclusive hypotheses. First, both species can be  
427 independently attracted to the same areas because of prey availability in these areas.

428 Since most carnivore habitat selection is driven by resource availability (Hopcraft,  
429 Sinclair & Packer, 2005; Davidson *et al.*, 2012; Elbroch & Wittmer, 2012; Kock *et al.*,  
430 2013), it logically follows that both predator species should favour these areas. Second,  
431 hyaenas may limit encounters with lions in areas intensively used by them by avoiding  
432 them temporarily instead of spatially (as observed for cheetahs by Broekhuis *et al.*,  
433 2013). For instance, with lions making intensive use of waterhole areas (Valeix *et al.*,  
434 2009, 2010; Courbin *et al.*, 2019) and then moving to a different area after most of their  
435 kills (Valeix *et al.*, 2011), there are abundant opportunities for hyaenas to use these  
436 same waterholes when lions are absent. Third, hyaenas could be using the areas  
437 intensively used by lions looking for kleptoparasitism and scavenging opportunities,  
438 although this may put them at risk (Prugh & Sivy, 2020). Such behaviour has been  
439 observed in wolverine, *Gulo gulo*, following lynx, *Lynx lynx* (van Dijk *et al.*, 2008a)  
440 and red fox following striped hyaena, *Hyaena hyaena* (Macdonald, 1978). Following  
441 lions could provide hyaenas with easy meals, which seems to be the case in the wet  
442 season when encounters between lions and hyaenas occur mostly around carcasses with  
443 a pattern clearly suggesting that hyaenas look for scavenging opportunities (Cusack *et*  
444 *al.*, 2017; Périquet *et al.*, 2021).

445 In the second approach (SSF with the dynamic immediate risk), we did not find any  
446 effect of distance to the closest lion on hyaena habitat selection, which suggests that  
447 overall, hyaenas do not tend to be found closer (or further) from lion than expected at  
448 random. We believe this arises from the combined high inter-individual (cf. our results  
449 and discussion section below) and intra-individual in hyaena behavioural responses to a  
450 close lion. Such variability in individual hyaena behaviour has also been found in  
451 Amboseli National Park, Kenya, where Watts *et al.* (2010a) studied their response to

452 simulated lion presence. Such variability arises because of the existence of very  
453 contrasted situations, which depend upon the individual itself, but also the presence of a  
454 carcass, the respective hunger state of the lion and the hyaena, the presence of a male  
455 lion and the respective hyaena and lion group size known to influence the outcome of an  
456 aggressive encounter (Cooper, 1991). We suggest that global patterns are unlikely to  
457 emerge since these parameters are highly dynamic in time and space. We reach here the  
458 limit of studies based on GPS collar data only, as there is a lack of information about  
459 the context around the GPS-collared individual (group size or presence of a carcass,  
460 most importantly). We also acknowledge that our GPS data were collected at 1h  
461 intervals which might not be enough to detect hyaena's fine-scale response to lions.  
462 Additionally, even though all efforts were made to have at least one individual collared  
463 in each lion pride and coalition in the study area, we cannot rule out that some transient  
464 groups or individuals were not monitored and their encounter with collared hyaenas  
465 would have therefore been undetected. Furthermore, despite the fact that lion social  
466 groups showed very low fission-fusion dynamics in the area, fission does occur and  
467 might have led to lions forming subgroups without any individual collared.

468 We also expected that night brightness would affect habitat selection by hyaenas, by  
469 affecting the perceived risk associated to lions. Moonlight has the dual effect of  
470 allowing both predators and prey to see better, and has a stronger effect on species  
471 relying primarily on vision, particularly in open areas. Further, lions in Hwange have  
472 been reported to have higher hunting success on dark nights (Preston *et al.*, 2019) and  
473 have been shown to be more active during dark nights in Etosha National Park, Namibia  
474 and the Okavango Delta, Botswana (Barker *et al.*, 2023). Nonetheless, we could detect  
475 no biologically meaningful effect of moonlight on hyaena habitat selection. This is,

476 however, consistent with a study that showed that diurnal predators, such as cheetah and  
477 wild dog, increased their activity levels during full moon nights, whereas nocturnal  
478 predators, such as lions or hyaenas, did not (Cozzi *et al.*, 2012).

479 ***Individual and population-level habitat selection patterns***

480 As expected, our results show substantial individual variation in habitat selection  
481 patterns, leading to weak population-level effects. Whereas at the population level,  
482 hyaenas can appear as generalists in habitat selection, the high inter-individual  
483 variability reveals that this does not mean that all hyaenas are generalists, as some  
484 individuals have marked patterns of habitat selection. Here, we did not detect any  
485 population-level effect of distance to water on hyaena habitat selection, but some  
486 individuals clearly avoided areas near waterholes whereas others selected these areas  
487 and others had a habitat selection independent from water areas. This contrasts  
488 markedly with the situation of lions, for which water is a clear determinant of their  
489 habitat selection at the population level in Hwange (Valeix *et al.*, 2010; Davidson *et al.*,  
490 2012; Courbin *et al.*, 2019). However, this finding for hyaenas is consistent with  
491 observations in other ecosystems. For instance, Broekhuis *et al.* (2013) found that  
492 hyaenas use habitat randomly within their home ranges in the Okavango Delta,  
493 Botswana. In Hwange, the only habitat that appears selected at the population level by  
494 hyaenas in both seasons is open vegetation. Open areas represent a tiny proportion of  
495 the study ecosystem, but they are usually associated with high prey richness (Davidson  
496 *et al.*, 2012; Courbin *et al.*, 2016). They also provide ideal hunting grounds for cursorial  
497 predators such as hyaenas, which can easily maintain visual contact with their quarry  
498 during the chase (Kruuk, 1972; Mills, 1990). However, our study highlights that this  
499 selection is also underpinned by a very high inter-individual variability, with some

500 individuals selecting for open areas while others did not. The nature and strength of  
501 habitat selection and behavioural responses to changes may indeed vary amongst  
502 individuals, as has been shown in many groups, such as birds or fish (*e.g.* Eurasian  
503 perch, Svanbäck *et al.*, 2015; Forest's tetra, Cardozo *et al.*, 2021). While studies have  
504 focused on individual variations based on sex and social status on diet and response to  
505 risk (Pangle & Holekamp, 2010 and ; Watts *et al.*, 2010b in spotted hyaena; Edwards *et*  
506 *al.*, 2018 in cheetah; Balme *et al.*, 2019 in leopard), research on the importance of  
507 individuality in large carnivores' habitat selection lags behind (but see Lesmerises & St-  
508 Laurent, 2017 for black bears). This would be particularly relevant for spotted hyaenas  
509 that live in clans in which social status strongly affects access to resources and  
510 reproduction success (Holekamp *et al.*, 1997; Boydston *et al.*, 2005; White, 2005, 2007;  
511 Watts *et al.*, 2010b) and, therefore, has the potential to influence resource and habitat  
512 selection.

513

514 ***Carnivore spatial behaviour: the complexity of integrating dynamic interspecific***  
515 ***interactions and inter-individual heterogeneity***

516 Overall, our study highlights two caveats in our understanding of habitat selection in  
517 apex carnivores: (1) the need to consider the richness and dynamics of their interactions,  
518 and (2) the need to study and take into account individuality in habitat selection, and  
519 responses to other carnivores.

520 Intraguild interactions among carnivores have been primarily studied in cases where  
521 one species is clearly dominant over the other one, and the subordinate species avoids  
522 proactively and/or reactively the dominant one. This often implies avoiding prey-rich  
523 areas to minimise the risk of potentially negative, sometimes lethal, encounters with the

524 dominant species. However, because lions and spotted hyaenas, the two largest African  
525 carnivores, form cooperative social groups and can benefit from each others' kills,  
526 either from scavenging or kleptoparasitism, their interactions seem to be much more  
527 complex and dynamic in space and time. Even though interactions with lions can result  
528 in severe injury and death for hyaenas, it seems this risk is not high enough to cause  
529 spatial proactive avoidance of areas that are intensively used by lions. This, therefore,  
530 allows hyaenas to maintain access to prey-rich areas. The use of these areas also  
531 provides them with more scavenging opportunities. However, some broad-scale spatial  
532 avoidance has been shown in meso-carnivores of similar body size and social  
533 organisation (*e.g.* Arctic and red fox, Hersteinsson & Macdonald, 1992). This might be  
534 explained by the fact that Arctic fox, in this case, has little scavenging opportunities to  
535 gain from using the same areas as red foxes since their prey are small and likely to be  
536 consumed entirely, leaving nothing to scavenge. Intraguild killing and predation occur  
537 mainly between species with intermediate differences in body size (Palomares & Caro,  
538 1999; Donadio & Buskirk, 2006; Prugh & Sivy, 2020). In cases of more symmetrical  
539 interactions between carnivores of comparable body size and sociality, hence of similar  
540 ecology, overall avoidance is less likely to occur (Monterroso *et al.*, 2020), and it  
541 appears that interactions are more dynamic to allow for coexistence.

542 Further, our work supports recent acknowledgement of the importance of  
543 conceptualising, measuring and considering inter-individual variation in habitat  
544 selection behaviour (Bastille- Rousseau & Wittemyer, 2022). The importance of  
545 individuality might be even more marked and essential to consider in social species with  
546 clearly defined hierarchies, such as spotted hyaenas. In this species, dominant  
547 individuals secure priority access to food resources over subordinate ones (Kruuk, 1972;

548 Höner *et al.*, 2005), and dominant individuals likely secure the highest quality habitats  
549 (proximity to waterholes in semi-arid ecosystems, for instance), while subordinate  
550 animals are pushed toward less profitable habitats. This is an important research  
551 direction for future studies.

552

553

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579

#### 580 **DATA AVAILABILITY**

581 Analyses reported in this article can be reproduced using the data available upon  
582 request on Movebank for the GPS tracking data and by emailing the authors to obtain  
583 the GIS layers for the vegetation cover and waterholes location.

584

#### 585 **AUTHORS CONTRIBUTION**

586 SP, MV, NC, HF and ER conceived the ideas and designed methodology; SP and EB  
587 collected the hyaena data; AL and DM provided the lion data; SP and NC analysed the  
588 data; SP, NC and MV interpreted the results; SP, MV and NC led the writing of the  
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591

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- 882

883 **TABLE 1** **RSF POP MODEL OUTPUT**

884 Population-level coefficient estimates with their associated standard error (SE) and  
 885 95% confidence intervals (CI) of the Resource Selection Function model, including the  
 886 triple interaction between vegetation type, distance to water and static long-term risk of  
 887 encountering lions. Significant effects (with 95% CI excluding 0) are represented in  
 888 bold black lettering. *Distance to water* represents the distance to the closest pumped  
 889 waterhole and *Static risk* is the static long-term risk of encountering lions. The reference  
 890 vegetation type is wooded vegetation.

	<i>Estimates ± SE (95% CI)</i>	
	<i>Dry season</i>	<i>Wet season</i>
<i>Wooded vegetation (intercept)</i>	-2.895 ± 0.046 (-3.002 ; -2.789)	-2.844 ± 0.037 (-2.93 ; -2.758)
<i>Bushed vegetation</i>	0.124 ± 0.082 (-0.064 ; 0.312)	0.081 ± 0.102 (-0.154 ; 0.316)
<i>Open vegetation</i>	<b>1.114 ± 0.357 (0.291 ; 1.938)</b>	<b>1.066 ± 0.25 (0.491 ; 1.642)</b>
<i>Distance to water (Wooded)</i>	-0.004 ± 0.11 (-0.257 ; 0.25)	-0.067 ± 0.119 (-0.341 ; 0.207)
<i>Static risk (Wooded)</i>	<b>0.236 ± 0.033 (0.161 ; 0.312)</b>	<b>0.134 ± 0.033 (0.059 ; 0.209)</b>
<i>Bushed vegetation x Distance to water</i>	0.025 ± 0.134 (-0.285 ; 0.335)	0.129 ± 0.078 (-0.051 ; 0.308)
<i>Open vegetation x Distance to water</i>	0.156 ± 0.358 (-0.67 ; 0.982)	0.152 ± 0.182 (-0.267 ; 0.572)
<i>Bushed vegetation x Static risk</i>	<b>0.276 ± 0.061 (0.136 ; 0.417)</b>	-0.088 ± 0.054 (-0.212 ; 0.036)
<i>Open vegetation x Static risk</i>	-0.422 ± 0.2 (-0.883 ; 0.038)	<b>0.444 ± 0.161 (0.074 ; 0.815)</b>
<i>Static risk x Distance to water</i>	-0.006 ± 0.068 (-0.162 ; 0.15)	<b>0.194 ± 0.045 (0.091 ; 0.298)</b>
<i>Bushed vegetation x Distance to water x Static risk</i>	0.146 ± 0.109 (-0.104 ; 0.397)	<b>-0.181 ± 0.061 (-0.321 ; -0.04)</b>
<i>Open vegetation x Distance to water x Static risk</i>	<b>-0.254 ± 0.108 (-0.504 ; -0.004)</b>	0.139 ± 0.155 (-0.218 ; 0.496)

