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

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ABSTRACT

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

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

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

4. We showed a spatial response of lions to the presence of offspring, with females with cubs less likely to select areas close to waterholes or in the periphery of the territory than females without cubs. In contrast, these areas were more selected by males when there were cubs in the pride. We also found social responses. Males spent more time with females as habitat openness increased, but the presence of cubs in the pride did not influence the average likelihood of observing males with females. Furthermore, rival males relocated further after an encounter with pride males when cubs were present in the prides, suggesting that the presence of cubs leads to a more vigorous repulsion of competitors. Males with cubs in their pride were more likely to interact with male competitors on the edge of the pride's home range and far from the waterholes, suggesting that they are particularly assiduous in detecting and repelling rival males during these periods.

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

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

1. INTRODUCTION

Animal movement decisions are naturally shaped by factors in their environment (resources, refuges, breeding areas), but they are also influenced by social interactions. For example, depending on species, sex, age, and other factors, individuals may be attracted to, or avoid, a food source already being used by a conspecific. Individuals can also track the movement of potential mates and avoid sexual competitors or repel them to minimize sexual competition for mates. Socially-influenced movements occur continuously in group-living species (Fichtel et al., 2011), and even solitary animals respond to the presence of conspecifics, as they need at times to engage in exploration to find a mate to reproduce (Leyhausen, 1964). Despite social and spatial behaviours being intertwined, studies investigating these processes simultaneously are rare, especially because social behaviour is traditionally studied from direct observation of focal groups whereas spatial behaviour is mostly studied at the landscape-scale (Webber et al., 2023).

The presence of offspring is a major source of adjustment of the social and spatial behaviours in animals, especially regarding the risk of predation on offspring or the risk of infanticide. For example, species that live in fission-fusion societies can form larger groups, potentially in safer habitats, to prevent the risk of predation on offspring (Bond et al., 2019; Holmes et al., 2016). Even carnivores adjust their movement rate to the presence of offspring in response to the risk of intra-guild predation (Goodheart et al., 2022). Among taxa in which infanticide occurs, such as primates, carnivores, and rodents (Agrell et al., 1998), the infant safety hypothesis proposes that females with offspring are less gregarious and avoid males to reduce the risk of infanticide (Otali & Gilchrist, 2006;

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Smith et al., 2008). Such social-avoidance behaviours are expected to shape the spatial behaviour of females. For example, adult females with offspring move further from territory edges and maintain smaller home ranges (Benson & Chamberlain, 2007; Boydston et al., 2003; Klevtcova et al., 2021). However, females have the option to adjust many other behaviours to decrease the risk of infanticide (Agrell et al., 1998), such as by increasing the frequency and intensity of agonistic interactions (Elwood et al., 1990), or by the formation of maternal groups (Grinnell & McComb, 1996).

In social species, males also adopt counterstrategies to infanticide (Agrell et al., 1998). Two strategies may exist for territorial males to reduce the risk of infanticide: staying close to females to protect offspring against rivals (here formulated as the "infant-defence hypothesis"; Van Schaik & Kappeler, 1997) or patrolling the territory more intensely to prevent the intrusion of rivals (here formulated as the "territorial-defence hypothesis"; McLean, 1983). However, such socio-spatial responses to the presence of offspring can be in competition. By staying close to females with offspring, males reduce their patrols throughout their territory, and, conversely, increasing their patrols reduces the time available to spend close to females to protect offspring. Therefore, although the two hypotheses are not mutually exclusive, it is necessary to investigate how social-territorial animals simultaneously adjust their social and spatial behaviours to the presence of offspring to distinguish their associated predictions.

Temporal variations in interactions between groupmates, driven by reproductive status and presence of offspring, have been described quantitatively mainly through detailed and continuous field observations of focal groups (Clutton-Brock, 2016). Knowledge of the associated changes in habitat selection has accumulated because of these studies, but generally only at a relatively small spatial scale or at a coarse grain (individuals seen/not seen with others, ignoring the locations of the unseen individuals). Rigorous quantification of how habitat selection is modified with changing social circumstances, such as in the presence of offspring, has lagged (Webber et al., 2023; Westley et al.,

2018). In particular, little is known about how conspecifics influence habitat selection among mammals (Buxton et al., 2020). Here, we address this gap by investigating how social, territorial, and infanticidal animals adjust their spatial and social behaviours in response to the presence of offspring, when they face a trade-off between protecting offspring and patrolling territory.

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

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

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

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

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

2. MATERIALS AND METHODS

2.1. Study area and environmental data

The study was carried out in the north-eastern region of Hwange National Park, Zimbabwe. The park covers 14,600 km² of semi-arid savanna. Natural rain-fed pans dry during the dry season from May to October, and water remains available only in some waterholes in which underground water is pumped (Chamaillé-Jammes et al., 2007). Vegetation is dominated by bushlands and woodlands interspersed with patches of grasslands, particularly near waterholes. For the study conducted here, we built a map of vegetation openness: we used the 30-m resolution vegetation map produced by

(Arraut et al., 2018) to calculate, for each pixel, the proportion of open vegetation (category 'grassland' and 'open bushlands' in the original map) in a radius of 250 m.

