

1 **COUNTER-STRATEGIES TO INFANTICIDE: THE IMPORTANCE OF CUBS IN**

2 **DETERMINING LION HABITAT SELECTION AND SOCIAL INTERACTIONS**

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20 **ABSTRACT**

21 1. Animal social and spatial behaviours are inextricably linked. Animal movements are
22 driven by environmental factors and social interactions. Habitat structure and changing
23 patterns of animal space use can also shape social interactions.

24 2. Animals adjust their social and spatial behaviours to reduce the risk of offspring
25 mortality. In territorial infanticidal species, two strategies are possible for males: they
26 can stay close to offspring to protect them against rivals (infant-defence hypothesis) or
27 patrol the territory more intensively to prevent rival intrusions (territorial-defence
28 hypothesis). Here, we tested these hypotheses in African lions (*Panthera leo*) by
29 investigating how males and females adjust their social and spatial behaviours in the
30 presence of offspring.

31 3. We combined data sets on the demography and movement of lions, collected
32 between 2002 and 2016 in Hwange National Park (Zimbabwe), to document the
33 presence of cubs (field observations) and the simultaneous movements of groupmates
34 and competitors (GPS tracking).

35 4. We showed a spatial response of lions to the presence of offspring, with females with
36 cubs less likely to select areas close to waterholes or in the periphery of the territory
37 than females without cubs. In contrast, these areas were more selected by males when
38 there were cubs in the pride. We also found social responses. Males spent more time
39 with females as habitat openness increased, but the presence of cubs in the pride did
40 not influence the average likelihood of observing males with females. Furthermore,
41 rival males relocated further after an encounter with pride males when cubs were

42 present in the prides, suggesting that the presence of cubs leads to a more vigorous
43 repulsion of competitors. Males with cubs in their pride were more likely to interact
44 with male competitors on the edge of the pride's home range and far from the
45 waterholes, suggesting that they are particularly assiduous in detecting and repelling
46 rival males during these periods.

47 5. In general, the strategies to avoid infanticide exhibited by male lions supported the
48 territorial-defence hypothesis. Our study contributes to answer the recent call for a
49 behavioural ecology at the spatial-social interface.

50 Keywords: habitat selection; infanticide; male-female association; movement ecology;
51 *Panthera leo*; social behaviour; social environment; territoriality

52 **1. INTRODUCTION**

53 Animal movement decisions are naturally shaped by factors in their environment
54 (resources, refuges, breeding areas), but they are also influenced by social interactions.
55 For example, depending on species, sex, age, and other factors, individuals may be
56 attracted to, or avoid, a food source already being used by a conspecific. Individuals can
57 also track the movement of potential mates and avoid sexual competitors or repel
58 them to minimize sexual competition for mates. Socially-influenced movements occur
59 continuously in group-living species (Fichtel et al., 2011), and even solitary animals
60 respond to the presence of conspecifics, as they need at times to engage in exploration
61 to find a mate to reproduce (Leyhausen, 1964). Despite social and spatial behaviours
62 being intertwined, studies investigating these processes simultaneously are rare,
63 especially because social behaviour is traditionally studied from direct observation of

64 focal groups whereas spatial behaviour is mostly studied at the landscape-scale
65 (Webber et al., 2023).

66 The presence of offspring is a major source of adjustment of the social and
67 spatial behaviours in animals, especially regarding the risk of predation on offspring or
68 the risk of infanticide. For example, species that live in fission-fusion societies can form
69 larger groups, potentially in safer habitats, to prevent the risk of predation on offspring
70 (Bond et al., 2019; Holmes et al., 2016). Even carnivores adjust their movement rate to
71 the presence of offspring in response to the risk of intra-guild predation (Goodheart et
72 al., 2022). Among taxa in which infanticide occurs, such as primates, carnivores, and
73 rodents (Agrell et al., 1998), the infant safety hypothesis proposes that females with
74 offspring are less gregarious and avoid males to reduce the risk of infanticide (Otali &
75 Gilchrist, 2006; Smith et al., 2008). Such social-avoidance behaviours are expected to
76 shape the spatial behaviour of females. For example, adult females with offspring move
77 further from territory edges and maintain smaller home ranges (Benson &
78 Chamberlain, 2007; Boydston et al., 2003; Klevtcova et al., 2021). However, females
79 have the option to adjust many other behaviours to decrease the risk of infanticide
80 (Agrell et al., 1998), such as by increasing the frequency and intensity of agonistic
81 interactions (Elwood et al., 1990), or by the formation of maternal groups (Grinnell &
82 McComb, 1996).

83 In social species, males also adopt counterstrategies to infanticide (Agrell et al.,
84 1998). Two strategies may exist for territorial males to reduce the risk of infanticide:
85 staying close to females to protect offspring against rivals (here formulated as the
86 “infant-defence hypothesis”; Van Schaik & Kappeler, 1997) or patrolling the territory

87 more intensely to prevent the intrusion of rivals (here formulated as the “territorial-
88 defence hypothesis”; McLean, 1983). However, such socio-spatial responses to the
89 presence of offspring can be in competition. By staying close to females with offspring,
90 males reduce their patrols throughout their territory, and, conversely, increasing their
91 patrols reduces the time available to spend close to females to protect offspring.
92 Therefore, although the two hypotheses are not mutually exclusive, it is necessary to
93 investigate how social-territorial animals simultaneously adjust their social and spatial
94 behaviours to the presence of offspring to distinguish their associated predictions.

95 Temporal variations in interactions between groupmates, driven by reproductive
96 status and presence of offspring, have been described quantitatively mainly through
97 detailed and continuous field observations of focal groups (Clutton-Brock, 2016).
98 Knowledge of the associated changes in habitat selection has accumulated because of
99 these studies, but generally only at a relatively small spatial scale or at a coarse grain
100 (individuals seen/not seen with others, ignoring the locations of the unseen
101 individuals). Rigorous quantification of how habitat selection is modified with changing
102 social circumstances, such as in the presence of offspring, has lagged (Webber et al.,
103 2023; Westley et al., 2018). In particular, little is known about how conspecifics influence
104 habitat selection among mammals (Buxton et al., 2020). Here, we address this gap by
105 investigating how social, territorial, and infanticidal animals adjust their spatial and
106 social behaviours in response to the presence of offspring, when they face a trade-off
107 between protecting offspring and patrolling territory.

108 African lions (*Panthera leo* ; lions hereafter) are territorial animals that live in
109 social groups (prides) composed of related females and a coalition of males (“pride

110 males" hereafter) that compete with other coalitions for exclusive access to females
111 (Bygott et al., 1979; Schaller, 1972). The arrival of a new coalition of males in a pride
112 leads to infanticide of the existing cubs (Schaller, 1972) or to the rapid eviction of
113 subadults, which are unlikely to survive dispersal if they are younger than 3 years
114 ('delayed infanticide' *sensu* (Elliot et al., 2014)). Since cubs suffer high mortality from
115 infanticidal males until about 1 year (Packer, 2000), we expect major adjustments of the
116 spatial and social behaviour of females to their presence, but also of pride males to
117 secure pride tenure long enough for cubs to reach independence and disperse (Packer
118 & Pusey, 1983). Even in the absence of male takeovers, lion cubs suffer from
119 opportunistic infanticide by females from neighbouring prides or transient males
120 traveling within the territory, or suffer from intraguild predation, particularly from
121 spotted hyaenas *Crocuta crocuta* (Curveira-Santos et al., 2022; Mosser & Packer, 2009;
122 Schaller, 1972). Although pride females form nursery groups to protect cubs (Packer et
123 al., 1990; Packer & Pusey, 1983), paternal care and male strategies to avoid infanticide
124 have been overlooked. Here, we used the intensive long-term monitoring of a lion
125 population in Hwange National Park, (Zimbabwe), and combined demographic and
126 GPS-tracking data to investigate the spatial and social responses of lions to the
127 presence of cubs. To test the infant-defence and territorial-defence hypotheses, we
128 specifically addressed three questions:

129 Question 1: How do lions respond spatially to the presence of cubs? We tested whether
130 the presence of cubs influences the selection of habitat by female and male lions.
131 Following the infant-defence hypothesis, we predicted that when there are cubs in a
132 pride, both females and males should select habitats that minimize the risk of

133 encountering a rival male (i.e., areas more central to their home range, and far from
134 water sources known to attract lions (Davidson et al., 2012)) and cub detection by rival
135 males (i.e., selection of denser vegetation).

136 Question 2: How does the presence of cubs influence the association between pride
137 females and males? According to the infant-defence hypothesis, we predicted that pride
138 males should be observed more frequently and for longer periods with their pride
139 females when there are cubs in the pride. We further predicted that males should stay
140 near females even more when the habitat within the pride territory is open, since a
141 greater visibility may mean that males need to patrol less (Funston et al., 1998).

142 Question 3: How does the presence of cubs influence the interactions between rival
143 males? The territorial-defence hypothesis states that pride males patrol their territory
144 more, and attempt more stringently to keep out rival males, in the presence of cubs.
145 This more assiduous defensive behaviour would be interpreted as an adaptation to
146 reduce the risk of intrusion by potentially infanticidal males into the pride territory.
147 Accordingly, we predicted that male-male interactions should be more frequent, further
148 from the territory core, and more intense, with the consequence that rival males
149 relocate further from the encounter site with a pride male, at time when there are cubs
150 in the pride.

151 **2. MATERIALS AND METHODS**

152 **2.1. Study area and environmental data**

153 The study was carried out in the north-eastern region of Hwange National Park,
154 Zimbabwe. The park covers 14,600 km² of semi-arid savanna. Natural rain-fed pans dry

155 during the dry season from May to October, and water remains available only in some
156 waterholes in which underground water is pumped (Chamaillé-Jammes et al., 2007).
157 Vegetation is dominated by bushlands and woodlands interspersed with patches of
158 grasslands, particularly near waterholes. For the study conducted here, we built a map
159 of vegetation openness: we used the 30-m resolution vegetation map produced by
160 (Arraut et al., 2018) to calculate, for each pixel, the proportion of open vegetation
161 (category 'grassland' and 'open bushlands' in the original map) in a radius of 250 m.