891

892 **TABLE 2** **SSF**

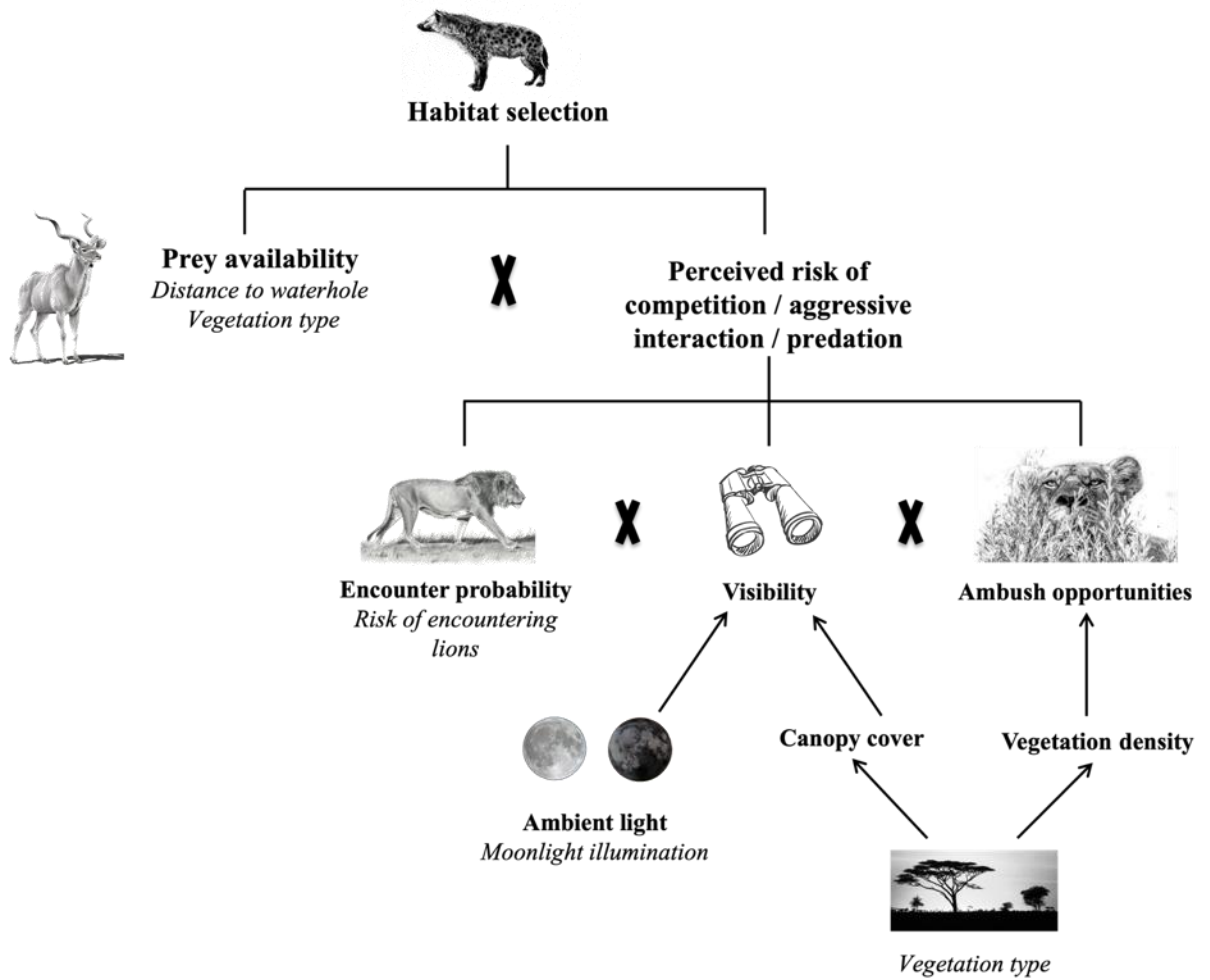
893 Population level coefficient estimates with their associated standard error (SE) and  
 894 95% confidence intervals (CI) of the paired-design Step Selection Function at the end of  
 895 steps, including a triple interaction between vegetation type, night brightness (full vs  
 896 new moon) and distance to lion (log-transformed). The reference vegetation type is  
 897 wooded vegetation.

	<i>Estimates ± SE (95% CI)</i>	
	<i>Dry season</i>	<i>Wet season</i>
<i>Step length</i>	0 ± 0 (0 ; 0)	0 ± 0 (0 ; 0)
<i>log(step length)</i>	0.011 ± 0.034 (-0.069 ; 0.091)	-0.006 ± 0.037 (-0.09 ; 0.079)
<i>cos(turning angle)</i>	-0.054 ± 0.08 (-0.244 ; 0.137)	-0.023 ± 0.037 (-0.109 ; 0.063)
<i>Bushed vegetation</i>	0.233 ± 0.941 (-1.994 ; 2.459)	1.316 ± 0.858 (-0.663 ; 3.296)
<i>Open vegetation</i>	-0.846 ± 1.116 (-3.485 ; 1.793)	-0.153 ± 1.377 (-3.328 ; 3.022)
<i>Distance to lion</i>	-0.354 ± 0.154 (-0.717 ; 0.01)	-0.235 ± 0.134 (-0.544 ; 0.073)
<i>Bushed vegetation x Distance to lion</i>	0 ± 0.115 (-0.273 ; 0.273)	-0.129 ± 0.102 (-0.363 ; 0.106)
<i>Open vegetation x Distance to lion</i>	0.194 ± 0.119 (-0.087 ; 0.474)	0.104 ± 0.161 (-0.267 ; 0.475)
<i>Distance to lion x New moon</i>	0.297 ± 0.18 (-0.127 ; 0.722)	-0.186 ± 0.141 (-0.511 ; 0.138)
<i>Bushed vegetation x New moon</i>	0.315 ± 0.829 (-1.644 ; 2.274)	-0.865 ± 1.357 (-3.993 ; 2.263)
<i>Open vegetation x New moon</i>	1.441 ± 2.484 (-4.433 ; 7.315)	-0.565 ± 1.432 (-3.868 ; 2.738)
<i>Bushed vegetation x Distance to lion x New moon</i>	-0.034 ± 0.091 (-0.25 ; 0.182)	0.083 ± 0.152 (-0.268 ; 0.434)
<i>Open vegetation x Distance to lion x New moon</i>	-0.16 ± 0.269 (-0.796 ; 0.475)	0.09 ± 0.157 (-0.271 ; 0.452)

898

899 **FIGURE 1** **FRAMEWORK**

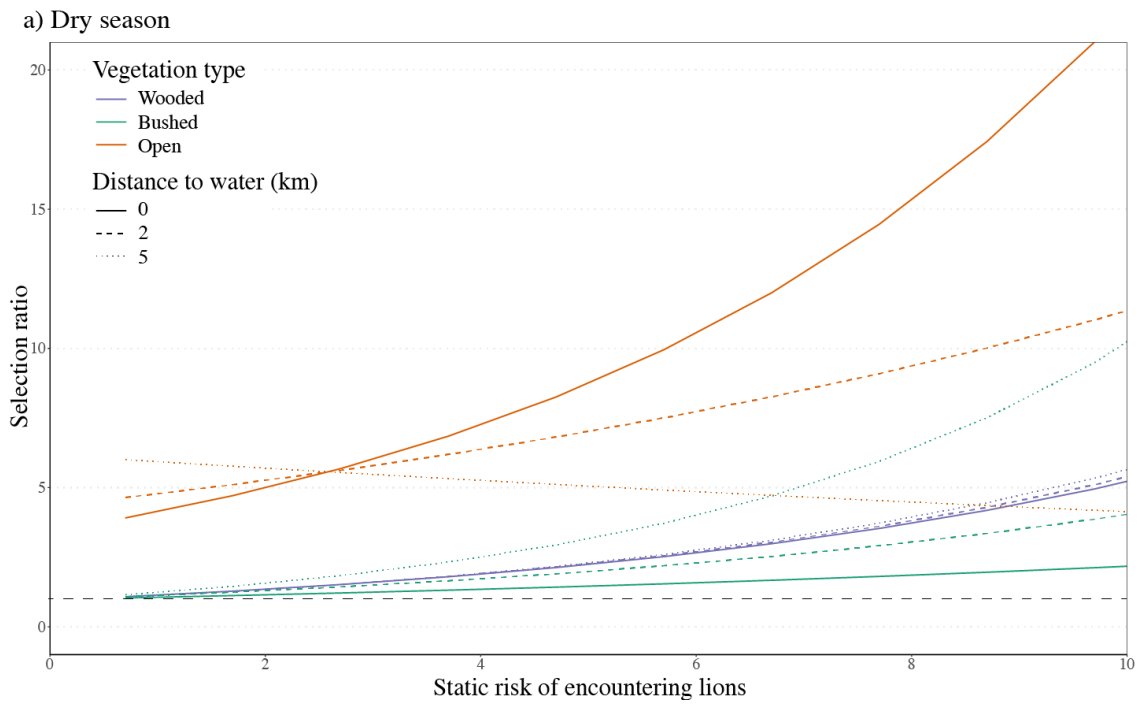
900 Factors likely to influence habitat selection in hyaenas (in bold) and variables used as  
 901 their proxies (in italics).



902  
 903

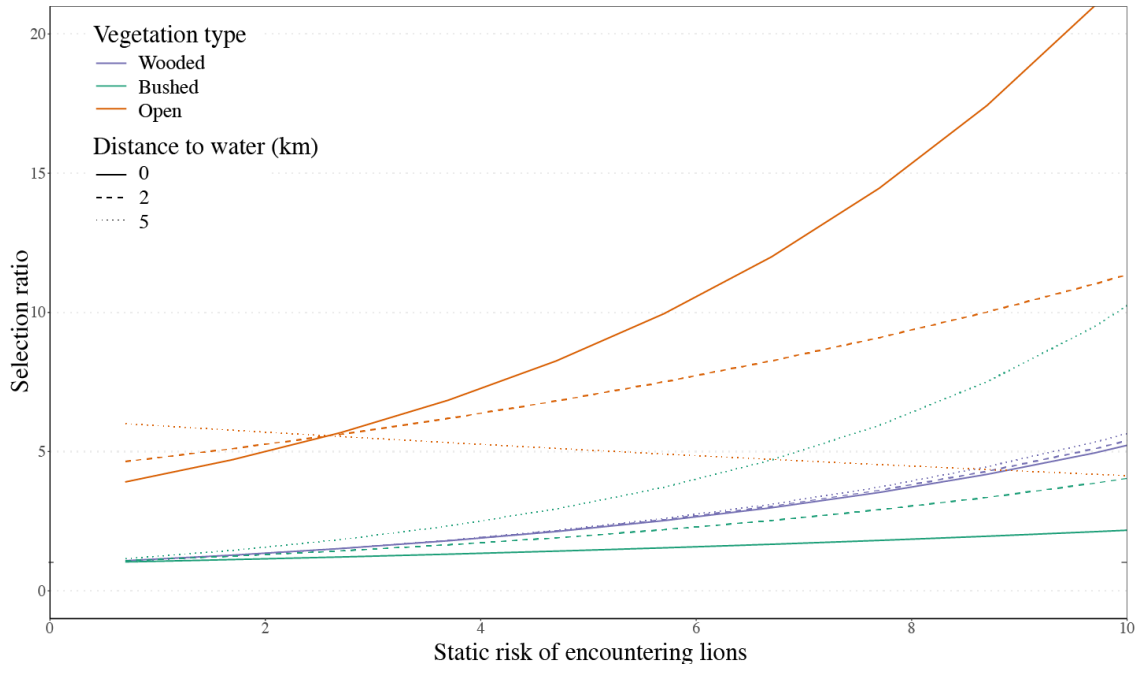
904 **FIGURE 2** **RSF RESPONSE**

905 Effects of the static risk of encountering lions, vegetation type and distance to water  
906 on hyaena habitat selection in the dry (a) and wet (b) seasons. Effects are shown as  
907 selection ratios computed based on population-level models. The horizontal line at  
908  $SR=1$  represents the threshold between avoidance ( $SR<1$ ) and selection ( $SR>1$ ).



909

b) Wet season

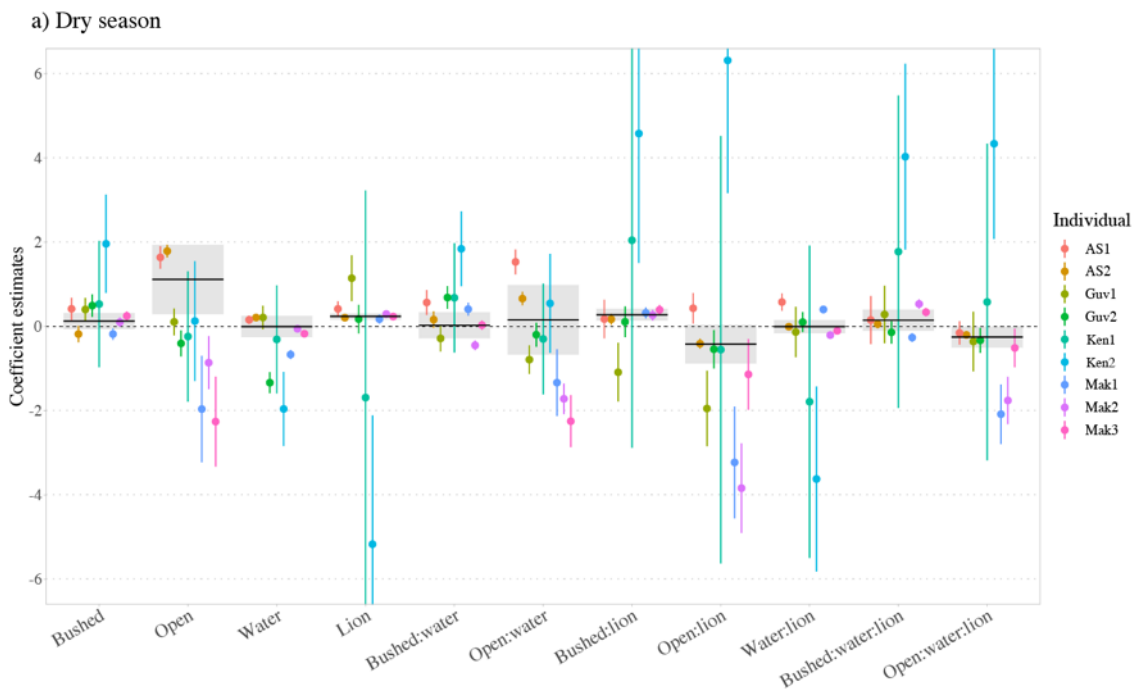


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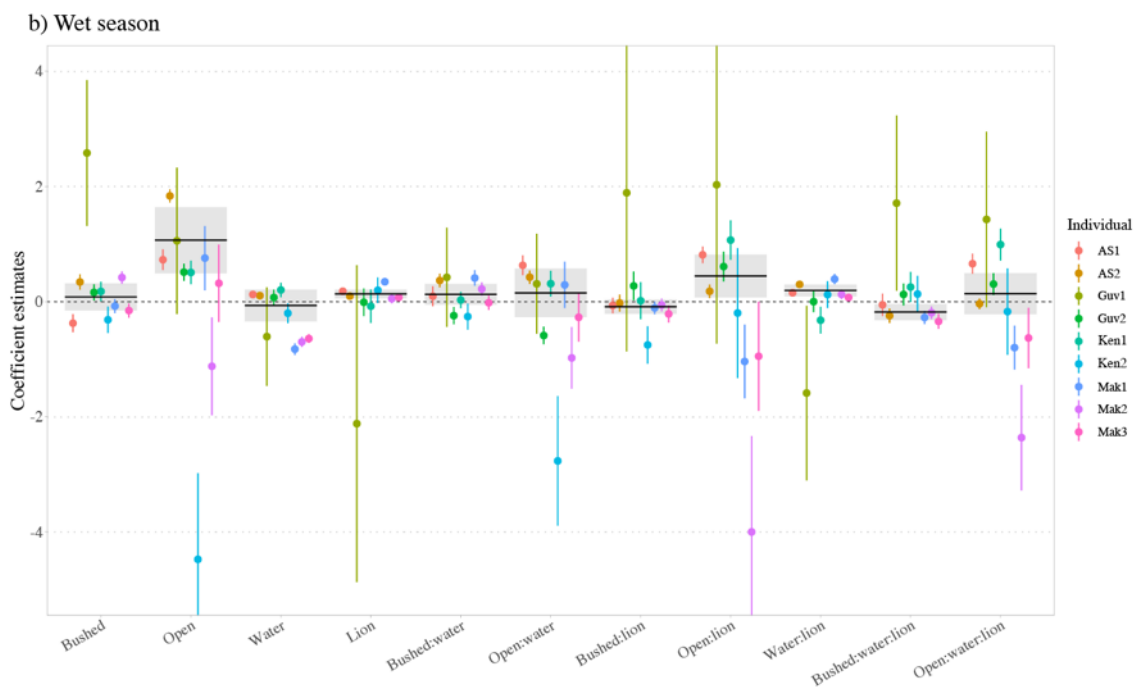
911