2.2. Lion Population Monitoring

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

2.3. GPS data collection

Animal handling and ethical care statement

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

Identification of proximity events between tracked lions

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

Data sets used for Questions 1, 2 and 3

Due to the spatial and temporal variations in the collar deployments, the raw dataset (i.e., GPS data from 81 lions) needed to be subsampled differently to address each question of the study. First, to explore the spatial response of female lions to the presence of cubs, we used GPS data collected on 19 females that had at least 500 GPS locations in each situation of interest, i.e., with and without cubs in the pride (question 1). Second, we explored the spatial (question 1) social (question 2) responses of male lions to the presence of cubs on 17 dyads of one male and one female tracked simultaneously in the same pride. For each male-female dyad, the collared male (1) has been seen in a mating event with a female from the pride, (2) did not reproduce with females from other prides during the tracking period, and (3) the collared female was not dispersing from its pride during the tracking period. The average tracking period per male-female dyad was longer than 8 months [quartile 1 = 5 months; median = 6 months; quartile 3 = 13 months]. Among the 17 pride males, 15

encountered (i.e., simultaneous locations <1km) at least once another GPS tracked male that could be a competitor, i.e., a male outside of their coalition, resulting in 30 dyads of rival males (question 3). We provide an illustration of the GPS tracking data recorded for (1) pride male – pride female dyads, and (2) pride male – competitor male dyads in Figure S3.1 (Appendix S3) and Figure S4.1 (Appendix S4), respectively.

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

We used a resource selection function (RSF) to estimate the habitat selection of lions within their home range in the presence and absence of cubs. For both female and male datasets, to reduce the non-independence among observations, we kept only three locations per night (18h, 24h, 6h), which resulted in 2982 locations (± 1901 s.d.) per female and 716 locations (± 542 s.d.) per male. For each used location, we sampled 10 random locations within the 90% utilization distribution of a kernel-based home range estimate, using the *adehabitatHR* and *amt* packages (Calenge, 2007; Signer et al., 2019). We then associated to the used and random locations the following information: (1) whether at least one cub was present in the pride at the corresponding date, (2) the habitat characteristics known to affect the selection of lion habitat, i.e., the distance to water and habitat openness, (3) the distance to the centroid of the home range, to estimate the strength of selection for the home range core area, and (4) for males only, whether males were close (<1km) to females. We did not include a season variable since lion reproduction is not seasonal (Bertram, 1975), and preliminary analyses did not show a major influence of seasons on lion selection for areas close to waterholes (see also Valeix et al., 2010). For the female model, we added interaction terms between the cub presence/absence and (i) the distance to water, (ii) the habitat openness, and (iii) the distance to the home range centroid. For the male model, we combined the two categorical variables, i.e., proximity to females (<1km or >1km) and presence / absence of cubs, into one variable (with four categories) to test such multiplicative effects. The RSF models were fitted using generalized linear mixed models with a logit link and a binomial distribution of errors. To deal with the unequal number of locations among lions,

we added a random intercept with individual identity as a random factor. The goodness-of-fit of our models were evaluated using the Spearman rank correlation based on k-fold cross-validation (Boyce et al., 2002) with 5 folds, 20 bins and 20 repetitions. Following Chamaillé-Jammes (2019), RSF scores were converted into selection ratios for interpretability.

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

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

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

Since vegetation structure may influence the propensity of males to stay close to their pride (Funston et al., 1998), we also measured, for each male-female dyad, the mean habitat openness within the core of the pride territory (50% utilization distribution of a kernel-based home range estimate). We added to each model an interaction term between cub-presence and habitat-openness variables to test whether pride males would accompany pride females more when they had cubs, and especially among prides whose territories were composed of open areas (i.e., higher detectability of rivals, reduced need for males to patrol).