162 **2.2. Lion Population Monitoring**

163 The demographic characteristics of lion prides (mating partners, births, deaths) were
164 recorded about five times per month (with at least one observation of each pride per
165 month) since the beginning of the monitoring of this population in 1999. Prides are on
166 average made up of 4.8 (\pm 2.5 s.d.) adult males and females in the study area (Mbizah et
167 al., 2019). Lion individuals are recognized by whisker patterns, natural markings, such
168 as scars, muzzle spots, and tooth irregularities (Pennycuick & Rudnai, 1970). In this
169 analysis, we focus on two cub classes: cubs younger than 1 year old, whose survival
170 depends heavily on adult protection (Packer, 2000) and cubs younger than 6-month-old,
171 which corresponds to the duration of the lactation period and to the period when cubs
172 are less mobile (Schaller, 1972; Smuts et al., 1978). All subsequent analyses were
173 performed with respect to these two categories; as the results were similar, we present
174 here only those with cubs younger than 1 year old (results with 6-month-old cubs are
175 available in Appendix S1).

176 **2.3. GPS data collection**

177 *Animal handling and ethical care statement*

178 The lions were immobilized and equipped with a GPS collar by project staff trained and
179 certified by the Zimbabwe Veterinary Association, Wildlife Group, and Medicines
180 Control Authority, Zimbabwe. Lion handling and collaring was carried out with the
181 permission of the Zimbabwe Parks and Wildlife Management Authority. Animal
182 handling and care protocols were consistent with the guidelines provided in the 'Code
183 of Practice for Biologists using Animals', Department of Zoology, University of Oxford,
184 and approved by the University of Oxford, Biomedical Sciences, Animal Welfare and
185 Ethics Review Body.

186 *Identification of proximity events between tracked lions*

187 We used proximity between individuals, estimated using GPS data, as a proxy for social
188 interactions (see the following section for details on the distribution of collars within
189 and among prides). However, since GPS fixes were not acquired at the same time
190 intervals for each lion (1 hour or 2 hours) and to avoid the use of a wide temporal
191 window to define simultaneous fixes, we initially interpolated lion trajectories to hourly
192 locations using a continuous-time correlated random walk model, as implemented in
193 the R package *crawl*. All proximity estimations were performed using the interpolated
194 dataset and between simultaneous fixes. We defined a proximity event between two
195 individuals as successive pairs of simultaneous locations of the two individuals closer
196 than 1km. Within this 1 km distance threshold, we considered that individuals were in
197 sufficiently close proximity to facilitate encounters and associated social interactions.
198 We considered that a location beyond that distance threshold could occur before
199 terminating a given proximity event (these decisions are discussed in Appendix S2).

200 *Data sets used for Questions 1, 2 and 3*

201 Due to the spatial and temporal variations in the collar deployments, the raw dataset
202 (i.e., GPS data from 81 lions) needed to be subsampled differently to address each
203 question of the study. First, to explore the spatial response of female lions to the
204 presence of cubs, we used GPS data collected on 19 females that had at least 500 GPS
205 locations in each situation of interest, i.e., with and without cubs in the pride (question
206 1). Second, we explored the spatial (question 1) social (question 2) responses of male
207 lions to the presence of cubs on 17 dyads of one male and one female tracked
208 simultaneously in the same pride. For each male-female dyad, the collared male (1) has
209 been seen in a mating event with a female from the pride, (2) did not reproduce with
210 females from other prides during the tracking period, and (3) the collared female was
211 not dispersing from its pride during the tracking period. The average tracking period
212 per male-female dyad was longer than 8 months [quartile 1 = 5 months; median = 6
213 months; quartile 3 = 13 months]. Among the 17 pride males, 15 encountered (i.e.,
214 simultaneous locations <1km) at least once another GPS tracked male that could be a
215 competitor, i.e., a male outside of their coalition, resulting in 30 dyads of rival males
216 (question 3). We provide an illustration of the GPS tracking data recorded for (1) pride
217 male – pride female dyads, and (2) pride male – competitor male dyads in Figure S3.1
218 (Appendix S3) and Figure S4.1 (Appendix S4), respectively.

219 **2.4. Spatial response of lions to the presence of cubs (Question 1)**

220 We used a resource selection function (RSF) to estimate the habitat selection of lions
221 within their home range in the presence and absence of cubs. For both female and
222 male datasets, to reduce the non-independence among observations, we kept only

223 three locations per night (18h, 24h, 6h), which resulted in 2982 locations (\pm 1901 s.d.)
224 per female and 716 locations (\pm 542 s.d.) per male. For each used location, we sampled
225 10 random locations within the 90% utilization distribution of a kernel-based home
226 range estimate, using the *adehabitatHR* and *amt* packages (Calenge, 2007; Signer et al.,
227 2019). We then associated to the used and random locations the following information:
228 (1) whether at least one cub was present in the pride at the corresponding date, (2) the
229 habitat characteristics known to affect the selection of lion habitat, i.e., the distance to
230 water and habitat openness, (3) the distance to the centroid of the home range, to
231 estimate the strength of selection for the home range core area, and (4) for males only,
232 whether males were close (<1 km) to females. We did not include a season variable since
233 lion reproduction is not seasonal (Bertram, 1975), and preliminary analyses did not
234 show a major influence of seasons on lion selection for areas close to waterholes (see
235 also Valeix et al., 2010). For the female model, we added interaction terms between the
236 cub presence/absence and (i) the distance to water, (ii) the habitat openness, and (iii)
237 the distance to the home range centroid. For the male model, we combined the two
238 categorical variables, i.e., proximity to females (<1 km or >1 km) and presence / absence
239 of cubs, into one variable (with four categories) to test such multiplicative effects. The
240 RSF models were fitted using generalized linear mixed models with a logit link and a
241 binomial distribution of errors. To deal with the unequal number of locations among
242 lions, we added a random intercept with individual identity as a random factor. The
243 goodness-of-fit of our models were evaluated using the Spearman rank correlation
244 based on k-fold cross-validation (Boyce et al., 2002) with 5 folds, 20 bins and 20

245 repetitions. Following Chamaillé-Jammes (2019), RSF scores were converted into
246 selection ratios for interpretability.

247 **2.5. Social response of lions to the presence of cubs (Question 2)**

248 We used GPS data collected in the 17 dyads of pride males and females to assess the
249 influence of the presence of cubs on the spatial association between pride females and
250 males. In total, we obtained 1600 proximity events between pride males and females.
251 In Figure S2.2 in Appendix S2, we present an investigation of how the duration and
252 frequency of proximity events varies when using different distance thresholds to define
253 proximity events.

254 We tested whether pride males accompanied more pride females when they had
255 cubs. We did this by calculating for each male-female dyad (1) the percentage of time
256 pride males spent with pride females (i.e., the number of fixes in proximity divided by
257 the total number of fixes), (2) the frequency, and (3) the duration of proximity events.
258 Since the percentage of time that pride males spent with pride females, as well as the
259 duration of proximity events, exhibited overdispersion in Poisson models, we used
260 negative binomial mixed models for these response variables and a Poisson mixed
261 model for the 'frequency' response variable. For each model, we added a random
262 intercept with dyad identity.

263 Since vegetation structure may influence the propensity of males to stay close to
264 their pride (Funston et al., 1998), we also measured, for each male-female dyad, the
265 mean habitat openness within the core of the pride territory (50% utilization
266 distribution of a kernel-based home range estimate). We added to each model an

267 interaction term between cub-presence and habitat-openness variables to test whether
268 pride males would accompany pride females more when they had cubs, and especially
269 among prides whose territories were composed of open areas (i.e., higher detectability
270 of rivals, reduced need for males to patrol).

271 **2.6. Influence of the social and spatial response of lions on interactions with** 272 **competitors (Question 3)**

273 We used GPS data collected on the 30 male-male dyads to test the influence of the
274 presence of cubs on interactions between rival males. We recorded 450 close locations
275 (<1km) between pride males and their competitors, corresponding to 141 proximity
276 events.

277 *Frequency of proximity events between rival males*

278 For each pride male, we calculated the frequency of proximity events and tested the
279 influence of the presence of cubs using a negative binomial mixed model adding a
280 random intercept with dyad identity. Following (Wielgus et al., 2020), we also controlled
281 for the impact of the spatial overlap between the two collared males on the frequency
282 of male-male distinct proximity events. We used the Bhattacharyya affinity index to
283 compare the utilization distributions of pride and rival males during the dyad tracking
284 period, which ranges between 0 (no overlap) and 1 (identical utilization distribution)
285 (Benhamou et al., 2014; Bhattacharyya, 1943). We further investigated how the
286 frequency of male-male proximity events varied with the distance threshold used to
287 define proximity (see Figure S2.2 in Appendix S2).

288 *Habitat characteristics at the locations of proximity events between rival males*

289 We evaluated whether the presence of cubs influenced the locations of proximity
290 events between pride and rival males. To do this, we compared whether close locations
291 between pride males and rival males occurred more often outside or inside the male's
292 home range core than at other locations, and whether it changed when cubs were
293 present or not. We did this by fitting a mixed logistic regression, adding an interaction
294 term between the cub and rival variables and a random intercept with dyad identity. We
295 used the same approach to compare the likelihood of being close to waterholes (i.e.,
296 water sources < 1km) and within open areas (i.e., habitat openness > 0.5).

297 *Outcome of proximity events between rival males*

298 Finally, we kept the 103 proximity events interspaced by 24 hours to investigate the
299 likelihood for pride males to initiate the event, and the displacement of rival males after
300 the event. Following (Rafiq et al., 2020), we assumed that the male that was the farthest
301 from the proximity event site (over the 24 hours preceding the event) was the one that
302 initiated the event. We tested whether the presence of cubs influenced the likelihood
303 that pride males initiated the proximity event with rival males by fitting a GLMM with a
304 logit link and a binomial distribution for errors, adding a random intercept with dyad
305 identity. Using a log-linear model, we then tested whether the presence of cubs
306 influenced the competitor's displacement over the 24h following the event, viewed here
307 as an outcome of the proximity of the two males. Since a difference in age between
308 pride males and their competitors may influence the propensity for pride males to
309 initiate proximity events and the outcome of the proximity event, we also included an
310 age difference variable in our models.

311 **3. RESULTS**

312 **3.1. Spatial response of lions to the presence of cubs (Question 1)**

313 The RSF models had a high predictive power for both females (cross-validation: $\bar{r}_s = 0.89$
314 ± 0.02 , mean \pm SE) and males (cross-validation: $\bar{r}_s = 0.84 \pm 0.03$, mean \pm SE). Females
315 consistently selected areas close to the territory core, near waterholes, and in open
316 habitats (Fig. 1a, b, and c, respectively; Table S3.1 in Appendix S3). However, pride
317 females responded spatially to the presence of cubs by increasing the strength of their
318 selection for the territory core and weakening their selection for areas near waterholes,
319 and for open habitats (Fig. 1a, b, and c, respectively; Table S3.1 in Appendix S3).
320 Similarly, males moving close to females (i.e., < 1 km) selected areas close to the
321 territory core and near waterholes, with no detectable effect of the presence of cubs
322 (Figs. 1d and e, respectively; Table S3.2 in Appendix S3). In general, pride males moving
323 away from their pride (i.e., > 1 km) exhibited a greater selection of the features avoided
324 by females at the time they had cubs. In particular, when away from the pride, males
325 were more likely to use areas closer to territory edges, and this tendency was more
326 marked at times when cubs were present in the pride (Fig. 1d). Furthermore, when
327 moving away from their pride, males weakened the strength of their selection for
328 waterholes when there were no cubs in the pride, while they maintained the same
329 strength of selection for waterholes during periods when cubs were present (Fig. 1e).
330 We could not detect an influence of the presence of cubs on the male selection of open
331 habitats when they were away from their pride (Fig. 1f).