912 **FIGURE 3** **RSF MODEL OUTPUTS**

913 Model coefficients estimated from Resource Selection Functions during the dry (a)  
914 and wet (b) seasons, including the effects of the triple interaction between vegetation  
915 type, the static risk of encountering lions (variable "Lion" on the figure) and distance to  
916 water (variable "Water"). Colours show estimations for individual hyaenas with 95%  
917 confidence interval (CI) while the population estimate is represented by a bold  
918 horizontal bar and shaded rectangles for 95% CI. (Individual ID provided information  
919 on clan belonging: AS= Airstrip clan, Guv= Guvalal clan, Ken= Kennedy clan and  
920 Mak=Makwa clan).



921  
922

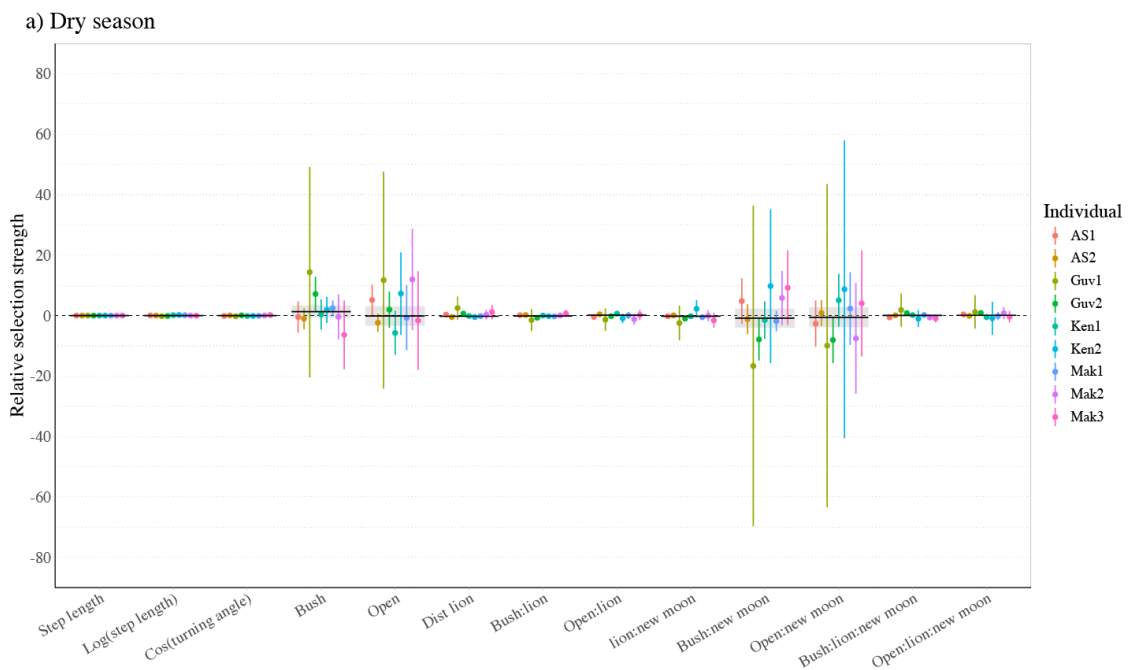


923

924 **FIGURE 4** **SSF MODEL OUTPUT**

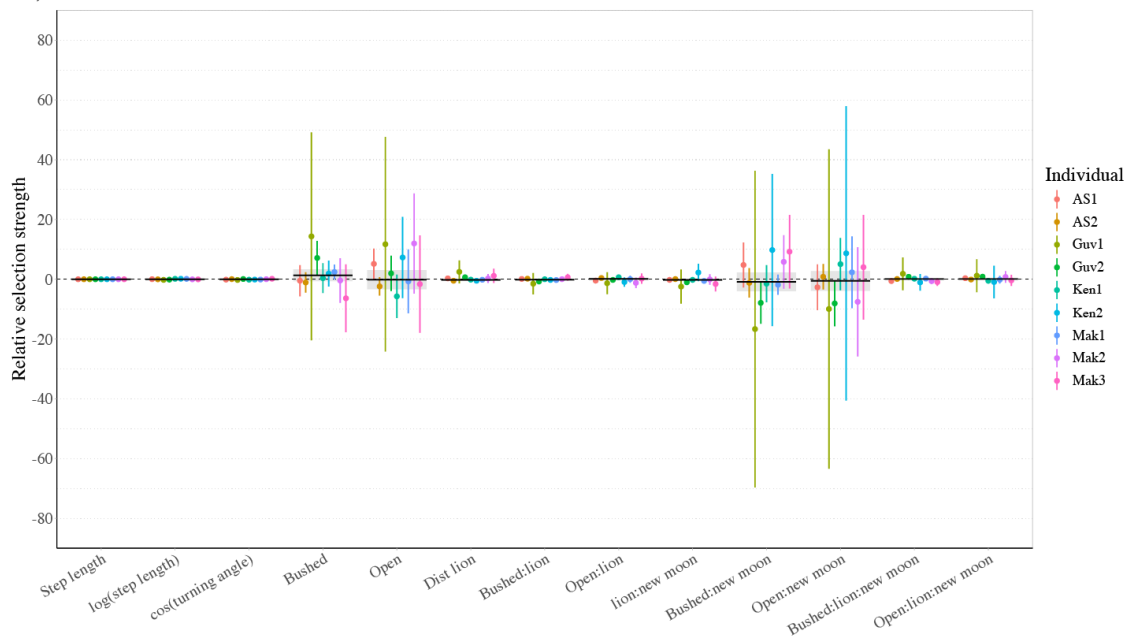
925 Coefficient estimates from Step Selection Functions during the dry (a) and wet (b)  
926 seasons, including the effects of the triple interaction between vegetation type, distance  
927 to lion and night brightness (new vs full moon) at the end of movement steps. Colours  
928 show estimations for individual hyaenas with 95% confidence interval (CI), while the  
929 population estimate is represented by a bold horizontal bar and shaded rectangles for  
930 95% CI. (Individual ID provided information on clan belonging: AS= Airstrip clan,  
931 Guv= Guvalal clan, Ken= Kennedy clan and Mak=Makwa clan).

932  
933



934  
935  
936

b) Wet season



937

938

939 **SUPPLEMENTARY MATERIAL S1: STUDY AREA DETAILS**

940 (S1.1) Location of the study area within Hwange National Park, Zimbabwe.

941

942 (S1.2) Vegetation structure in the study area of Main Camp, Hwange National Park,  
943 Zimbabwe.

944 The vegetation map has a 30m resolution and three vegetation classes with  
945 increasing woody plant density: open, bushed, and wooded.

946 Hyaena clan home ranges with clan names are also represented using location-based  
947 kernel density estimation, computed using data for all clan members.

948

949 (S1.3) Distribution of distances to pumped waterholes in the Main Camp area,  
950 Hwange National Park, Zimbabwe.

951 Hyaena clan home ranges are also represented using location-based kernel density  
952 estimation, computed using data for all clan members.

953

954 (S1.4) Distribution of the static long-term risk of encountering lions during the (a)  
955 dry and (b) wet seasons in the Main Camp area, Hwange National Park, Zimbabwe.

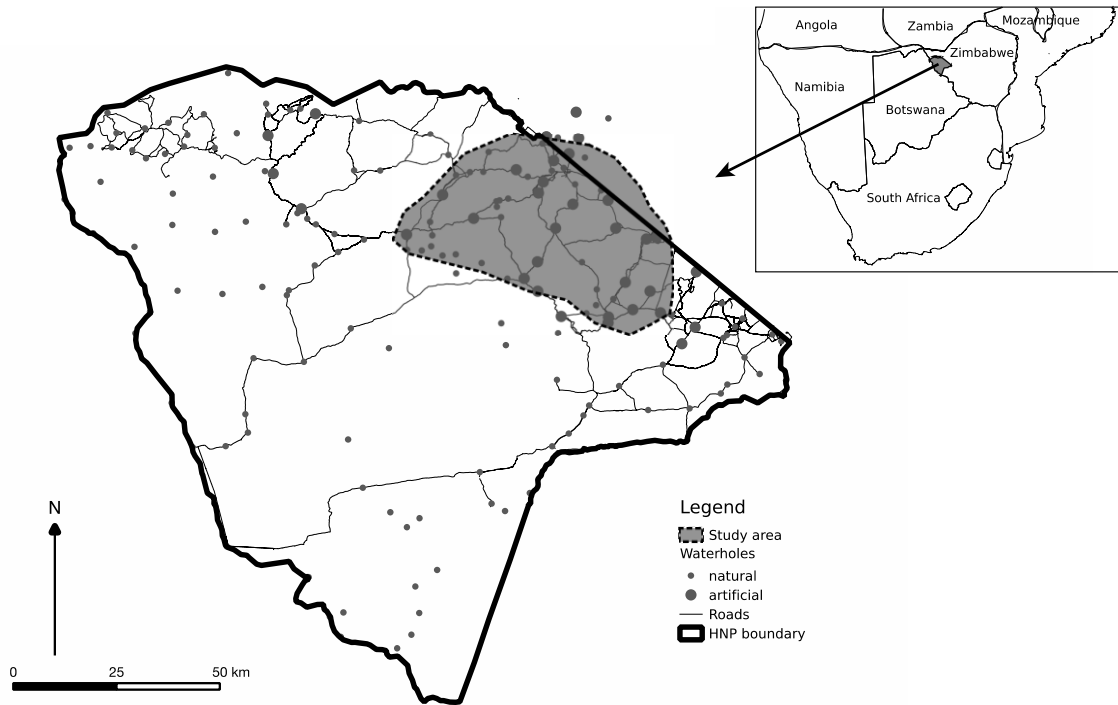
956 Probabilities were computed using movement-based Kernel Density Estimation of  
957 individual lions for each season. In the case of overlapping home ranges, the maximum  
958 value was used.

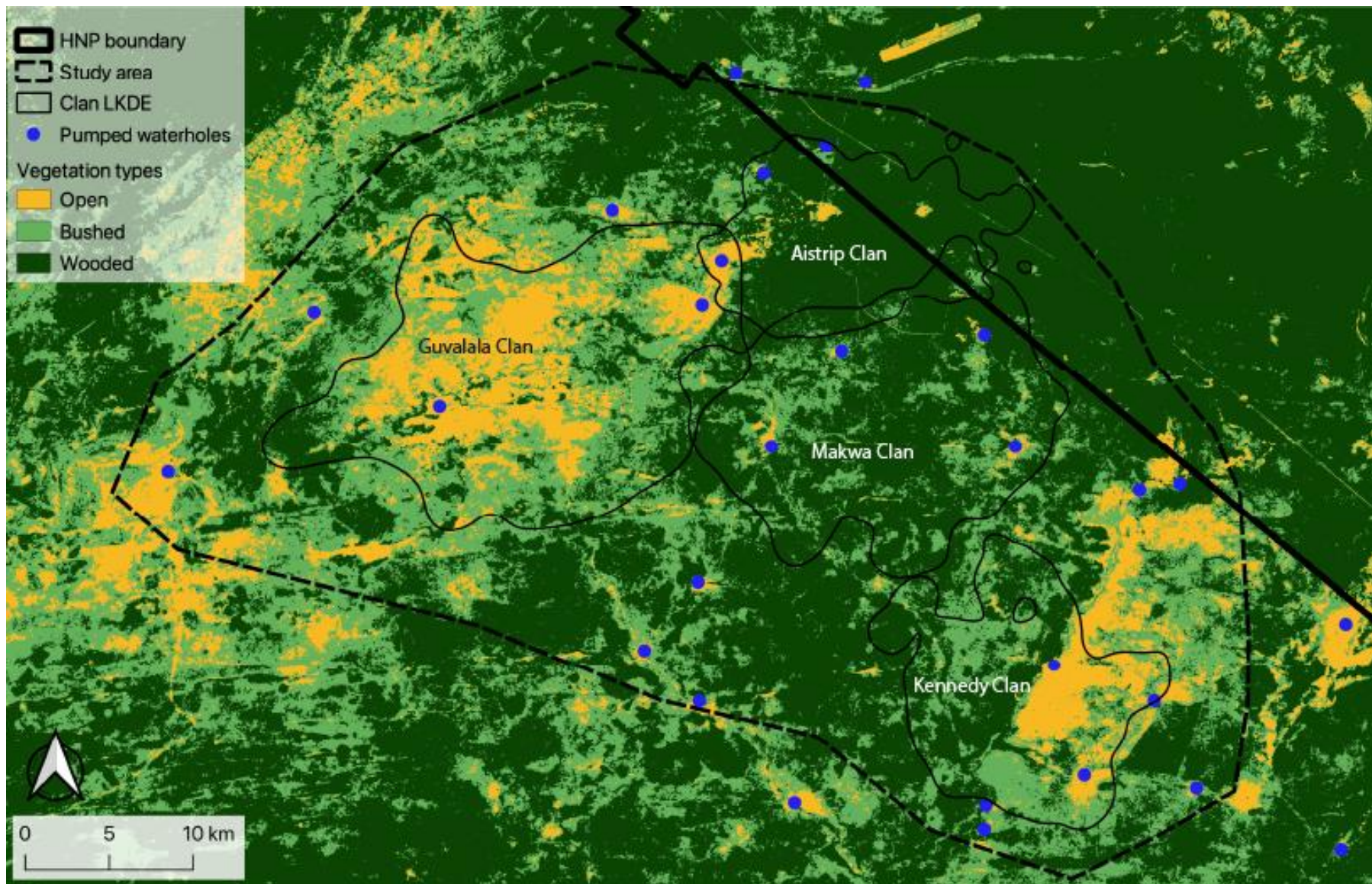
959 Hyaena clan home ranges are also represented using Location based Kernel Density  
960 Estimation computed using data for all individuals belonging to the clan.

961

962

*Figure S1.1*





*Figure S1.2*

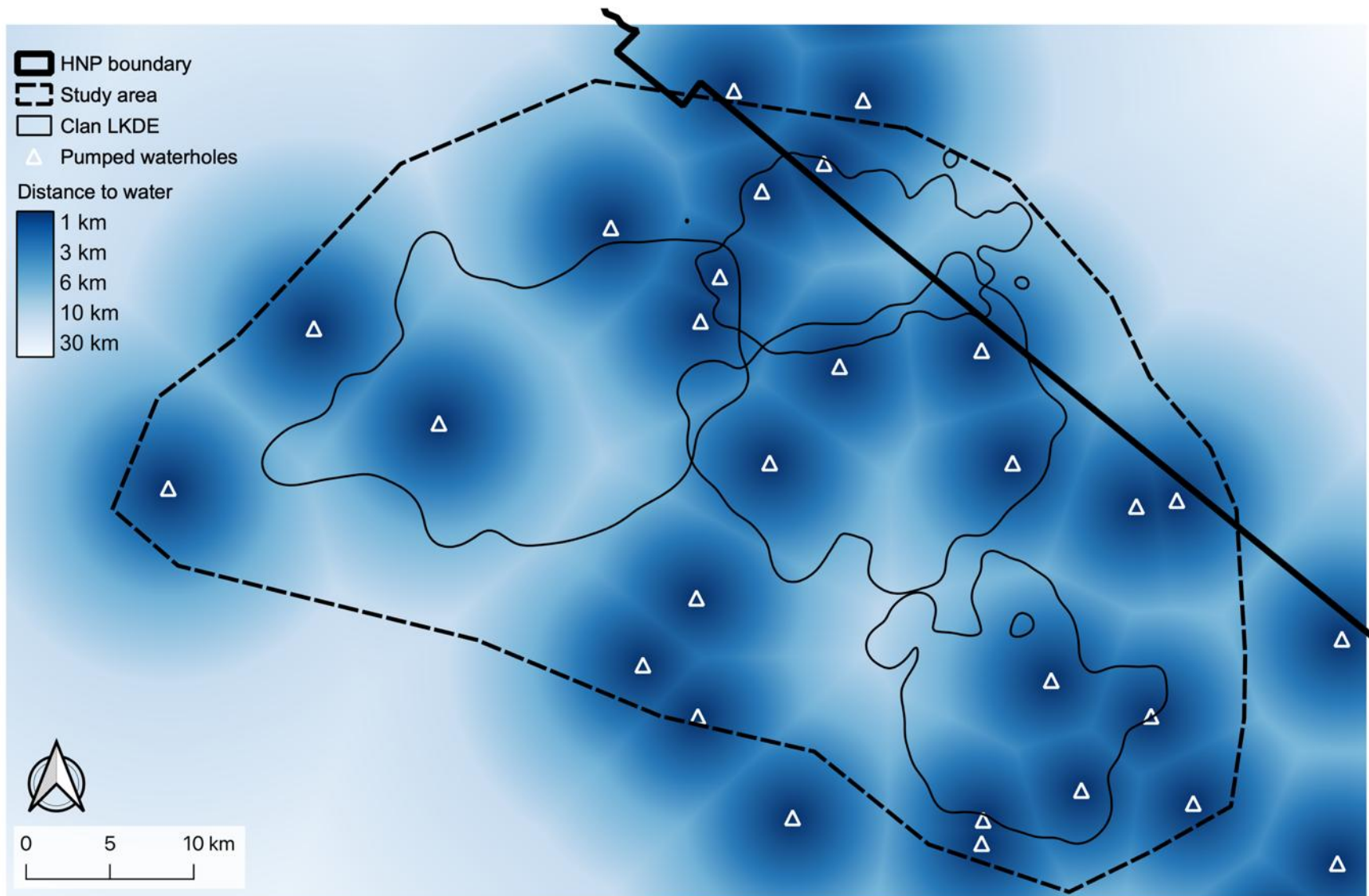
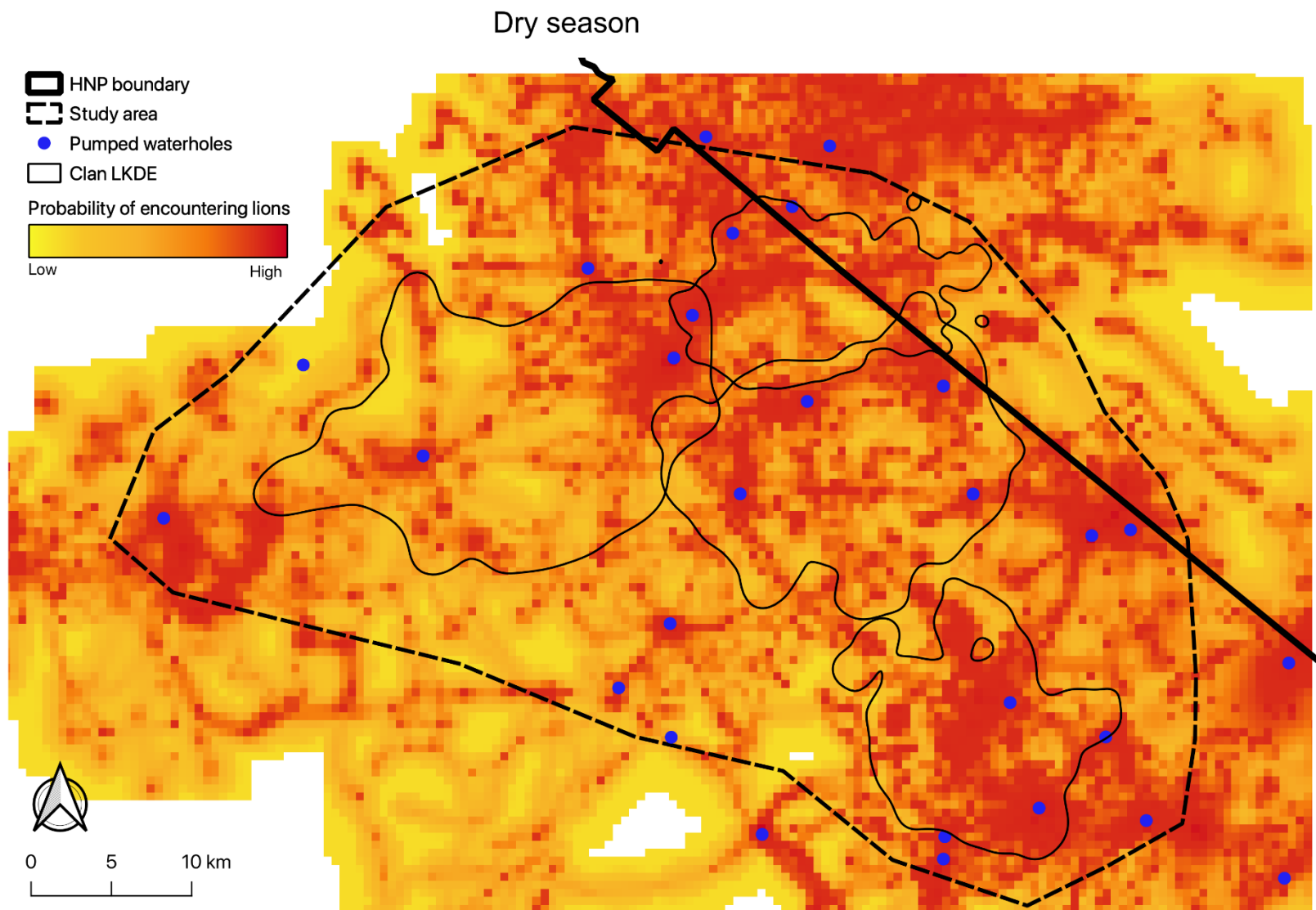
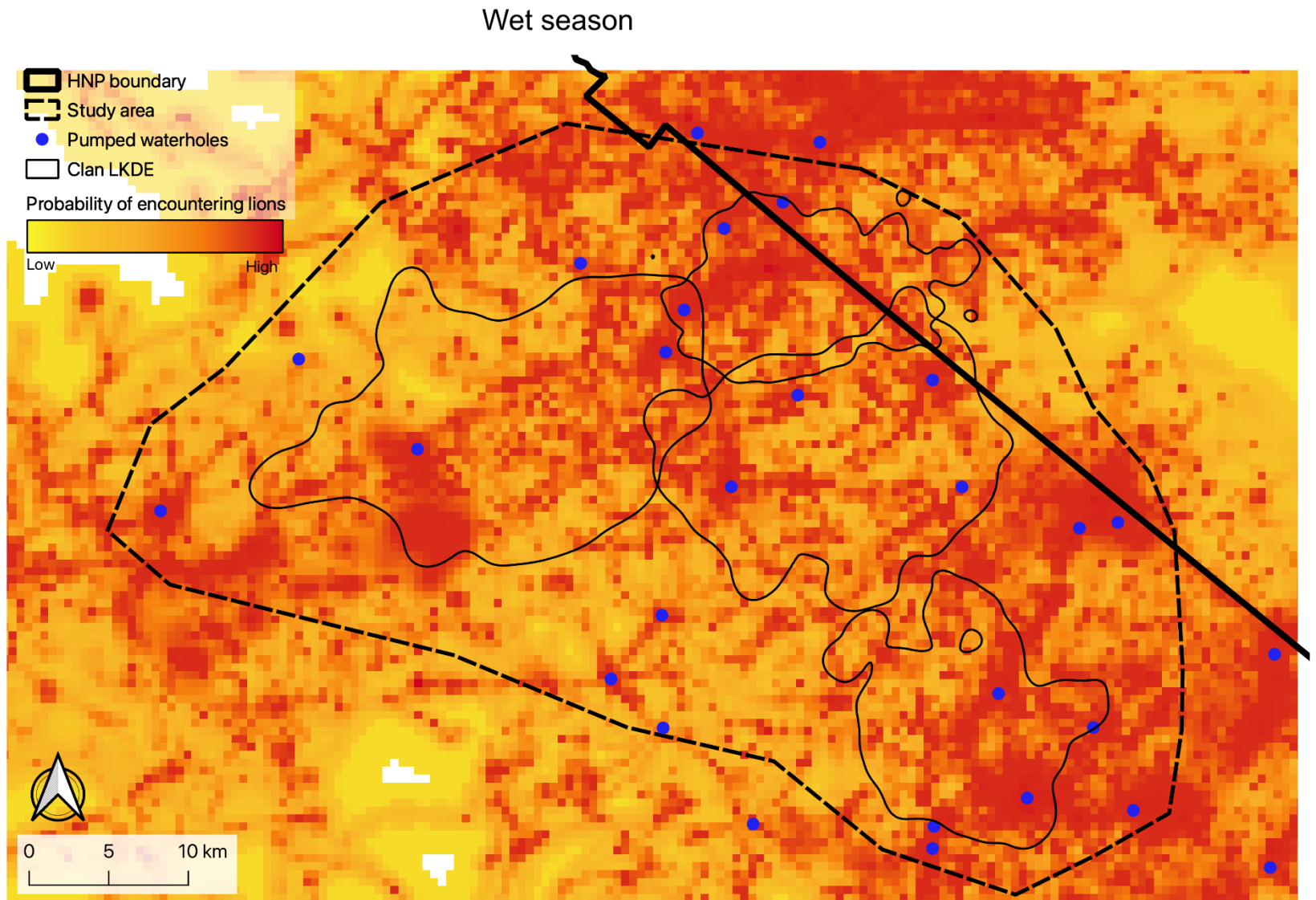


Figure S1.4





970 **SUPPLEMENTARY MATERIAL S2: MODELS SPECIFICATION AND COEFFICIENTS**

971 ***Resource Selection Function***

972 *Model specifications in R*

973 Individual models

974 `rsfi = glm(case ~ vegetation type * distance to water * long-term`  
 975 `risk of encountering lions, family=binomial(), data=di)`

976 With `rsfi` the model using the dataset `di` for individual `i`, `case=1` for used locations and 0  
 977 for random ones. For each individual model, this will result in a list of 11 beta coefficients  
 978 and their standard error (see table below).