332 **3.2 Social response of lions to the presence of cubs (Question 2)**

333 On average, male lions spent 33% of their time within 1 km of the collared female of
334 their pride [quartile 1 = 18%; median = 29%; quartile 3 = 41%], resulting from 14 distinct

335 proximity events per month [q1 = 7; med = 13; q3 = 17] lasting 18 hours each [q1 = 3;
336 med = 9; q3 = 23]. However, the percentage of time spent in proximity of females varied
337 greatly between males, ranging from 10% (averaged over 14 months) to 68% (averaged
338 over 5 months). Contrary to our predictions, we found no evidence that pride males
339 would spend longer periods close to females to protect cubs (Fig. 2; Table S3.3 in
340 Appendix S3). However, pride males were more likely to be in proximity of pride
341 females when the mean habitat openness within the core of the pride's territory was
342 high (Fig. 2a), a result arising from more frequent (Fig. 2b) and similarly long (Fig. 2c)
343 proximity events.

344 **3.3. Influence of the social and spatial response of lions on interactions with** 345 **competitors (Question 3)**

346 Pride males were in proximity to a collared rival on average 0.8 times a month [q1 = 0;
347 med = 0.4; q3 = 0.9] for a mean duration of 3.2 hours [q1 = 1.0; med = 2.0; q3 = 3.0].
348 These results are for one male-male dyad and do not consider the fact that a male may
349 have several potential rival males in surrounding territories. As expected, pride males
350 were more frequently in the proximity of rival males whose home range overlapped
351 more (Figure S4.2; Table S4.1 in Appendix S4). The presence of cubs in the pride did not
352 influence the frequency of proximity events between pride and rival males but
353 influenced where proximity events occurred (Fig. 3; Table S4.2 in Appendix S4). When
354 pride males had no cubs, habitats in which pride males were observed close to
355 competitors did not differ from habitats in which pride males were away from
356 competitors, neither relatively to their location inside or outside the male home range
357 core (Fig. 3a) nor to their openness (Fig. 3c), but they differed by being closer to

358 waterholes (Fig. 3b). However, this waterhole-proximity difference did not hold when
359 the pride had cubs, and in these cases habitats in which pride males were observed
360 close to competitors were more likely to be outside the male home range core.
361 Furthermore, we did not find any influence of the presence of cubs on the probability
362 that pride males would initiate a proximity event with rival males (Table S4.3 in
363 Appendix S4). However, rival males moved farther away after a proximity event with
364 pride males when the pride had cubs. For illustration, 12 hours after the proximity
365 event, rival males were on average 2.4 km away from the proximity event site when the
366 pride had cubs and 1.5 km away when the pride had no cubs.

367 **4. DISCUSSION**

368 A growing number of authors are urging movement ecologists to consider more fully
369 the social environment when seeking to explain habitat selection, a topic that has
370 traditionally been interpreted in terms of the influence of resources or of top-down
371 forces, such as predation risk or fear of people (He et al., 2019; Kanda et al., 2019;
372 Rouse et al., 2021; Q. M. R. Webber & Vander Wal, 2017; Westley et al., 2018). Here, we
373 illustrate the intricacies between the social and spatial behaviours of African lions.

374 **4.1. Spatial response of lions to the presence of cubs (Question 1)**

375 We showed intersexual differences in the spatial responses of lions to the presence of
376 cubs. Females with cubs were less likely than those without cubs to select areas close to
377 waterholes and territory peripheries, i.e., areas characterized by a high risk of
378 encountering other carnivores in general (i.e., risk of predation) and other lions and
379 rival males in particular (i.e., risk of infanticide). On the contrary, these features were

380 more frequently selected by pride males that moved away from females at times when
381 there were cubs in the pride.

382 The preference shown by females with cubs for safer habitats (i.e., territory core,
383 far from waterhole) is consistent with the pressure to protect cubs from infanticidal
384 rival males that are more likely to be near the territory edge and close to water sources
385 (Mosser & Packer, 2009; Valeix et al., 2010) representing a threat for cub survival
386 (Packer & Pusey, 1983). This selection of areas far from waterholes may also be
387 explained by the need to minimize the risk of intraguild predation, particularly from
388 spotted hyaenas, which pose a threat to the survival of lion cubs (Curveira-Santos et al.,
389 2022; Schaller, 1972). Reduced movement abilities of young cubs (i.e., < 2 months) (see
390 (Laurenson, 1994) for cheetahs *Acinonyx jubatus*) may also explain the increased use of
391 the cores of female home ranges. This reduction of female movements within their
392 home range core in response to offspring presence is consistent with studies on other
393 species, such as Louisiana black bears (*Ursus americanus luteolus*; (Benson &
394 Chamberlain, 2007)), Amur tigers (*Panthera tigris altaica*; (Klevtcova et al., 2021)),
395 spotted hyaenas (*Crocuta crocuta*; (Boydston et al., 2003)), or red foxes (*Vulpes vulpes*;
396 (Henry et al., 2005)).

397 Previous studies documented examples of paternal care, such as male brown
398 hyaenas (*Parahyaena brunnea*) bringing food to cubs (Mills, 1990) or bushbuck
399 (*Tragelaphus scriptus*) protecting calves (Wronski et al., 2006). However, studies
400 investigating the strategies used by males to avoid infanticide by rivals or intraguild
401 predation on offspring are rare. Although females with cubs avoided riskier locations,
402 males showed stronger preferences for these places when they moved away from their

403 pride, possibly because they invested more in territorial defence directed toward
404 potential intraspecific competitors. This result is in line with the territorial-defence
405 hypothesis, when males indirectly prevent intrusion from rivals by patrolling, scent-
406 marking, and roaring throughout their territory (McLean, 1983). However, using only
407 GPS-data, we cannot test whether male lions marked their territory more intensely or
408 more frequently when patrolling (e.g. through more frequent vocalizations) when there
409 are cubs in their pride. This question could be investigated in the future using acoustic
410 loggers, as was recently done on the influence of spatial features on lions' vocalization
411 (Wijers et al., 2021).

412 **4.2. Social response of lions to the presence of cubs (Questions 2-3)**

413 We found considerable intraspecific variations in the dynamics of association (i.e.,
414 frequency, duration of proximity events) between males and females among lion
415 prides. However, much of these intraspecific variations were explained by the
416 vegetation structure within the pride territory core, rather than by the presence of cubs
417 (see Section 4.3).

418 We predicted that males would be with females more frequently and over longer
419 periods to reduce the risk of infanticide when cubs are present (i.e., in accordance with
420 the infant-defence hypothesis), such as observed among primate societies (Van Schaik
421 & Kappeler, 1997), or to reduce the risk of intraguild predation on offspring. Our results
422 provide little support for this prediction. Perhaps the need for pride males to maintain
423 the integrity of their territory by patrolling can limit the time they have to be close to
424 females. Habitat structure shapes social interactions by modifying patterns of animal
425 space use (He et al., 2019), similarly, the need for territorial animals to patrol

426 throughout their territories can shape/constrain their social interactions with
427 groupmates and rivals. Overall, the formation of nursery groups by females (Packer et
428 al., 1990; Packer & Pusey, 1983) may be sufficient to protect pride cubs against
429 neighbouring infanticidal males, especially when males prevent intrusion from rivals.

430 The greater selection of the edges of the territory by male lions during periods
431 when the cubs are present in their pride (Section 4.1) did not translate into more
432 frequent interactions with rivals. However, when they occurred, such encounters were
433 more often in the territory peripheries at times when cubs were present in the pride
434 and may have resulted in more vigorous repulsion of rivals (i.e., rival males relocated
435 further away from the encounter site). The increased level of repulsion between rivals is
436 consistent with previous studies showing how reproductive status can influence the
437 aggressiveness of encounters between male competitors among song sparrows
438 (*Melospiza melodia*; Moser-Purdy et al., 2017) and black howler monkeys (*Alouatta pigra*;
439 Kitchen, 2004). Overall, our results suggest that males adjusted both their social and
440 spatial responses to the presence of cubs by investing more heavily in preventing the
441 intrusion of rivals within the territory core, which supports the territorial-defence
442 hypothesis.

443 **4.3. Influence of vegetation structures on the social behaviours of lions**

444 The structure of vegetation in a lion's territory core largely explained the variability in
445 male-female association rates. Similarly, Funston et al. (1998) investigated (in a cross-
446 site review) the ecological factors likely to impact the rate of male-female association
447 among lions, finding more frequent male-female association in open ecosystems,
448 which is consistent with our results observed at a finer scale. As discussed by Funston

449 et al. (1998), three hypotheses may explain the variability of male-female association
450 according to the habitat structure: (1) a lower hunting success for males in open areas
451 and hence a greater need to use kills from pride females and/or hunt with females, (2) a
452 greater ease for pride males to detect competitors in open areas reducing the need to
453 patrol, as well as a higher detectability of females and their cubs, resulting in a greater
454 need to accompany them, and (3) a greater need for lions to defend kills from hyaenas
455 in open areas, particularly important when cubs need to be fed. The influence of habitat
456 structure on association between groups (i.e., fission / fusion dynamics) has been
457 investigated, especially in herbivore species, such as plains bison (*Bison bison*; Fortin et
458 al., 2009), roe deer (*Capreolus capreolus*; Pays et al., 2007), and blackbuck antelope
459 (*Antilope cervica*; Isvaran, 2007) with fusion events facilitated by habitat openness.
460 However, it has rarely been explored in carnivore species, whose fission-fusion
461 dynamics and male-female associations have been mainly explored in light of prey
462 availability and size (Chakrabarti et al., 2021; Mbizah et al., 2020).

463 **CONCLUSION**

464 In general, our findings illustrate how the social and spatial behaviours of lions are
465 entwined, with animal movement in relation to the environment being influenced by
466 social context, but also social interactions being shaped by habitat structure and
467 potentially constrained by territoriality. The long-term demographic and spatial
468 monitoring of a lion population allowed us to assess the counterstrategy of male lions
469 to the risk of infanticide, with support to the territorial-defence hypothesis.