Individual #1	Beta coefficient	Beta Standard error
Vegetation – bush	Vb <sub>1</sub>	Vb <sub>1</sub> .SE
Vegetation – open	Vo <sub>1</sub>	Vo <sub>1</sub> .SE
Distance to water	W <sub>1</sub>	W <sub>1</sub> .SE
Risk of encountering lions	L <sub>1</sub>	L <sub>1</sub> .SE
Vegetation – bush x Distance to water	VbW <sub>1</sub>	VbW <sub>1</sub> .SE
Vegetation – open x Distance to water	VoW <sub>1</sub>	VoW <sub>1</sub> .SE
Vegetation – bush x Risk of encountering lions	VbL <sub>1</sub>	VoW <sub>1</sub> .SE
Vegetation – open x Risk of encountering lions	VoL <sub>1</sub>	VbL <sub>1</sub> .SE
Distance to water x Risk of encountering lions	WL <sub>1</sub>	VoL <sub>1</sub> .SE
Vegetation – bush x Distance to water x Risk of encountering lions	VbWL <sub>1</sub>	WL <sub>1</sub> .SE
Vegetation – open x Distance to water x Risk of encountering lions	VoWL <sub>1</sub>	VbWL <sub>1</sub> .SE

979

980 Population model for each predictor

981 `pop = lm(betaspredictor ~ 1, weights = (1/SEpredictor)2, data = param)`

982 With `param` being a data frame containing the coefficient estimates (betas) and their  
 983 standard error (SE) from the individual models for a given predictor. For instance, `param` for  
 984 the population model for the predictor distance to water would contain the list of the  
 985 coefficient for W and of W.SE for each of the nine individual models. Since each individual  
 986 model results in 11 beta coefficients, we therefore built 11 population models.

987

988

989 ***Step Selection Function***

990 *Model specifications in R*

991 **Individual models**

```
992 ssfi = clogit(case ~ step length + log(step length) + cos(turning  
993 angle) + distance to lion * vegetation type + moon * distance to  
994 lion+ moon * vegetation type + distance to lion * vegetation type *  
995 moon + strata(step_id), family=binomial())
```

996 With  $ssf_i$  being the model using the dataset  $d_i$  for individual  $i$ , case=1 for used locations  
997 and 0 for random ones. Vegetation type and distance to lions were measured at the end of the  
998 step.

999 **Population model for each predictor**

```
1000 pop = lm(betaspredictor ~ 1 , weights = (1/SEpredictor)2, data = param)
```

1001  $param$  is a data frame containing the coefficient estimates (betas) and their standard error  
1002 (SE) from the individual models for a given predictor.

1003

1004 *Table S2.1 Selection of the most appropriate transformation for the distance to lion*  
1005 *variable*

1006 We ran each individual model either with no transformation on the distance to lion  
1007 variable, or with log, inverse and square root transformation and compared their AIC to  
1008 determine which model was most fitting the data. For each individual, the model with lowest  
1009 AIC is represented in bold black lettering and models within  $\Delta AIC \leq 2$  are presented in black  
1010 lettering. We used the log transformation, leading to the best models in both seasons overall.

1011

1012

**Dry season**

<i>Individual</i>	<i>None</i>	<i>Transformation</i>		
		<i>Log</i>	<i>Inverse</i>	<i>Square root</i>
MAK1	1825.84	1823.59	1833.27	<b>1823.44</b>
KEN2	854.69	849.49	<b>844.64</b>	852.28
GUV1	<b>1385.71</b>	1387.03	1386.36	1386.73
MAK2	1919.79	1918.01	<b>1916.98</b>	1918.42
AS1	4090.82	<b>4074.74</b>	4079.78	4086.51
GUV2	2276.82	<b>2276.04</b>	2280.89	2279.32
AS2	1453.08	1451.05	<b>1449.25</b>	1452.11
MAK3	1978.78	1977.93	<b>1959.54</b>	1981.04

**Wet season**

<i>Individual</i>	<i>None</i>	<i>Transformation</i>		
		<i>Log</i>	<i>Inverse</i>	<i>Square root</i>
MAK1	2570.47	<b>2547.10</b>	2553.85	2567.06
GUV1	<b>3489.71</b>	3491.87	3492.38	3490.88
KEN2	933.02	929.69	<b>924.92</b>	933.30
GUB1	1413.24	1413.07	<b>1412.97</b>	1413.12
MAK2	<b>1431.72</b>	1432.05	1432.67	1431.95
AS1	8268.48	<b>8240.49</b>	8273.81	8263.22
GUV2	4223.17	<b>4217.94</b>	4218.41	4220.31
AS2	3218.93	3217.81	<b>3217.72</b>	3217.92
MAK3	1357.15	1356.21	1360.64	<b>1356.18</b>

1013

1014

1015 **SUPPLEMENTARY MATERIAL S3: MOON ILLUMINATION EFFECTS**

1016 *Effect of moon illumination on habitat use*

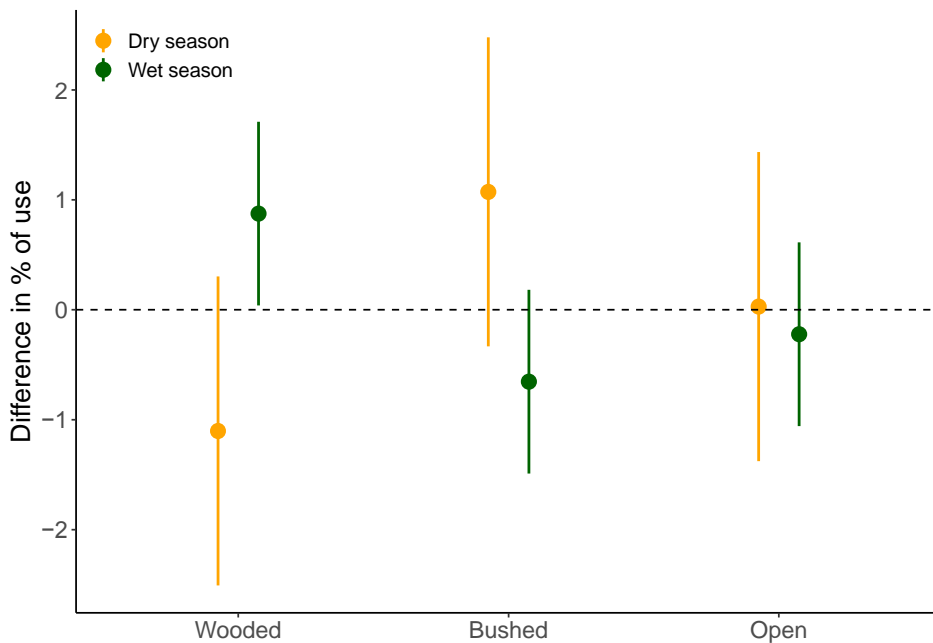
1017 *Table S3.1*

1018 Parameter estimates from Linear Mixed Effect Models with the difference in the  
 1019 proportion of use for each vegetation type between full and new moon nights as the response  
 1020 variable and hyaena identity as a random intercept. Estimates are given with their 95%  
 1021 confidence interval; values in bold are statistically different from zero.

Vegetation type	Dry season	Wet season
	<i>Wooded</i>	-1.1 (-2.48 ; 0.27)
<i>Bushed</i>	<b>2.18 (0.23 ; 4.12)</b>	<b>-1.53 (-2.68 ; -0.37)</b>
<i>Open</i>	1.13 (-0.81 ; 3.07)	-1.1 (-2.25 ; 0.06)

1026 *Figure S3.1 Difference in proportional use of each habitat type between full and new*  
 1027 *moon nights.*

1028 Error bars represent 95% confidence intervals.



1029

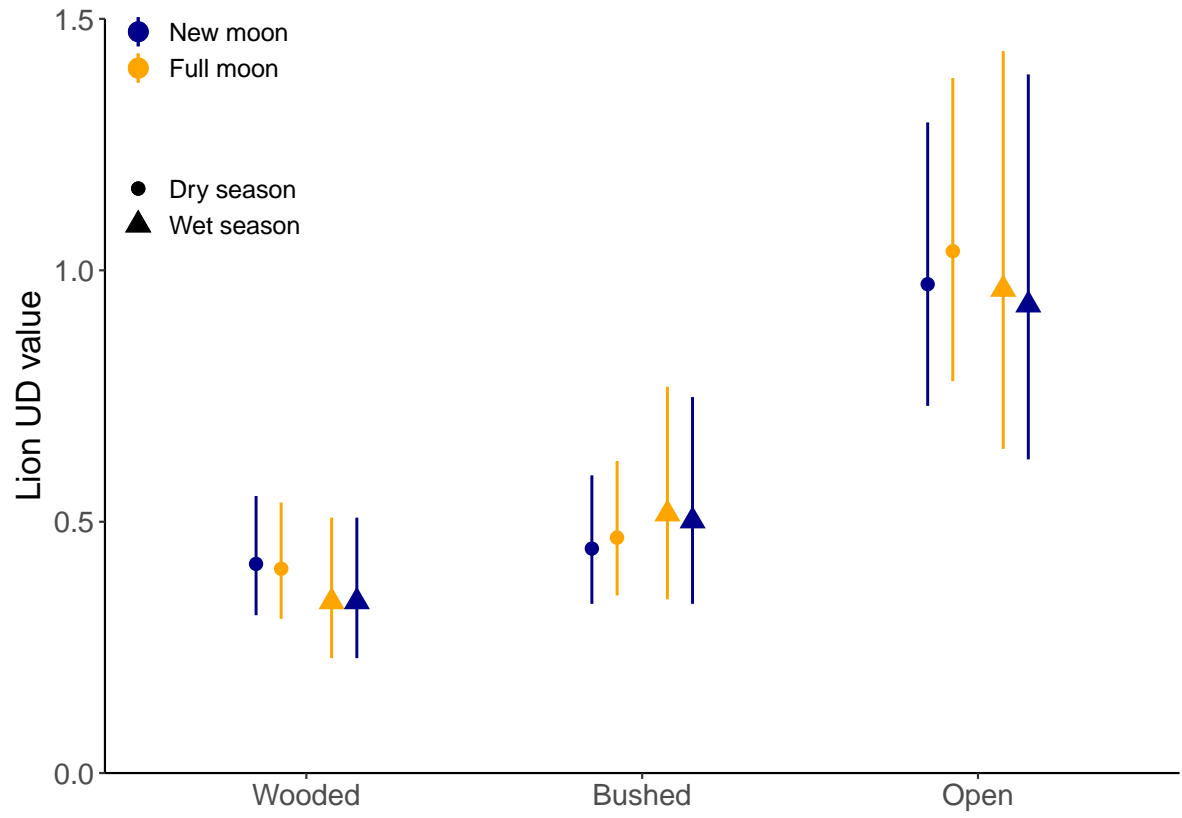
1030 *Effect of moon illumination and vegetation type on habitat use in terms of static long-*  
 1031 *term risk of encountering lions*

1032 *Table S3.2*

1033 Parameter estimates from Linear Mixed effect Models with the static long-term risk of  
 1034 encountering lions at used locations as the response variable and the interaction between  
 1035 moon illumination (full vs new moon) and vegetation type as predictors. Static long-term risk  
 1036 value was log-transformed to meet model assumption and hyaena identity was included as a  
 1037 random intercept. Estimates are given with their 95% confidence interval; values in bold show  
 1038 statistically significant effects.

	<i>Dry season</i>	<i>Wet season</i>
Intercept	-0.9 (-1.2 ; -0.61)	-1.08 (-1.5 ; -0.66)
Full moon	0.02 (-0.02 ; 0.07)	0 (-0.03 ; 0.03)
<b>Bushed vegetation</b>	<b>0.14 (0.09 ; 0.2)</b>	<b>0.41 (0.37 ; 0.45)</b>
<b>Open vegetation</b>	<b>0.94 (0.86 ; 1.02)</b>	<b>1.04 (0.99 ; 1.09)</b>
Full moon : Bushed vegetation	-0.07 (-0.15 ; 0.01)	-0.03 (-0.08 ; 0.02)
Full moon : Open vegetation	-0.09 (-0.19 ; 0.01)	-0.03 (-0.1 ; 0.03)

1044 *Figure S3.2 Effects of vegetation type and moon illumination on habitat use in terms*  
1045 *of long-term risk of encountering lions.*



1046

1047

1048 *Effect of moon illumination and distance to water on habitat use in terms of long-term*  
 1049 *risk of encountering lions*

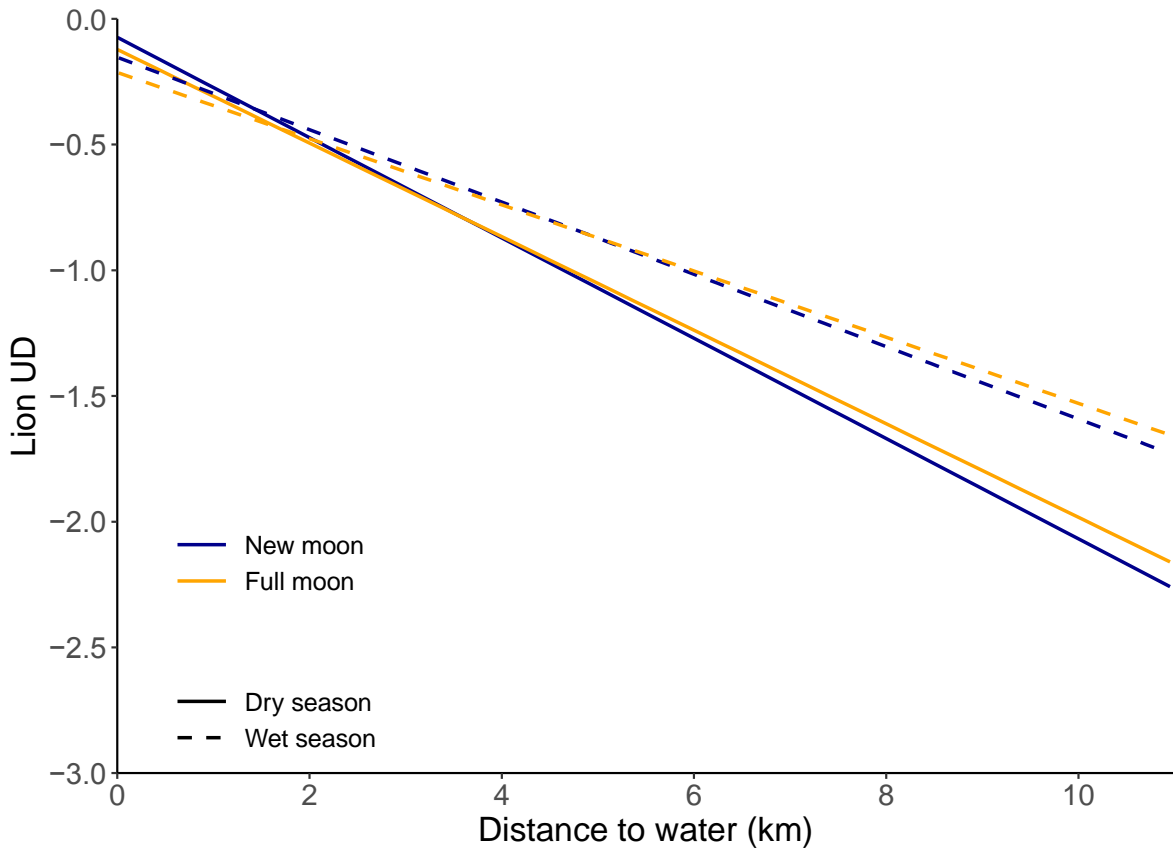
1050 *Table S3.3*

1051 Parameter estimates from Linear Mixed effect Model with the long-term lion risk at used  
 1052 locations as response variable and the interaction between moon illumination (full vs new  
 1053 moon) and distance to water as predictors. Long-term risk value was log-transformed to meet  
 1054 model assumption, and hyaena identity was included as a random intercept. Estimates are  
 1055 given with their 95% confidence interval; values in bold show statistically significant effects.