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481 **CONFLICT OF INTEREST**

482 The authors declare no competing interests.

483 **AUTHOR CONTRIBUTIONS**

484 Andrew J. Loveridge and David W. Macdonald initiated and directed the lion research
485 project in Hwange National Park, acquiring funding, coordinating data acquisition,
486 undertook and managed field work, and managed databases. Daphine Madhlamoto
487 facilitated the fieldwork. Romain Dejeante, Marion Valeix, and Simon Chamaillé-Jammes
488 conceived the ideas and designed the statistical methodology. Romain Dejeante
489 conducted the statistical analyses. Romain Dejeante, Andrew Loveridge, Marion Valeix,
490 and Simon Chamaillé-Jammes interpreted the results. Romain Dejeante led the writing
491 of the manuscript. All authors revised, edited the manuscript, and gave their final
492 approval for publication.

493 **DATA AVAILABILITY STATEMENT**

494 If accepted, the data used in this study will be publicly available in a figshare repository.

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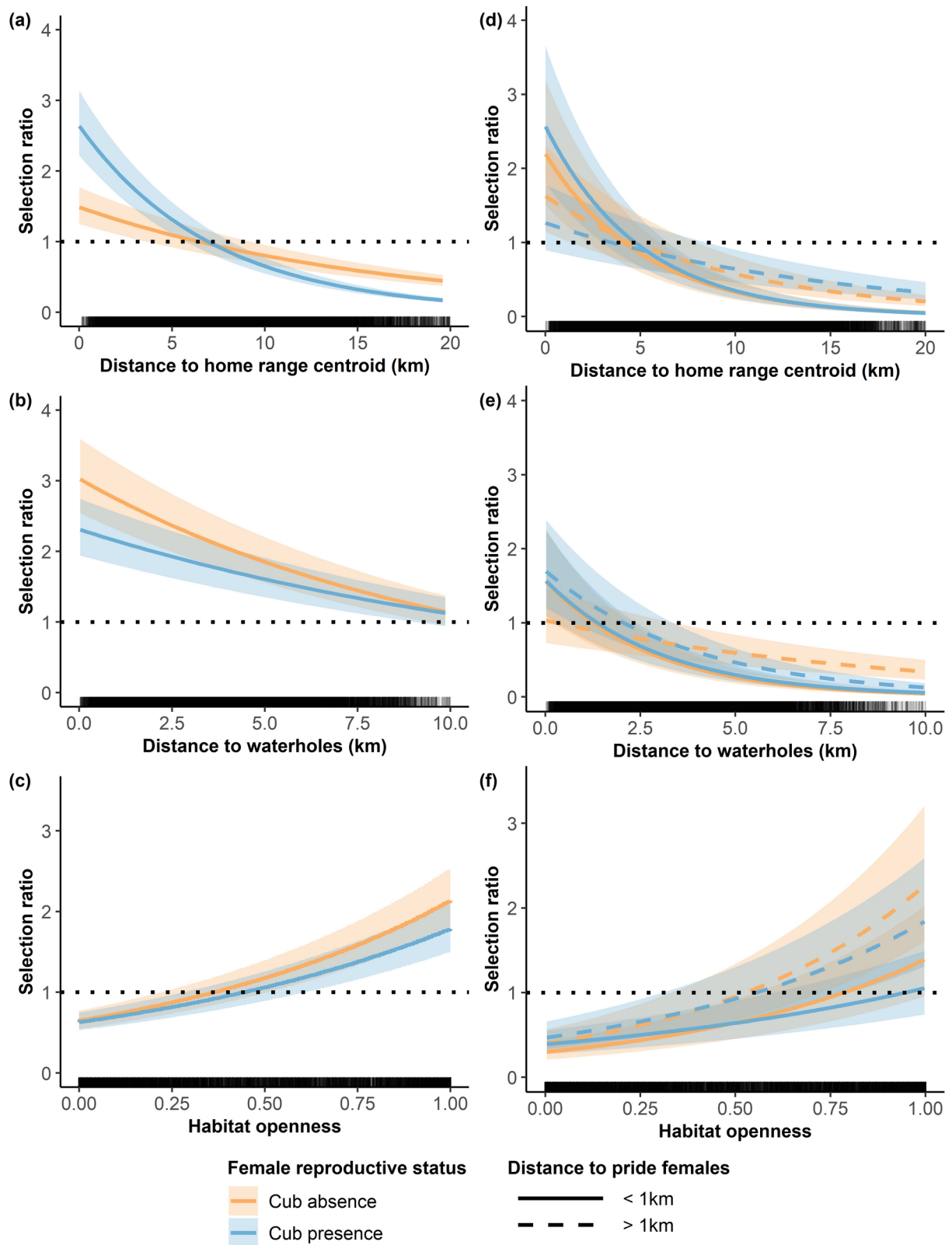
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686 **FIGURES**

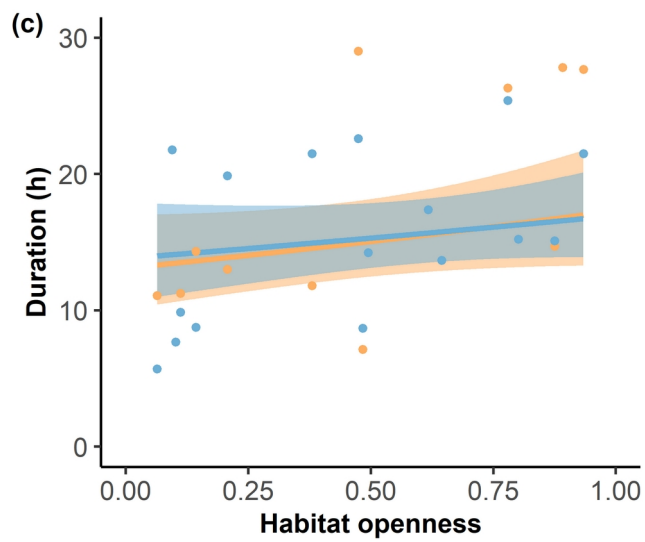
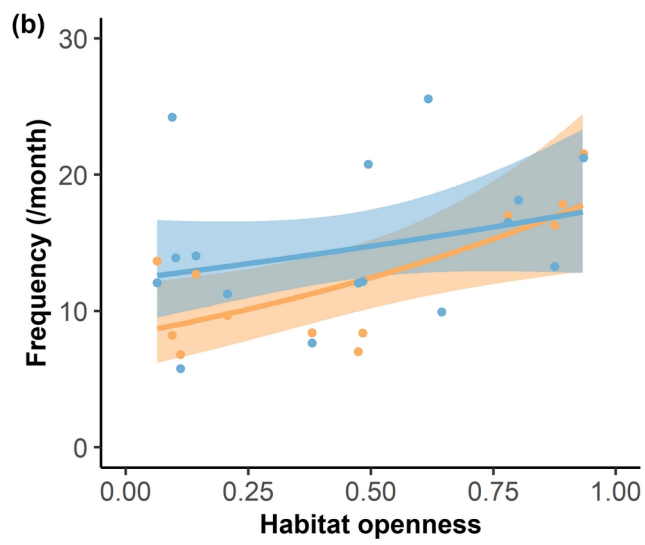
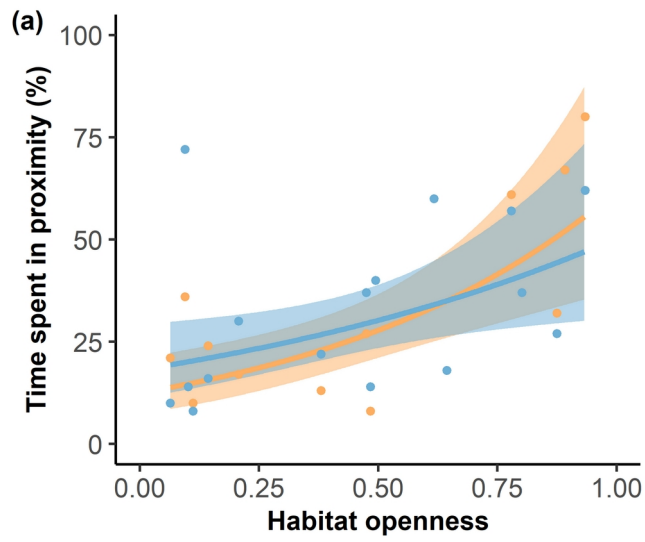
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689 Figure 1. Effects of the presence of cubs in the pride and, for males, of proximity to
 690 females, on female and male lion habitat selection. Figures show how the female (a-b-c)
 691 and male (d-e-f) selection ratio varies with (a-d) the distance to the home range

692 centroid, (b-e) the distance to the closest waterhole, and (c-f) the habitat openness,
693 according to the absence (orange) or presence (blue) of cubs within the pride and, for
694 males, to whether females were close by (<1km, solid symbols) or further away (dotted
695 symbols). The dotted horizontal line corresponds to a selection ratio of one, i.e., habitat
696 use proportional to habitat availability. Ribbon extremities show 95% confidence
697 interval, whereas lines show the mean value of selection ratio. Vertical bars at the
698 bottom of each panel show the distance to home range centroid (a-d), the distance to
699 waterholes (b-e) and the habitat openness (c-f) of the available locations (subsamped
700 to the same number of used locations).