	<i>Dry season</i>	<i>Wet season</i>
Intercept	-0.07 (-0.3 ; 0.15)	-0.15 (-0.51 ; 0.21)
Full moon	-0.05 (-0.11 ; 0.01)	-0.06 (-0.11 ; -0.01)
<b>Distance to water</b>	<b>-0.0002 (-0.0002 ; 0.0002)</b>	<b>-0.0001 (-0.0002 ; 0.0001)</b>
Full moon : Distance to water	0.00001 (-0.0000003 ; 0.00003)	0.00001 (-0.0000002 ; 0.00002)

1056  
 1057

1058 *Figure S3.3 Effects of vegetation type and distance to water on habitat use in terms of*  
1059 *long-term risk of encountering lions.*

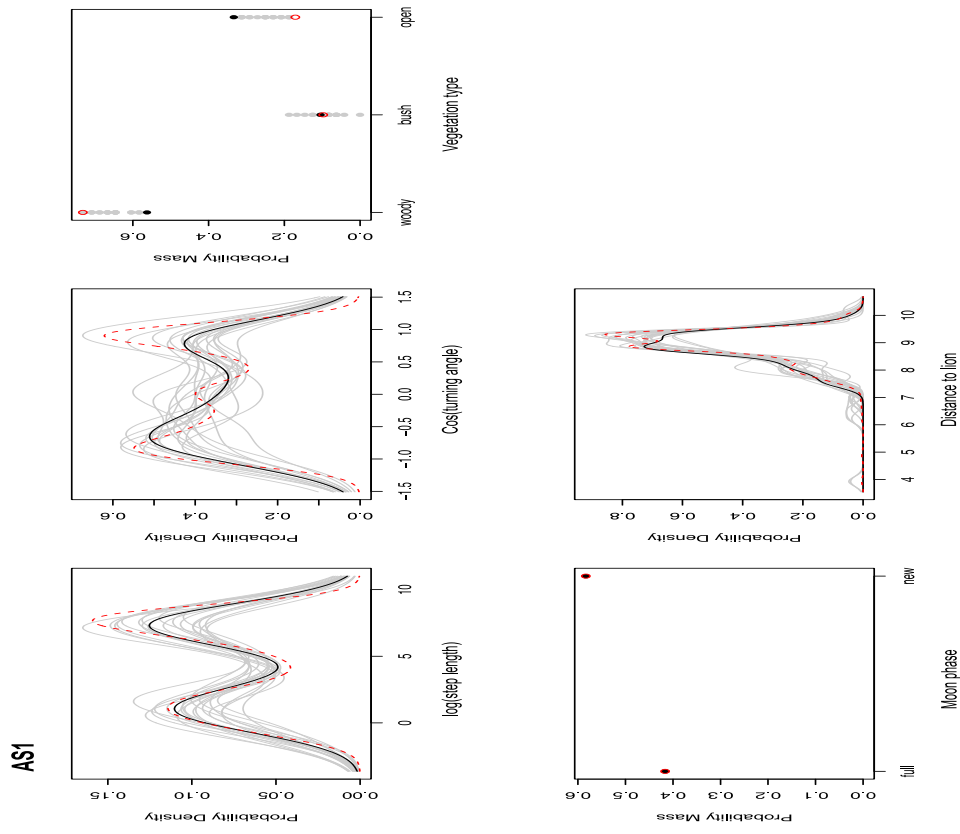


1060  
1061

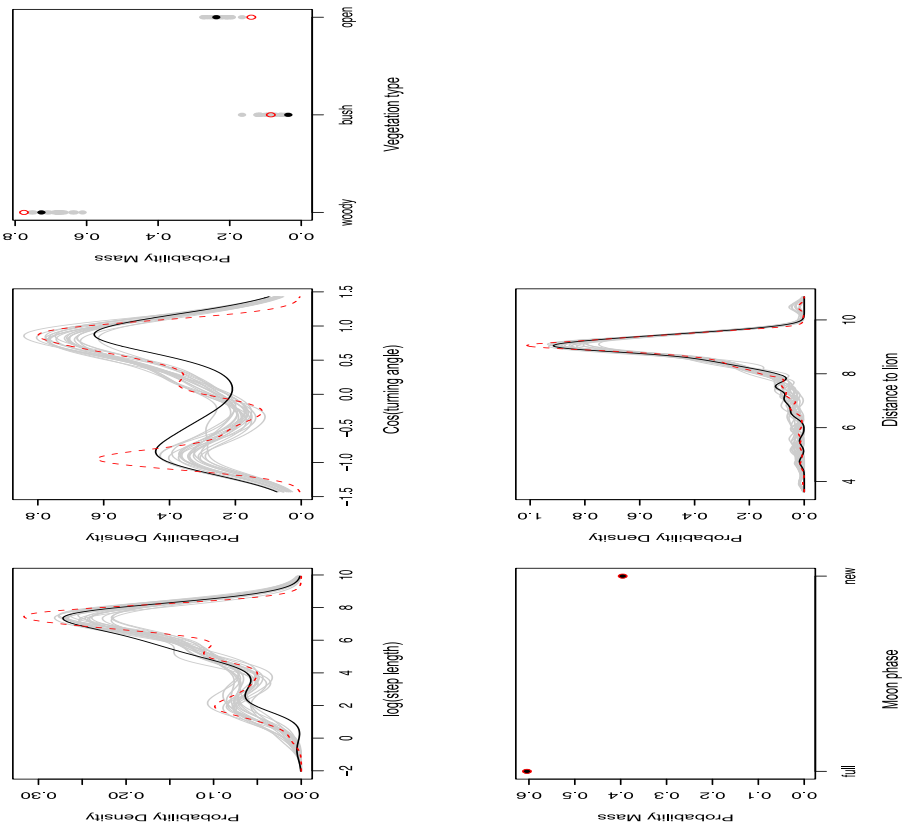
1062 **SUPPLEMENTARY MATERIAL S4: USED HABITAT CALIBRATION (UHC) PLOTS**

1063 This Supplementary material presents the UHC plots for each individual SSF as  
1064 recommended by Fieberg *et al.* (2018). We used 80% of the data of each individual as a  
1065 training set and the remaining 20% as a testing set and ran 20 simulations. In each figure, the  
1066 dotted red line represents the distribution of the predictor at available locations (i.e. the  
1067 availability), the black solid line is the distribution of predictor at the used locations and the  
1068 light grey solid lines, the results of the 20 simulations. In well-calibrated models, the black  
1069 line falls within the envelopes of the grey lines.

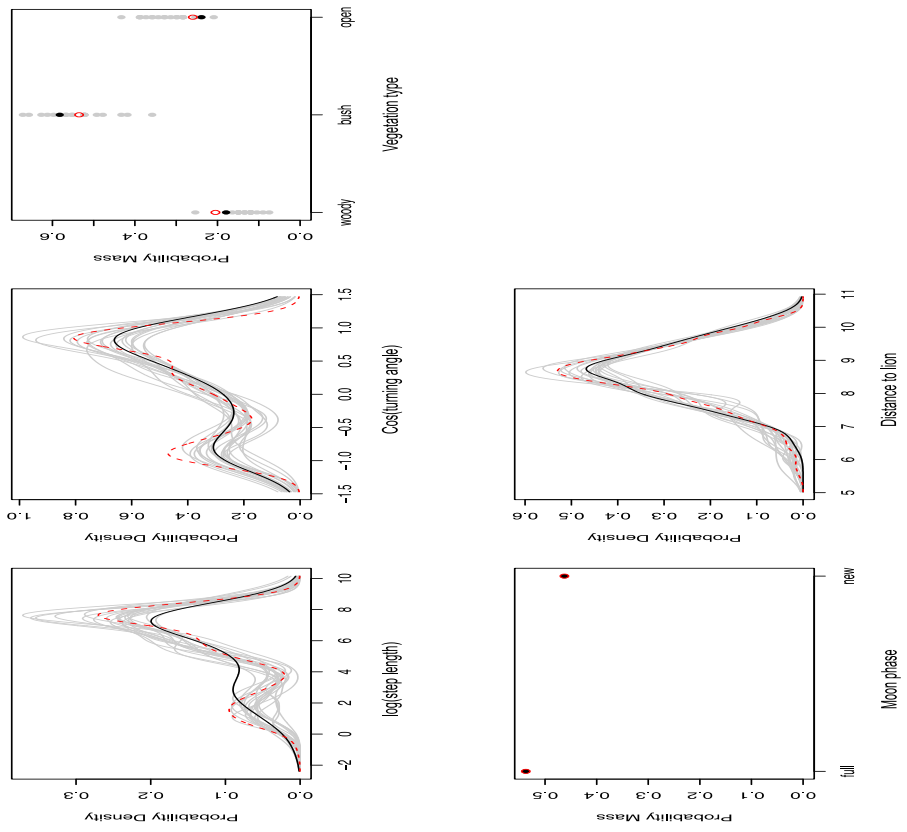
1070 *Figure S4.1: Dry season UHC plots*