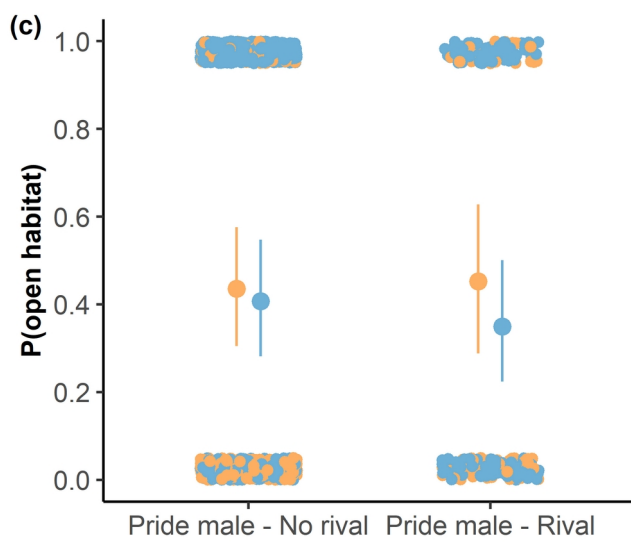
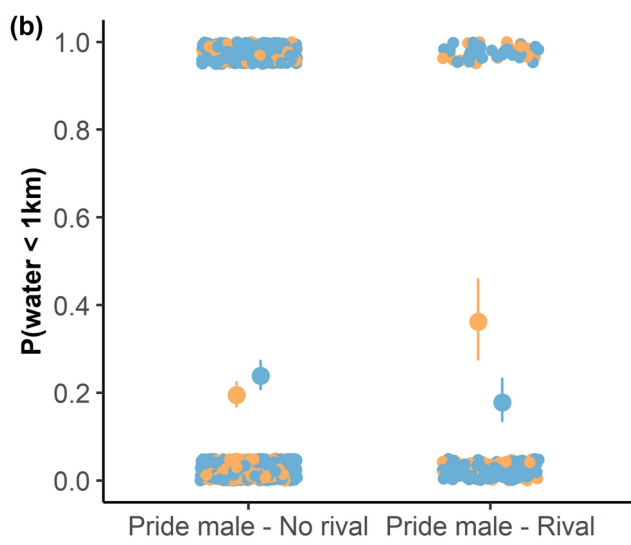
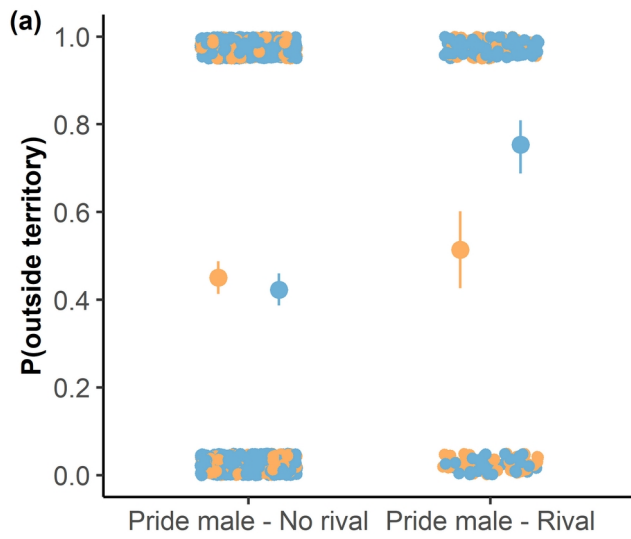


Female reproductive status

- Cub absence
- Cub presence

702 Figure 2. Effects of the presence of cubs in the pride, and of mean habitat openness in
703 the female home range, on (a) the percentage of time pride male and female lions
704 spend in proximity (distance <1km) to each other, (b) the frequency of these proximity
705 events and (c) the duration of these proximity events. Ribbon extremities show 95%
706 confidence interval, whereas solid lines show mean predicted values. Dots show the
707 percentage of time, frequency or duration of proximity events averaged per male-
708 female dyad in periods with and without cubs in the pride.

709



Female reproductive status

- Cub absence
- Cub presence

711 Figure 3. Spatial characteristics of proximity events (distance <1km) between pride
712 males and rival males. Likelihood for pride males to be (a) outside of their home range
713 core, (b) close from waterholes (<1km) and (c) in open areas according to the absence
714 (orange) and presence (blue) of cubs within the pride, and to the proximity of rival
715 males (pride male – no rival; pride male – rival < 1km). Dots show the statistical data
716 fitted to the logistic regression; i.e., one proximity event or one event with rival > 1km).

COUNTER-STRATEGIES TO INFANTICIDE: THE IMPORTANCE OF CUBS IN DETERMINING LION HABITAT SELECTION AND SOCIAL INTERACTIONS

Table S1.1. Coefficients (β) and standard errors (SE) for selection ratio model of lioness habitat selection for distance to water (WATER), open habitats (OPEN), and distance to the home range centroid (HR) accounting for the presence/absence of cubs within the pride (CUB ; without cub = 0, with cub = 1). Main effects estimate selection strength by females without cubs, and interaction terms estimate the additional effect on selection strength from having cubs in a pride. All continuous variables were scaled to compare their strength of selection.

Model - cubs < 6 months	β	SE	z-value	p-value
Intercept	-2,40	0,08	-29,33	<0.001
WATER	-0,21	0,01	-31,06	<0.001
OPEN	0,41	0,01	70,01	<0.001
HR	-0,29	0,01	-43,95	<0.001
CUB	-0,08	0,01	-7,97	<0.001
WATER x CUB	0,07	0,01	7,04	<0.001
OPEN x CUB	-0,01	0,01	-1,41	0.16
HR x CUB	-0,31	0,01	-31,19	<0.001

Table S1.2 Coefficients (β) and standard errors (SE) for selection ratio models of pride male habitat selection for distance to water (WATER), open habitats (OPEN), and distance to the home range centroid (HR) accounting for the presence/absence of cubs within the pride (CUB ; without cub = 0, with cub = 1) and for the presence/absence of females in proximity (FEM ; without female = 0, with female = 1). Main effects estimate selection strength by pride males without cubs but with females in proximity, and interaction terms estimate the additional effect on selection strength from having cubs in a pride. All continuous variables were scaled to compare their strength of selection.

Model - cubs < 6 months	β	SE	z-value	p-value
(Intercept)	-2,73	0,17	-15,58	<0.001
WATER	-0,51	0,04	-13,17	<0.001
OPEN	0,52	0,03	18,26	<0.001
HR	-0,69	0,04	-16,87	<0.001
(FEM & CUB)	-0,58	0,06	-9,30	<0.001
(no FEM & no CUB)	0,11	0,04	2,85	<0.01
(no FEM & CUB)	0,10	0,04	2,42	<0.05
WATER x (FEM & CUB)	-0,27	0,06	-4,43	<0.001
WATER x (no FEM & no CUB)	0,28	0,04	6,51	<0.001
WATER x (no FEM & CUB)	-0,05	0,04	-1,01	0.31
OPEN x (FEM & CUB)	-0,12	0,04	-2,86	<0.01
OPEN x (no FEM & no CUB)	0,16	0,03	4,78	<0.001
OPEN x (no FEM & CUB)	0,00	0,03	0,12	0.90
HR x (FEM & CUB)	-0,62	0,07	-9,33	<0.001
HR x (no FEM & no CUB)	0,24	0,05	5,33	<0.001

HR x (no FEM & CUB)	0,34	0,05	7,45	<0.001
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Table S1.3. Coefficients (β) and standard errors (SE) for the GLMMs testing the influence of the mean habitat openness (OPEN) and the presence of cubs (CUB) on (a) the percentage of time pride males spent in proximity with pride females, (b) the frequencies and (c) the duration of male-female proximity events.

Model – cubs < 6 months	β	SE	z-value	p-value
(a) Percentage of time spent in proximity – logistic regression				
(Intercept)	-0,71	0,16	-4,48	<0.001
CUB	-0,06	0,02	-3,07	<0.01
OPEN	0,57	0,15	3,86	<0.001
CUB x OPEN	-0,03	0,02	-1,51	0.13
(b) Frequency of proximity events – Poisson regression				
(Intercept)	2,51	0,10	25,46	<0.001
CUB	0,19	0,10	1,91	0.056
OPEN	0,21	0,10	2,18	<0.05
CUB x OPEN	-0,05	0,10	-0,52	0.60
(c) Duration of proximity events – negative binomial regression				
(Intercept)	2,94	0,06	50,07	<0.001
CUB	-0,12	0,05	-2,32	<0.05
OPEN	0,10	0,05	1,91	0,056
CUB x OPEN	-0,03	0,05	-0,62	0.54

Table S1.4. Frequency of pride male-competitor male proximity events according to the presence of cubs within the pride (CUB) and the overlap of the utilization distributions of pride and competitor males (UD overlap). We run a log-linear regression adding a random intercept with dyad identity.

Model - cubs < 6 months	β	SE	z-value	p-value
Intercept	-3,65	0,56	-6,56	<0.001
CUB	0,11	0,70	0,15	0.88
UD overlap	8,89	1,83	4,86	<0.001
CUB x UD overlap	0,19	2,45	0,08	0.94

Table S1.5. Spatial characteristics of proximity events between pride males and competitor males. Likelihood for pride males to use locations (a) outside of their core home range, (b) close to waterholes (<1km), and (c) within open areas, estimated using three logistic regressions adding a random intercept with dyad identity, according to the presence of cubs within the pride (CUB) and the presence of competitor males close (i.e. <1km) to the pride males (COMPETITOR).

Model – cubs < 6 months	β	SE	z-value	p-value
a) Likelihood for pride males to use locations outside of their core home range				
Intercept	0,05	0,06	0,73	0.47
CUB	-0,54	0,01	-41,10	<0.001
COMPETITOR	0,17	0,14	1,24	0.22
CUB x COMPETITOR	1,30	0,20	6,35	<0.001
b) Likelihood for pride males to use locations close to waterholes (<1km)				
Intercept	-1,50	0,10	-14,59	<0.001
CUB	0,45	0,02	30.0	<0.001
COMPETITOR	0.68	0,16	4.26	<0.001
CUB x COMPETITOR	-1.11	0,22	-5.0	<0.001
c) Likelihood for pride males to use open habitats				
Intercept	-0,51	0,28	-1,86	0.06
CUB	0,35	0,02	23,05	<0.001

COMPETITOR	0,03	0,18	0,14	0.89
CUB x COMPETITOR	-0,41	0,23	-1,74	0.08

Table S1.6. Outcome characteristics of proximity events between pride males and competitor males. (a) Likelihood for pride males to initiate the proximity events with competitor males, estimated using a logistic regression to the binary response variable (“initiated” or “ did not initiate”), (b) Logarithm of the competitor displacement to the proximity-event site with pride males, estimated using a log-linear regression model, according to the presence of cubs in the pride (CUB), the difference of age between the pride males and their competitors (AGE) and the time following the proximity event (HOUR).

Model - cubs < 6				
months	β	SE	z-value	p-value
a) Likelihood for pride males to initiate the proximity event with competitor males				
Intercept	0,36	0,28	1,29	0.20
CUB	0,50	0,31	1,59	0.11
AGE	0,01	0,21	0,03	0.98
b) Logarithm of the competitor displacement to the proximity event site with pride males				
Intercept	6,92	0,15	45,43	<0.001

Log(HOUR)	0,19	0,03	6,49	<0.001
CUB	0,26	0,09	2,84	<0.01
AGE	-0,39	0,15	-2,64	<0.01

COUNTER-STRATEGIES TO INFANTICIDE: THE IMPORTANCE OF CUBS IN DETERMINING LION HABITAT SELECTION AND SOCIAL INTERACTIONS

Appendix 2. Distance-based definition of proximity events, used as proxies for social interactions

Previous studies of carnivore dynamic interactions used lower distance thresholds (than 1km), such as 200m (Benhamou et al., 2014; Rafiq et al., 2020), 500m (Broekhuis et al., 2019), and 800m (Jordan et al., 2017), but using these did not lead to different patterns from when using 100m and 1km distance thresholds (Benhamou et al., 2014; Rafiq et al., 2020). Still, we preliminarily compared, for male-female dyads, the likelihood of simultaneous locations to be considered as being part of a proximity event using several distance thresholds, from 100m to 5km, with the classification of the distances obtained from a 2-state ('close' vs. 'far') univariate hidden-Markov model of the distances (see Figure S2.1 in Appendix S2). On average, 96% (respectively 83%) of dyad locations < 1km (respectively >1km) were classified by the hidden-Markov model as belonging to the 'close' state (respectively 'far' state).