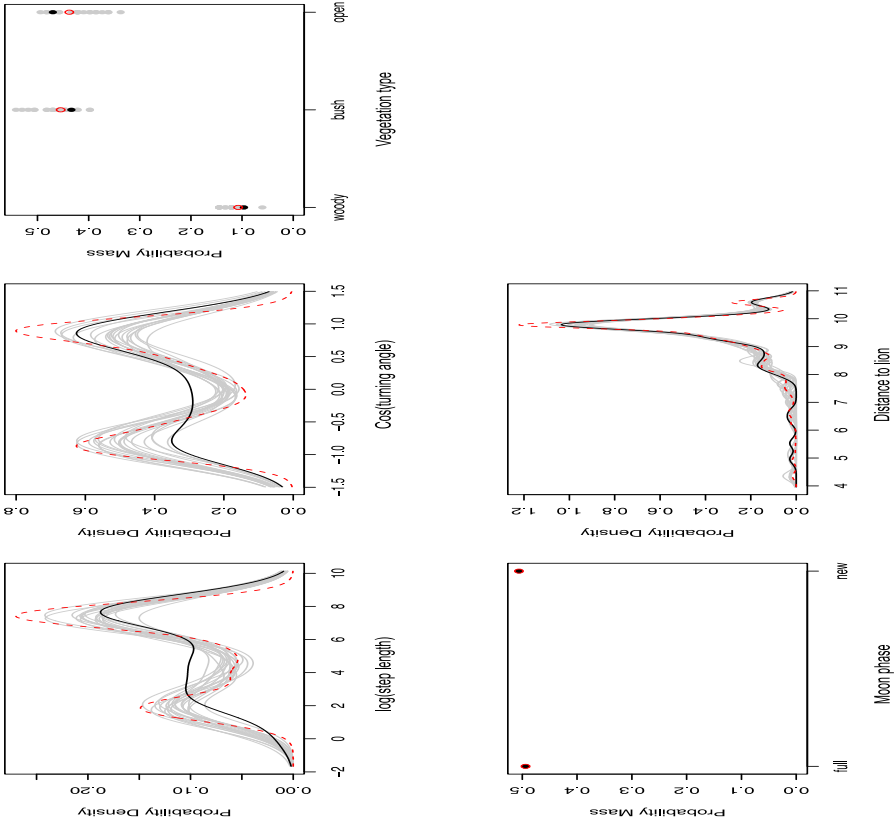
AS2

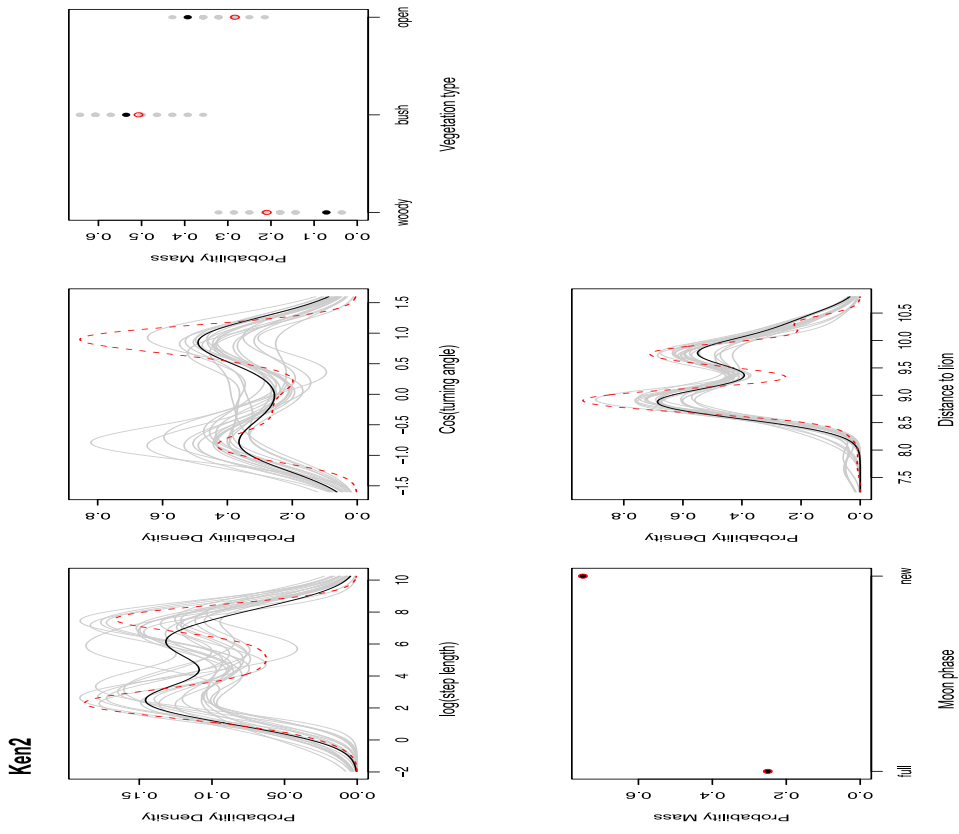


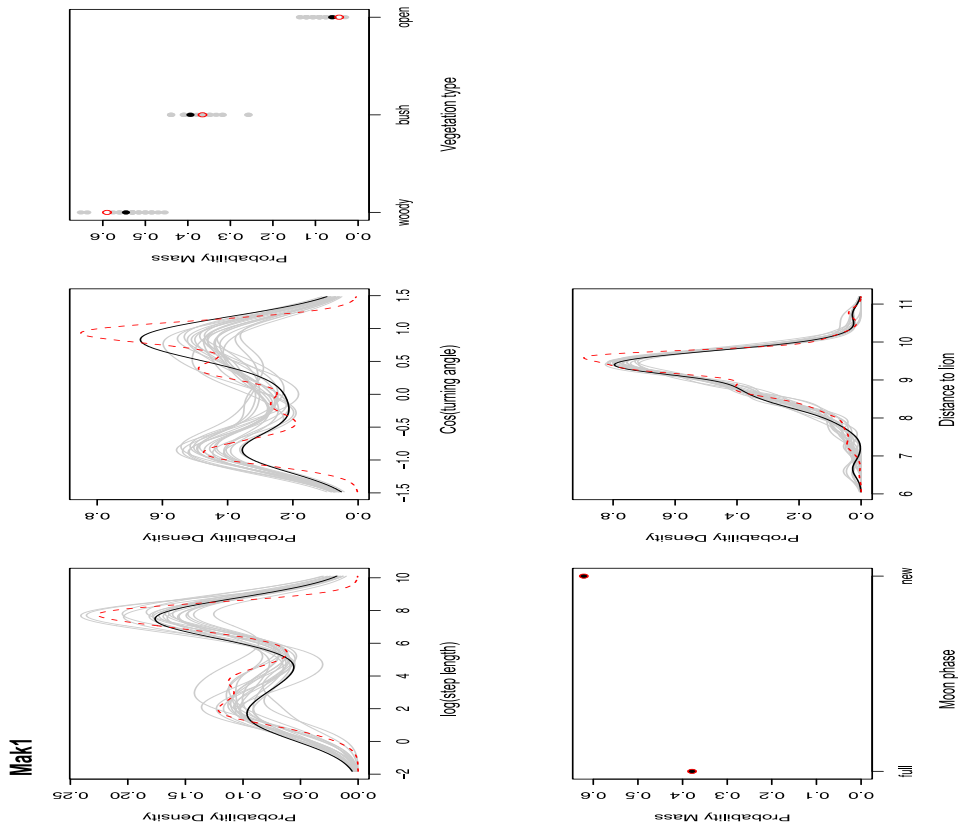
Guw1



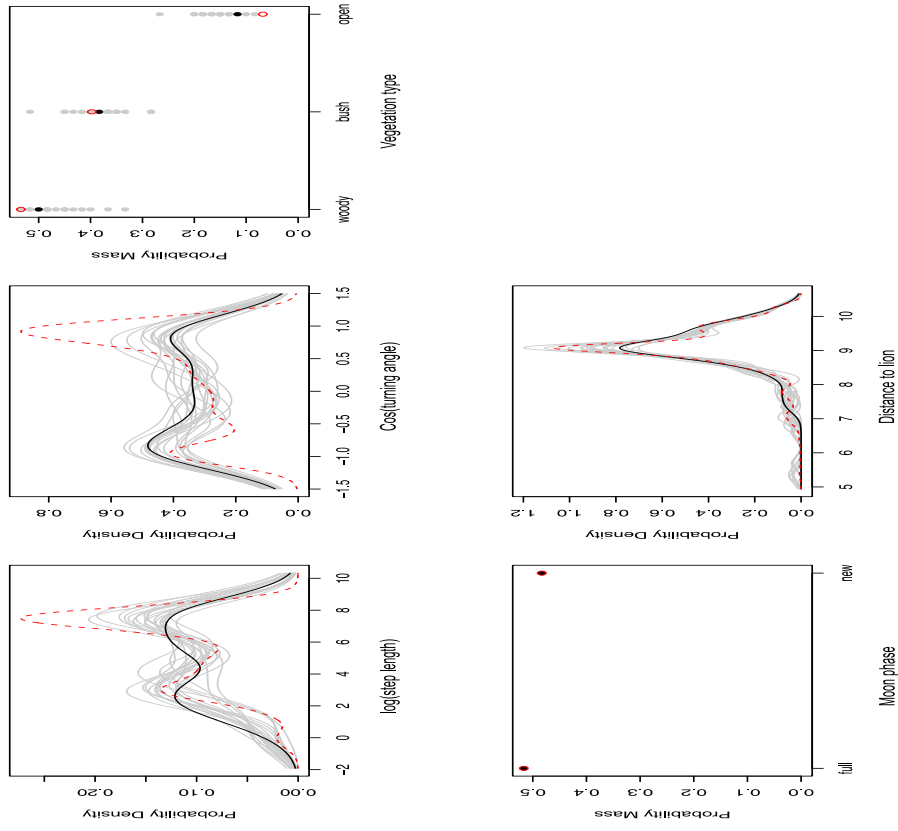
Gur2



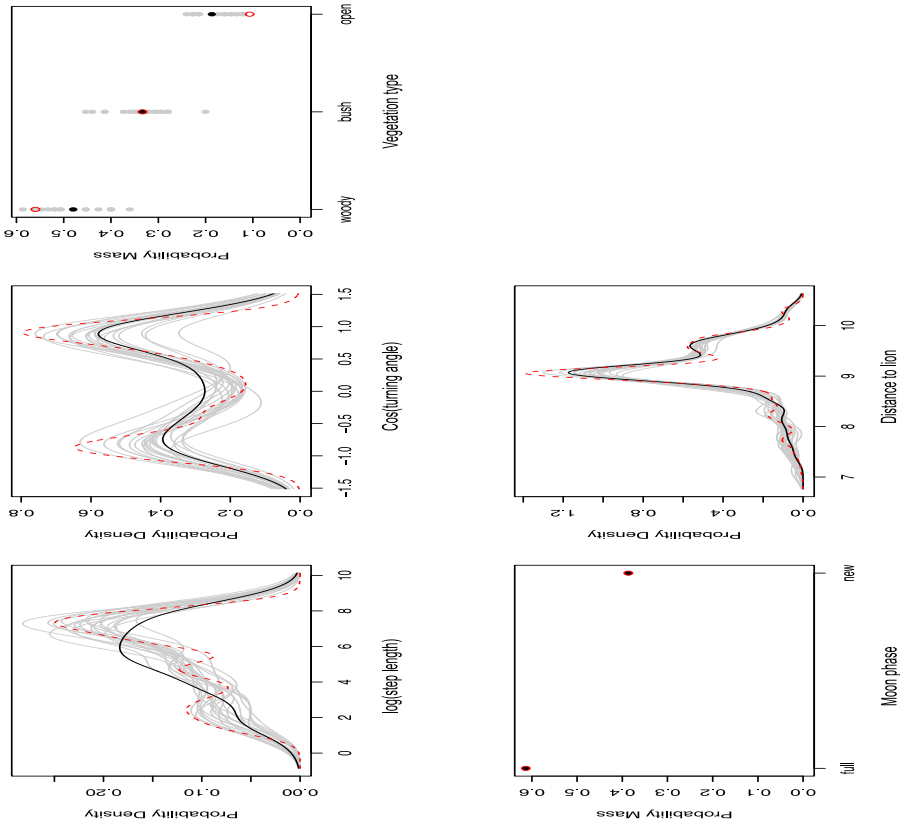




Mark2



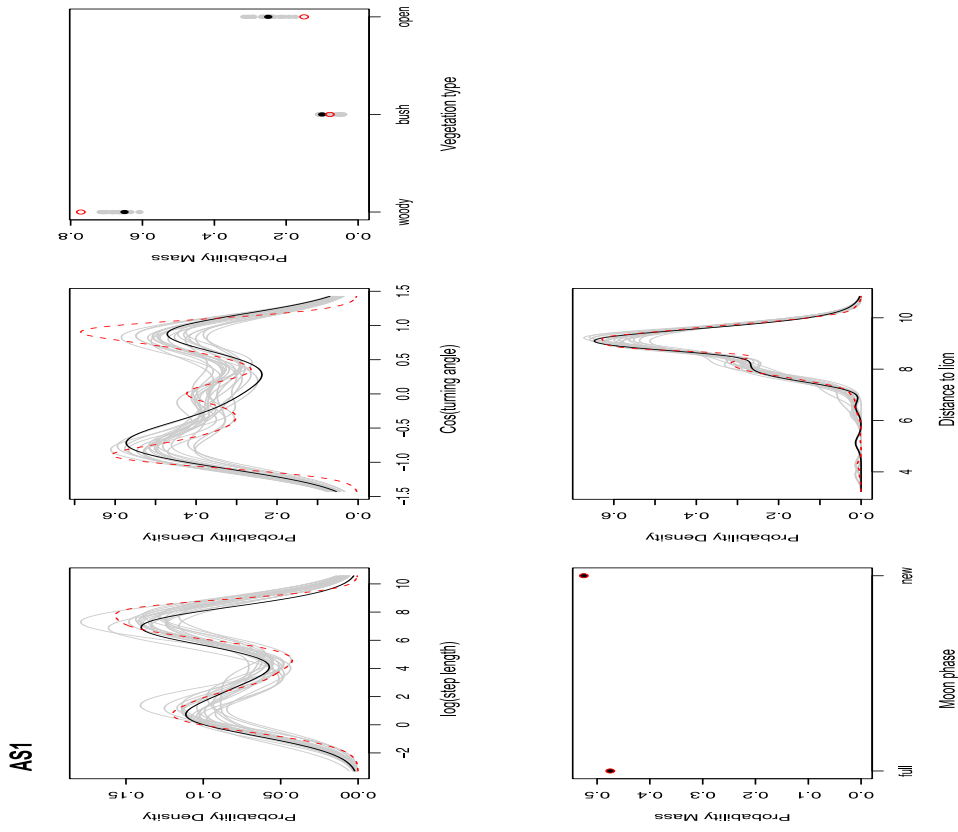
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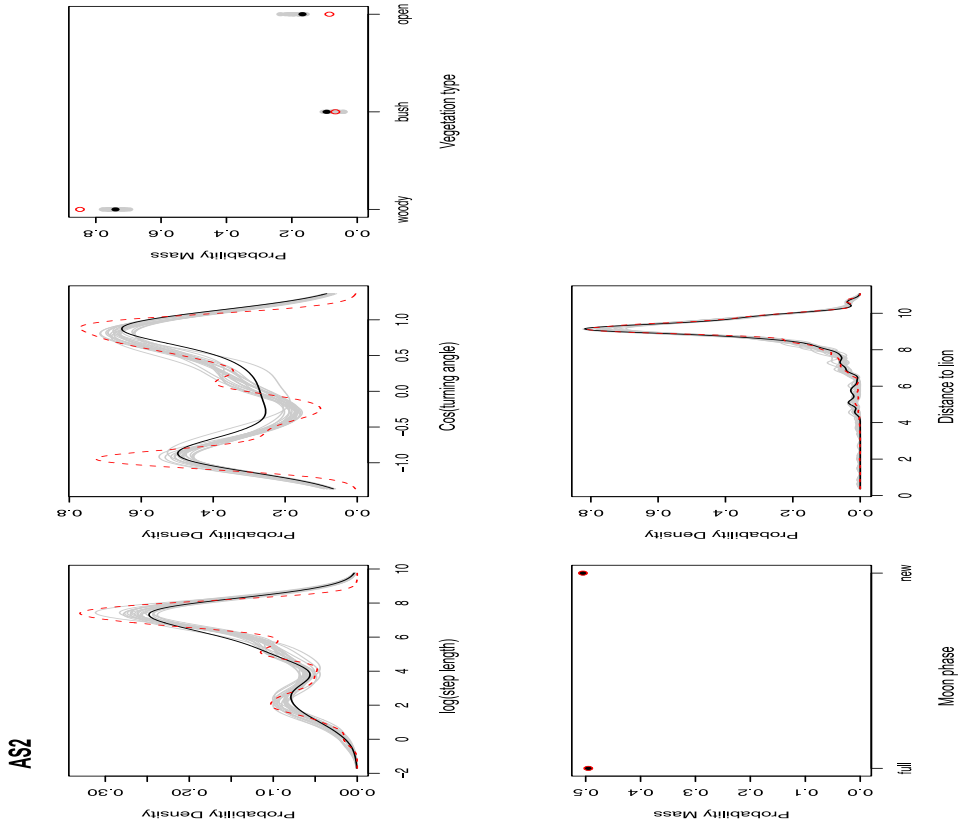


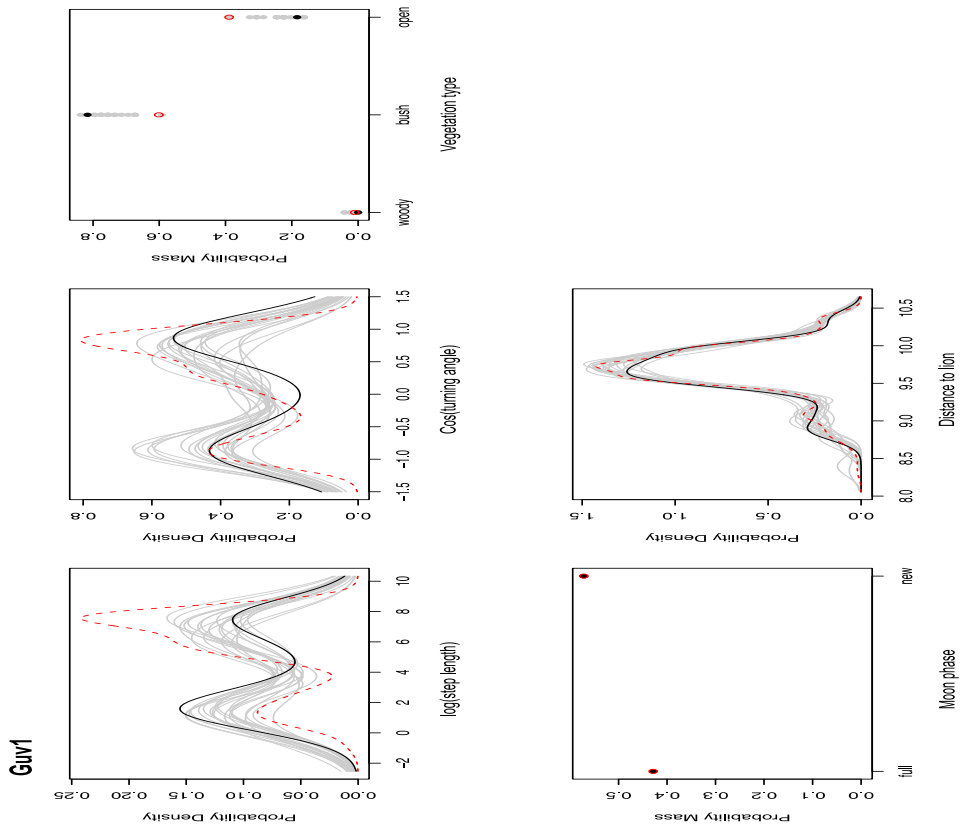
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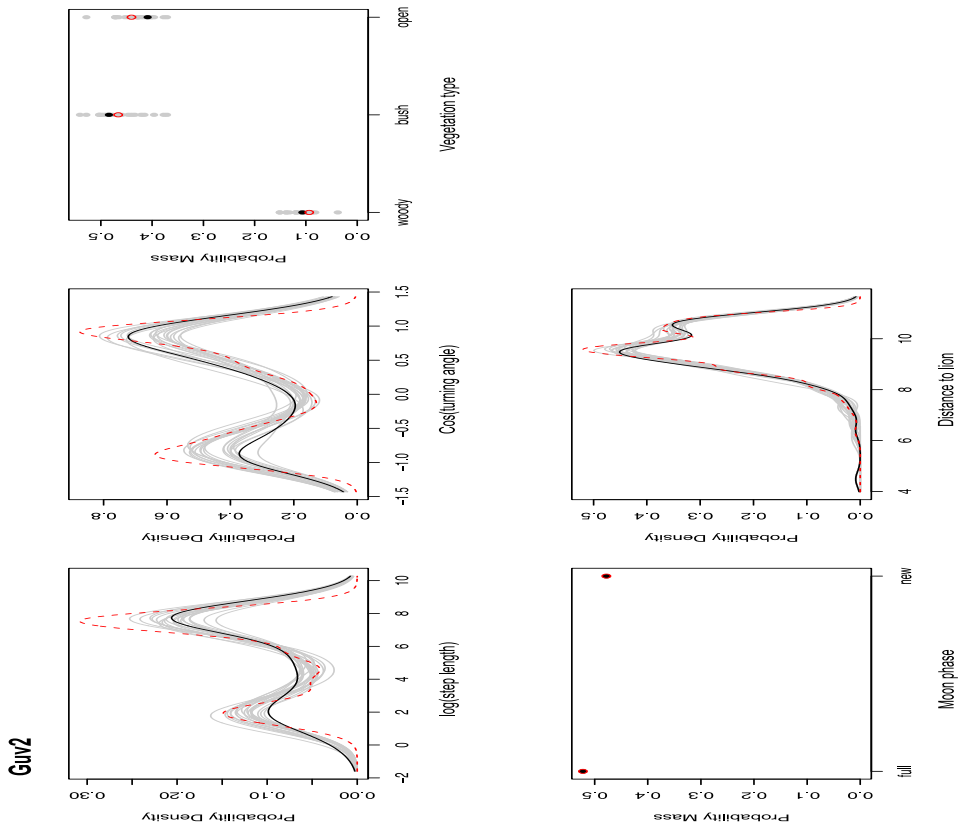
1079

Figure S4.1: Wet season UHC plots

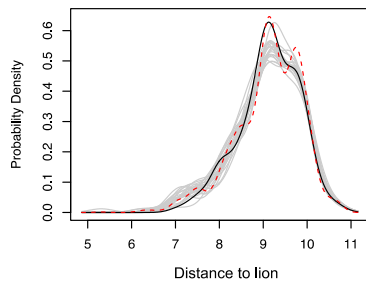
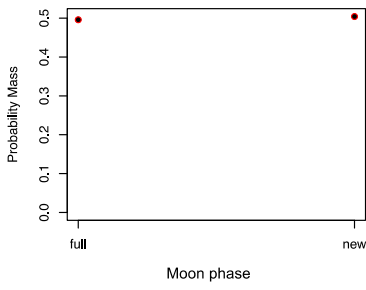
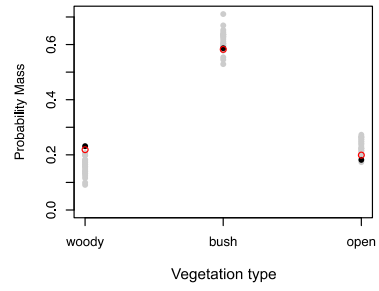
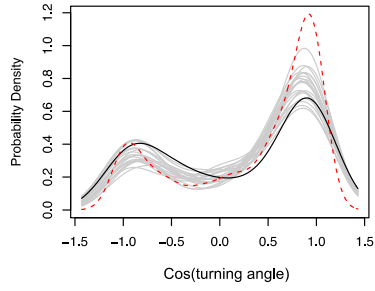
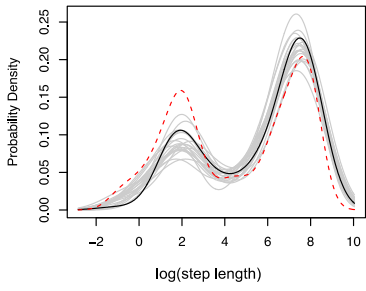




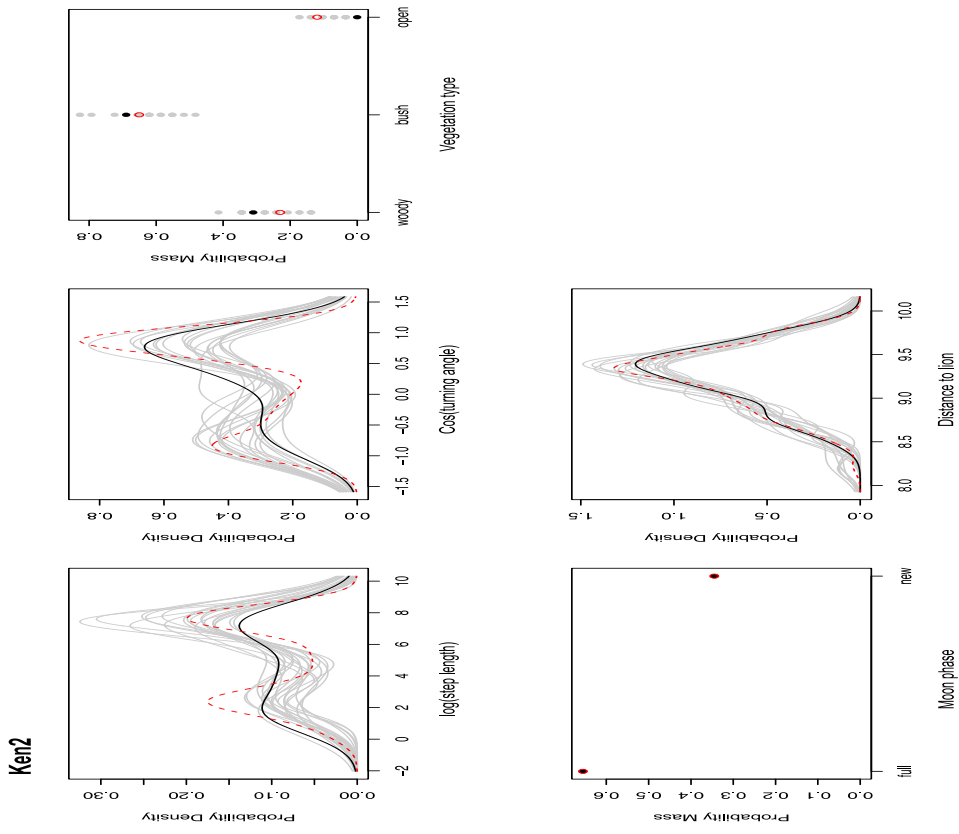




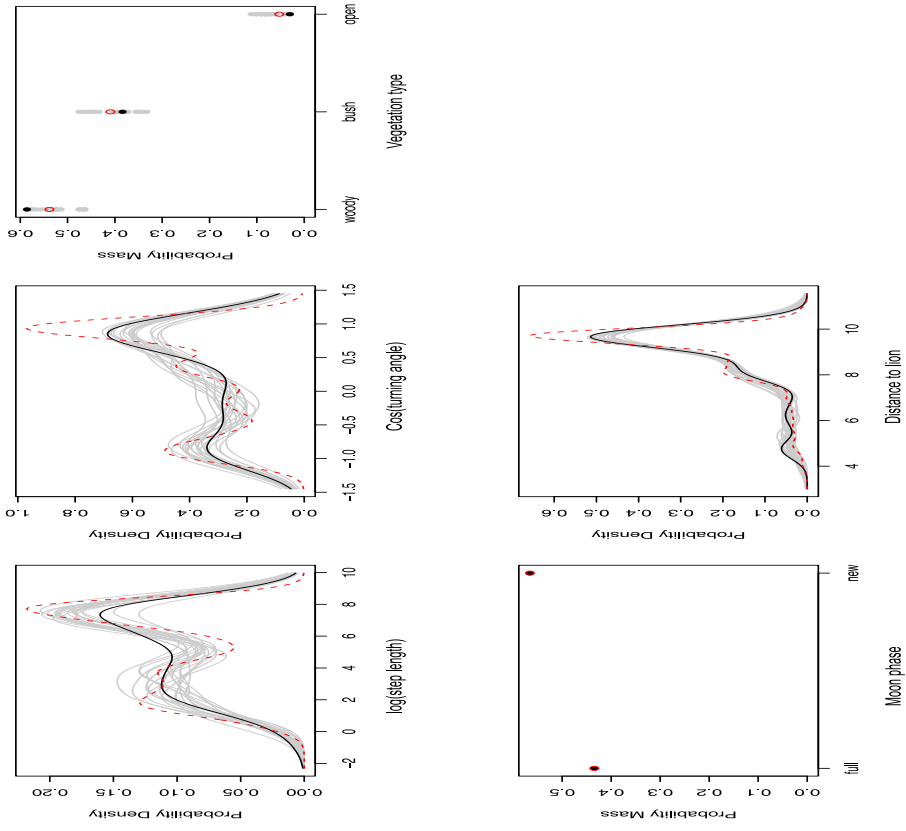
### Ken1

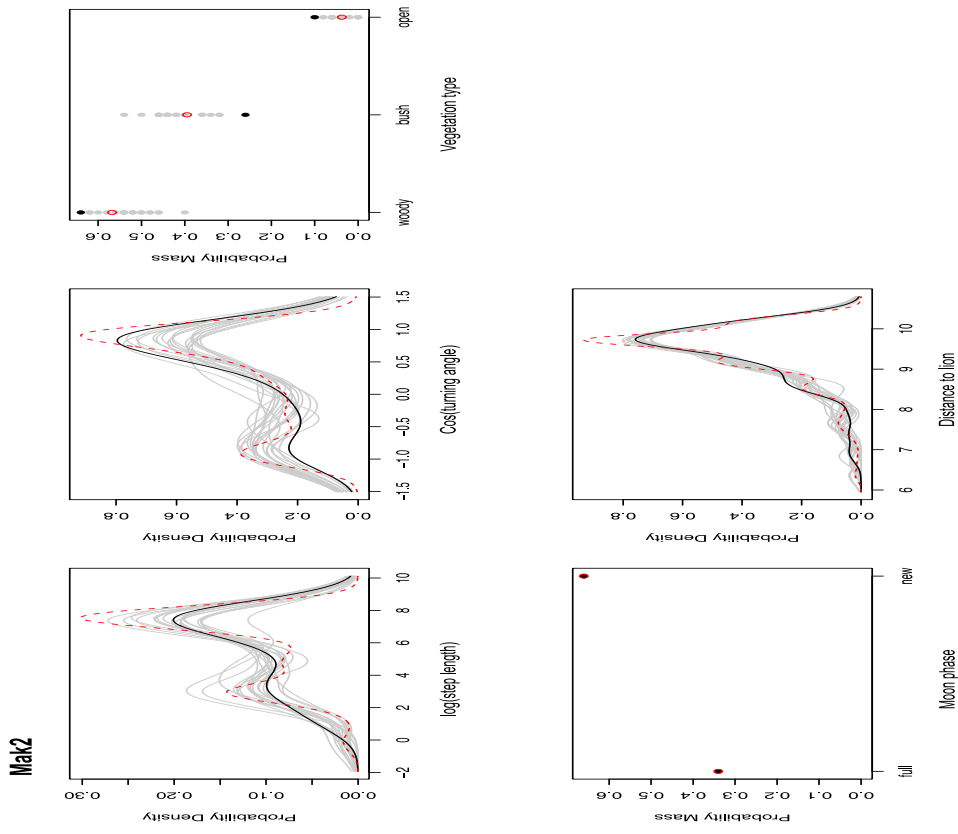


1085



Mak1





Mark3