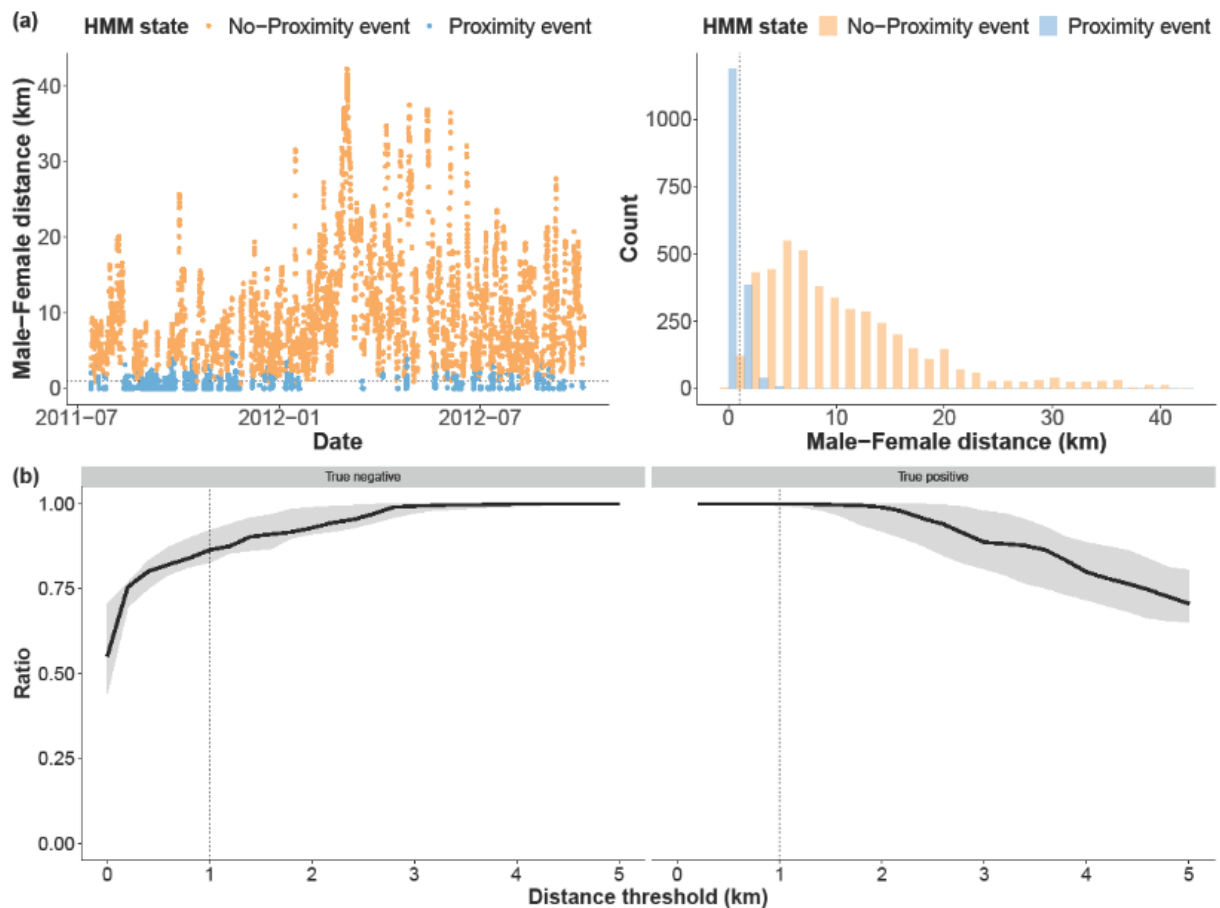


Figure S2.1 Methods to identify male-female interactions: comparison of male-female proximity events estimated by an univariate hidden-markov model based on the dyad distance, and estimated by a distance threshold from 100m to 5km. (a) Illustration of the temporal-dynamic of male-female distances (left) used to identify ‘close’ state (blue) and ‘far’ state (orange) based on the distribution of male-female distances (right). (b) Assessment of potential distance thresholds to identify male-female proximity events. The true negative ratio (resp. the true positive ratio) is the proportion of no-interaction cases (resp. interaction cases) identified by the HMM for which the pairwise distance was further (resp. closer) than the distance threshold. Ribbon extremities represent the first and third quartiles, whereas the black line represents the median value of the true negative and true positive ratios calculated on the 17 male-female dyads. The dotted

lines (a-b) show the 1km-distance threshold used in this paper. The HMM model was run by using the R package *depmixS4* (Visser and Speekenbrink 2010)

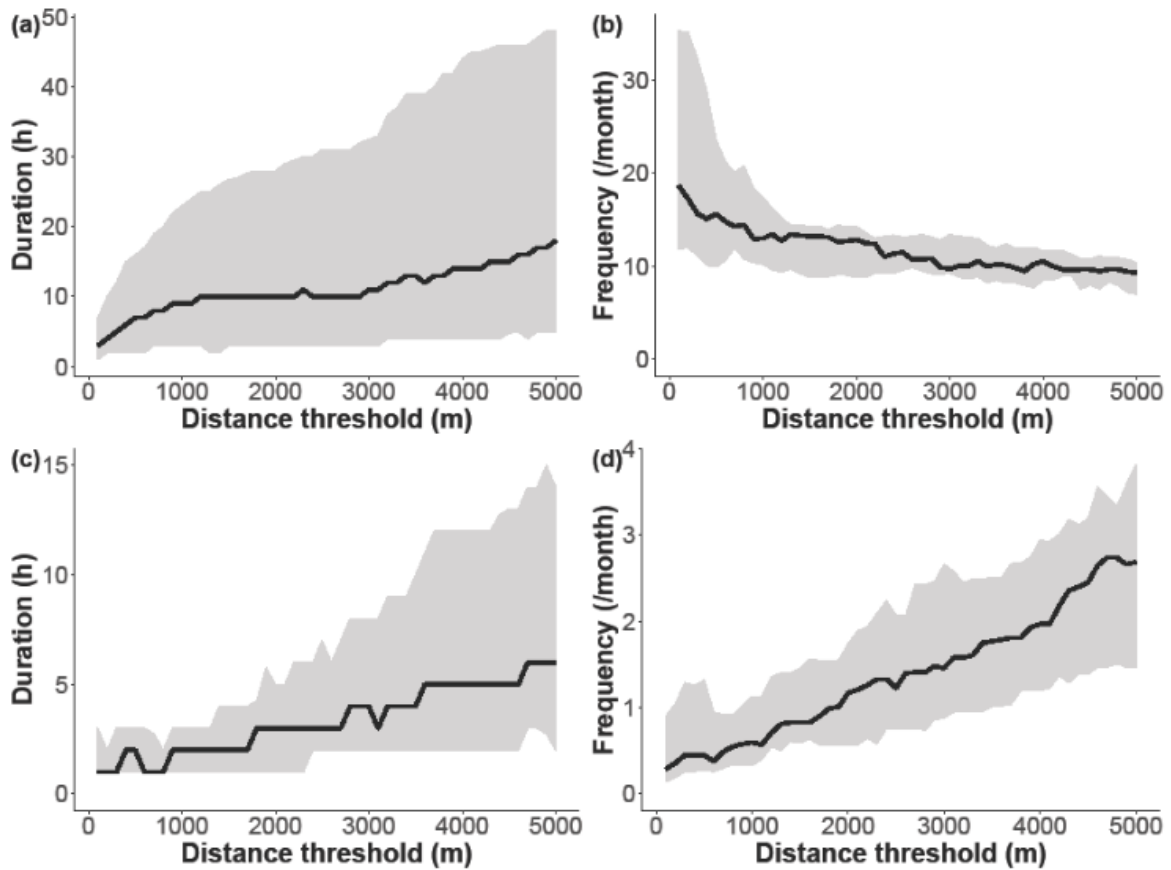


Figure S2.2 Distance-threshold sensitivity of the duration and frequency measures describing the temporal dynamics of male-female (a-b) and male-male proximity events (c-d). For male-female dyads ($n=17$), lower distance threshold induced higher segmentation risk of the proximity bouts and so lower durations and higher frequencies. For male-male dyads ($n=30$), higher distance threshold allows to detect more events of proximity between competing males. Ribbon extremities represent the first and third quartiles, whereas the black line represents the median value of the durations and frequencies.

Reference

Visser, I., & Speekenbrink, M. (2010). depmixS4: An R Package for Hidden Markov Models. *Journal of Statistical Software*, 36, 1–21. <https://doi.org/10.18637/jss.v036.i07>

COUNTER-STRATEGIES TO INFANTICIDE: THE IMPORTANCE OF CUBS IN DETERMINING LION HABITAT SELECTION AND SOCIAL INTERACTIONS

Appendix S3. Pride male-female association

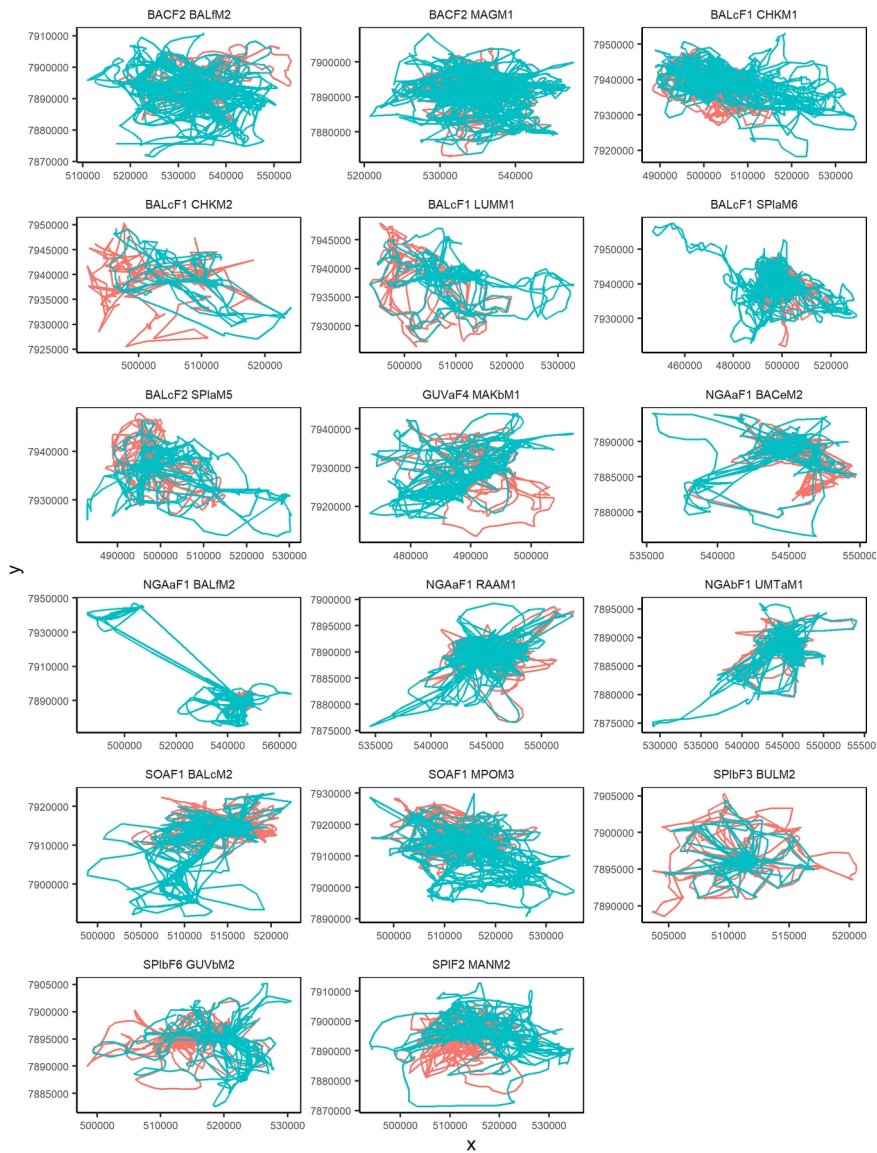


Figure S3.1. Locations and core home ranges of pride males (blue) and females (red), delineated from the 50% utilization distribution of a kernel-based home range estimate, using the *adehabitatHR* package (Calenge 2007). Similar overlaps between pride male

and female home ranges were observed from the 90% utilization distribution of a kernel-based home range estimate.

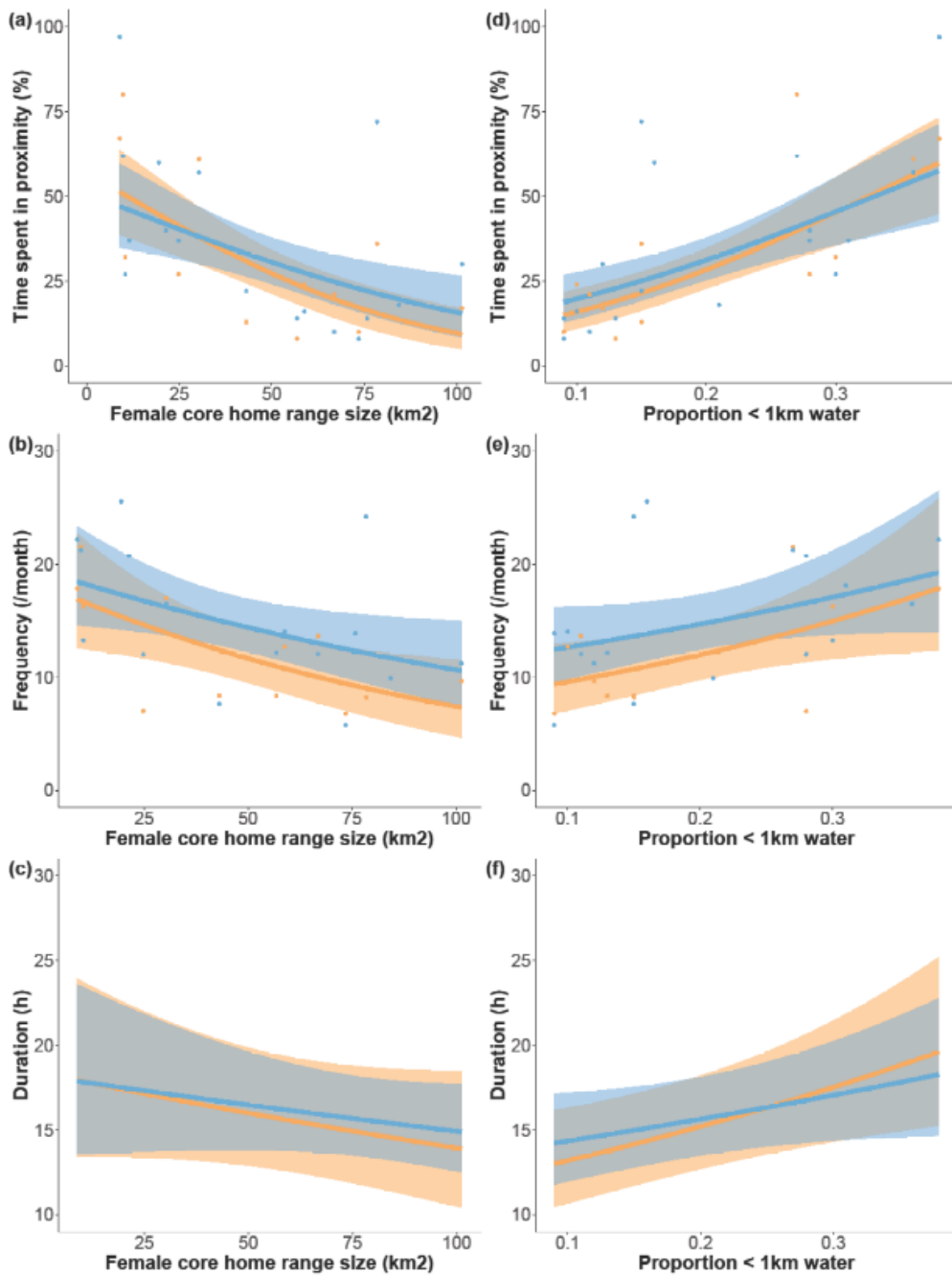


Figure S3.2 Temporal dynamic of pride male and female proximity events as a function to the size of the female core home range and to the proportion of habitats close to waterholes (i.e. <1km) within it, according to the presence (blue) and absence (orange) of cubs within the pride. We found high negative correlations between the mean

habitat openness in the female home range with its size (Pearson correlation = -0.74; $p < 0.001$) and with the proportion of habitats close to waterholes (Pearson correlation = 0.85; $p < 0.001$).

Table S3.1. Coefficients (β) and standard errors (SE) for selection ratio model of lioness habitat selection for distance to water (WATER), open habitats (OPEN), and distance to the home range centroid (HR) accounting for the presence/absence of cubs within the pride (CUB ; without cub = 0, with cub = 1). Main effects estimate selection strength by females without cubs, and interaction terms estimate the additional effect on selection strength from having cubs in a pride. All continuous variables were scaled to compare their strength of selection.

Model - cubs < 12 months	β	SE	z-value	p-value
Intercept	-2,41	0,09	-27,75	<0.001
WATER	-0,20	0,01	-26,22	<0.001
OPEN	0,44	0,01	65,32	<0.001
HR	-0,27	0,01	-36,68	<0.001
CUB	-0,07	0,01	-6,63	<0.001
WATER x CUB	0,05	0,01	5,00	<0.001
OPEN x CUB	-0,06	0,01	-6,47	<0.001
HR x CUB	-0,34	0,01	-33,95	<0.001

Table S3.2 Coefficients (β) and standard errors (SE) for selection ratio models of pride male habitat selection for distance to water (WATER), open habitats (OPEN), and distance to the home range centroid (HR) accounting for the presence/absence of cubs within the pride (CUB ; without cub = 0, with cub = 1) and for the presence/absence of females in proximity (FEM ; without female = 0, with female = 1). Main effects estimate selection strength by pride males without cubs but with females in proximity, and interaction terms estimate the additional effect on selection strength from having cubs in a pride. All continuous variables were scaled to compare their strength of selection.

Model – cubs < 12 months	β	SE	z-value	p-value
(Intercept)	-2,98	0,18	-16,61	<0.001
WATER	-0,66	0,05	-12,31	<0.001
OPEN	0,62	0,04	15,87	<0.001
HR	-0,92	0,06	-15,77	<0.001
(FEM & CUB)	0,08	0,07	1,21	0.23
(no FEM & no CUB)	0,36	0,06	6,39	<0.001
(no FEM & CUB)	0,39	0,06	6,80	<0.001
WATER x (FEM & CUB)	0,04	0,06	0,64	0.52
WATER x (no FEM & no CUB)	0,46	0,06	7,84	<0.01
WATER x (no FEM & CUB)	0,18	0,06	3,12	<0.001
OPEN x (FEM & CUB)	-0,22	0,05	-4,87	<0.001
OPEN x (no FEM & no CUB)	0,08	0,04	1,86	0.06
OPEN x (no FEM & CUB)	-0,07	0,04	-1,60	0.11
HR x (FEM & CUB)	-0,05	0,07	-0,69	0.49
HR x (no FEM & no CUB)	0,41	0,06	6,65	<0.001

HR x (no FEM & CUB)	0,59	0,06	9,69	<0.001
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Table S3.3. Coefficients (β) and standard errors (SE) for the GLMMs testing the influence of the mean habitat openness (OPEN) and the presence of cubs (CUB) on (a) the percentage of time pride males spent in proximity with pride females, (b) the frequencies and (c) the duration of male-female proximity events.

Model - cubs < 12 months	β	SE	z-value	p-value
(a) Percentage of time spent in proximity - logistic regression				
(Intercept)	-0,80	0,16	-4,92	<0.001
CUB	0,11	0,02	4,61	<0.001
OPEN	0,62	0,15	4,04	<0.001
CUB x OPEN	-0,14	0,02	-6,19	<0.001
(b) Frequency of proximity events - Poisson regression				
(Intercept)	2,49	0,10	24,85	<0.001
CUB	0,20	0,11	1,87	0.06
OPEN	0,26	0,10	2,73	<0.01
CUB x OPEN	-0,12	0,10	-1,18	0.24
(c) Duration of proximity events - negative binomial regression				
(Intercept)	2,86	0,07	42,44	<0.001
CUB	0,02	0,06	0,24	0.81
OPEN	0,08	0,05	1,47	0.14
CUB x OPEN	-0,02	0,06	-0,32	0.75

COUNTER-STRATEGIES TO INFANTICIDE: THE IMPORTANCE OF CUBS IN DETERMINING LION HABITAT SELECTION AND SOCIAL INTERACTIONS

Appendix 4. Pride male - competitor male association

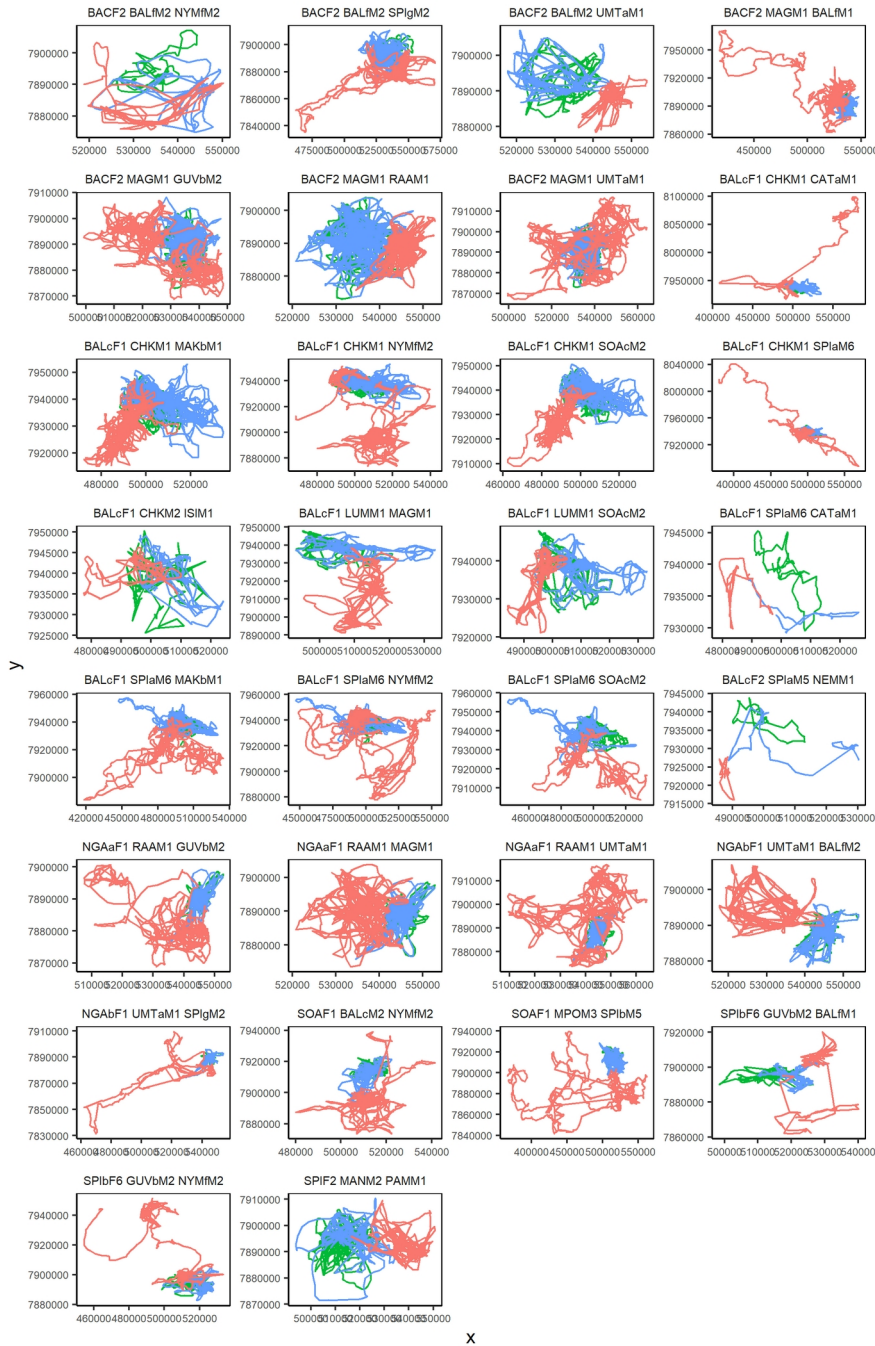


Figure S4.1. GPS locations of female (green), male (blue) and competitor (red) lions, for each of the 30 studied triads.

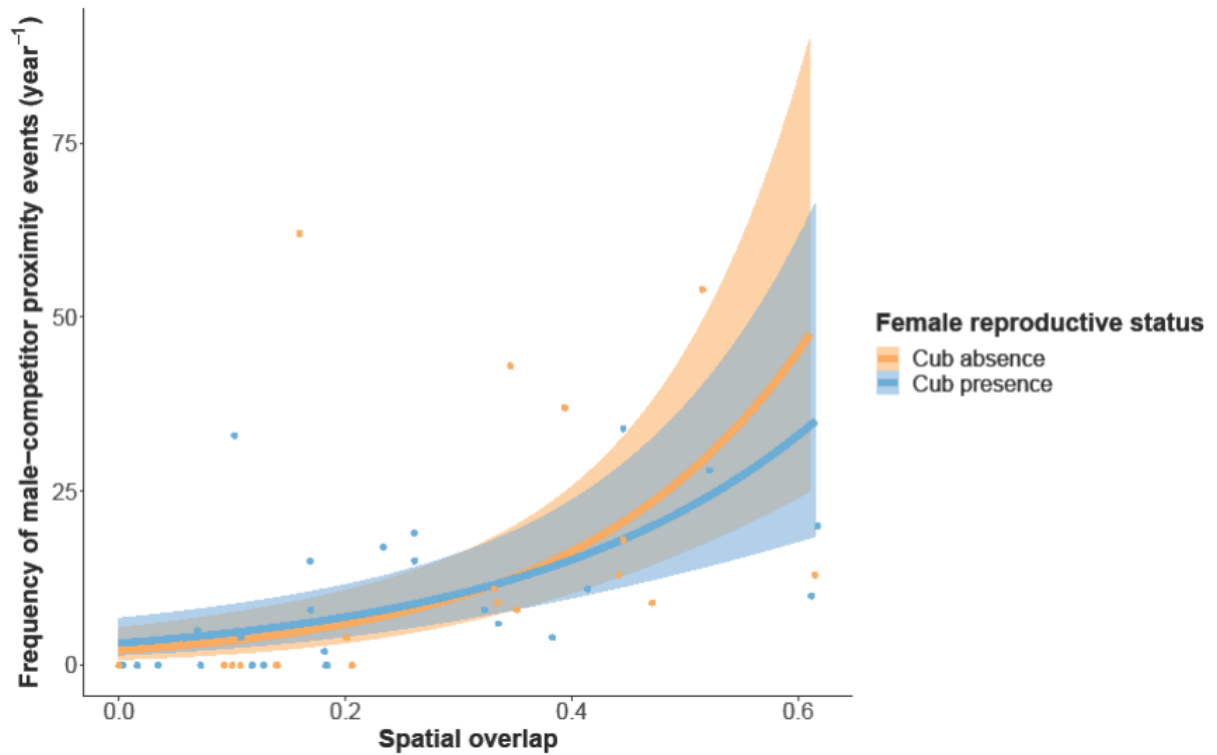


Figure S4.2. Relationship between the frequencies of proximity events between pride males and competitor males and the overlap of their utilization distribution (i.e. Bhattacharyya's affinity index) according to the presence (blue) and absence (orange) of cubs in the pride. Ribbon extremities represent 95% confidence interval, whereas solid lines represent mean frequencies of pride male-competitor male proximity events.

Table S4.1. Frequency of pride male-competitor male proximity events according to the presence of cubs within the pride (CUB) and the overlap of the utilization distributions of pride and competitor males (UD overlap). We run a log-linear regression adding a random intercept with dyad identity.

Model - cubs < 12 months	β	SE	z-value	p-value
Intercept	0,77	0,47	1,65	0.10
CUB	0,39	0,57	0,69	0.49
UD overlap	5,07	1,05	4,85	<0.001
CUB x UD overlap	-1,17	1,36	-086	0.39

Table S4.2. Spatial characteristics of proximity events between pride males and competitor males. Likelihood for pride males to use locations (a) outside of their core home range, (b) close to waterholes (<1km), and (c) within open areas, estimated using three logistic regressions adding a random intercept with dyad identity, according to the presence of cubs within the pride (CUB) and the presence of competitor males close (i.e. <1km) to the pride males (COMPETITOR).

Model - cubs < 12 months	β	SE	z-value	p-value
a) Likelihood for pride males to use locations outside of their core home range				
Intercept	-0,20	0,08	-2,58	<0.01
CUB	-0,11	0,02	-6,72	<0.001
COMPETITOR	0,26	0,16	1,56	0.12
CUB x COMPETITOR	1,17	0,22	5,29	<0.001
b) Likelihood for pride males to use locations close to waterholes (<1km)				
Intercept	-1,42	0,10	-14,56	<0.001
CUB	0,26	0,02	12,98	<0.001
COMPETITOR	0,85	0,19	4,61	<0.001
CUB x COMPETITOR	-1,22	0,24	-5,18	<0.001
c) Likelihood for pride males to use open habitats				
Intercept	-0,26	0,29	-0,90	0.37
CUB	-0,12	0,02	-5,59	<0.001

COMPETITOR	0,07	0,22	0,31	0,76
CUB x COMPETITOR	-0,31	0,26	-1,20	0,23

Table S4.3. Outcome characteristics of proximity events between pride males and competitor males. (a) Likelihood for pride males to initiate the proximity events with competitor males, estimated using a logistic regression to the binary response variable (“initiated” or “ did not initiate”), (b) Logarithm of the competitor displacement to the proximity-event site with pride males, estimated using a log-linear regression model, according to the presence of cubs in the pride (CUB), the difference of age between the pride males and their competitors (AGE) and the time following the proximity event (HOUR).

Model - cubs < 12				
months	β	SE	z-value	p-value
a) Likelihood for pride males to initiate the proximity event with competitor males				
Intercept	0,39	0,36	1,09	0.28
CUB	0,41	0,28	1,44	0.15
AGE	-0,08	0,23	-0,36	0.72
b) Logarithm of the competitor displacement to the proximity event site with pride males				
Intercept	6,85	0,16	43,98	<0.001
Log(HOUR)	0,18	0,03	6,27	<0.001
CUB	0,48	0,10	4,67	<0.001
AGE	-0,27	0,16	-1,73	0.08