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

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

Frequency of proximity events between rival males

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

Habitat characteristics at the locations of proximity events between rival males

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

Outcome of proximity events between rival males

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

3. RESULTS

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

The RSF models had a high predictive power for both females (cross-validation: $\overline{r_s}$ = 0.89 ± 0.02, mean ± SE) and males (cross-validation: $\overline{r_s}$ = 0.84 ± 0.03, mean ± SE). Females consistently selected areas close to the territory core, near waterholes, and in open habitats (Fig. 1a, b, and c, respectively; Table S3.1 in Appendix S3). However, pride females responded spatially to the presence of cubs by increasing the strength of their selection for the territory core and weakening their selection for areas near waterholes, and for open habitats (Fig. 1a, b, and c, respectively; Table S3.1 in Appendix S3). Similarly, males moving close to females (i.e., < 1km) selected areas close to the territory core and near waterholes, with no detectable effect of the presence of cubs (Figs. 1d and e, respectively; Table S3.2 in Appendix S3). In general, pride males moving away from their pride (i.e., > 1km) exhibited a greater selection of the features avoided by females at the time they had cubs. In particular, when away from the pride, males were more likely to use areas closer to territory edges,
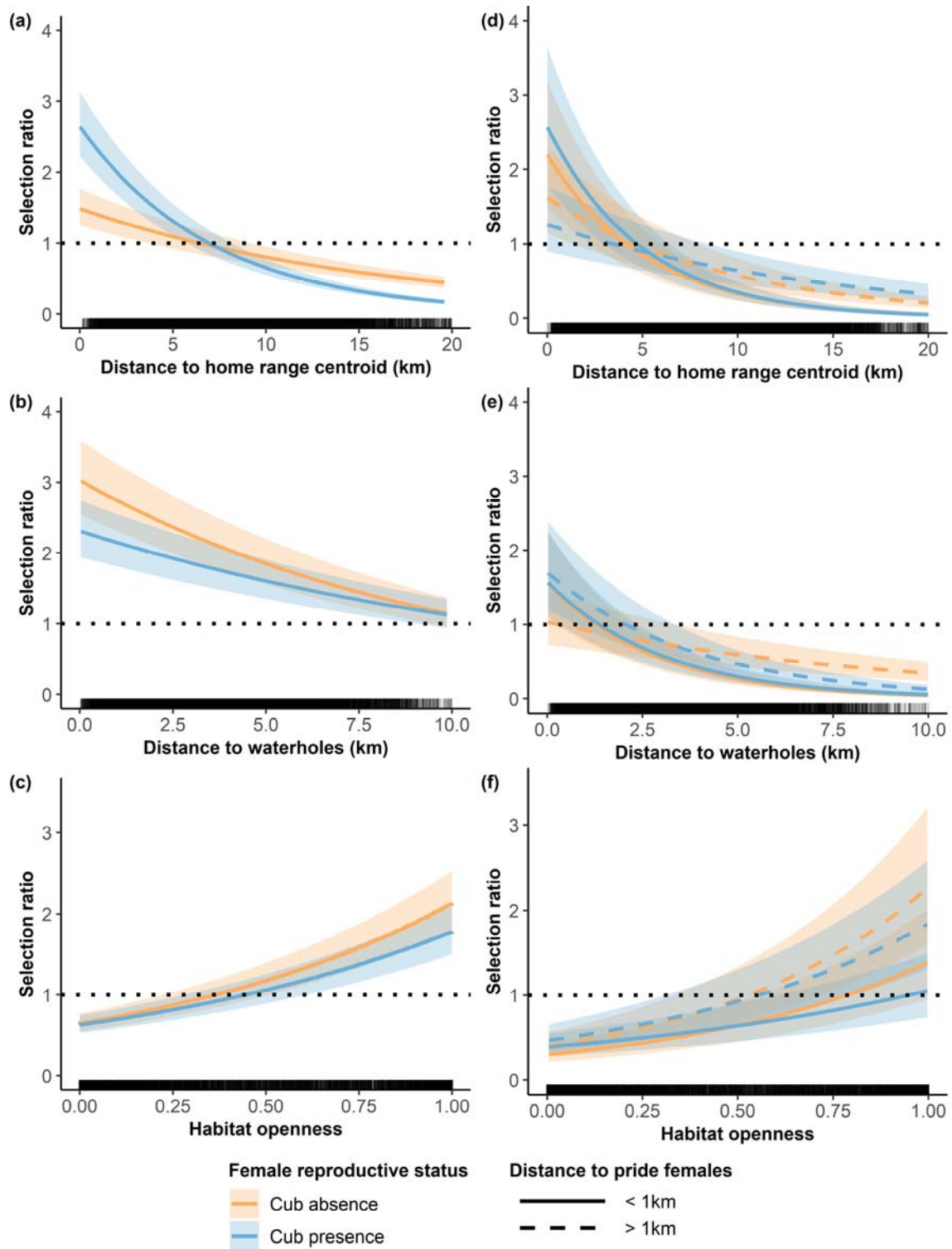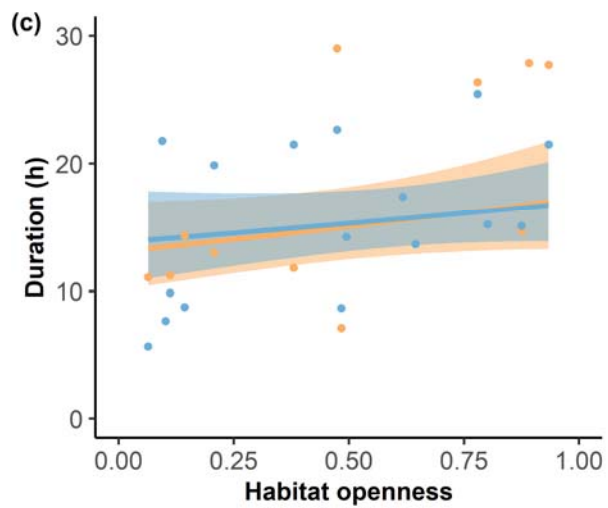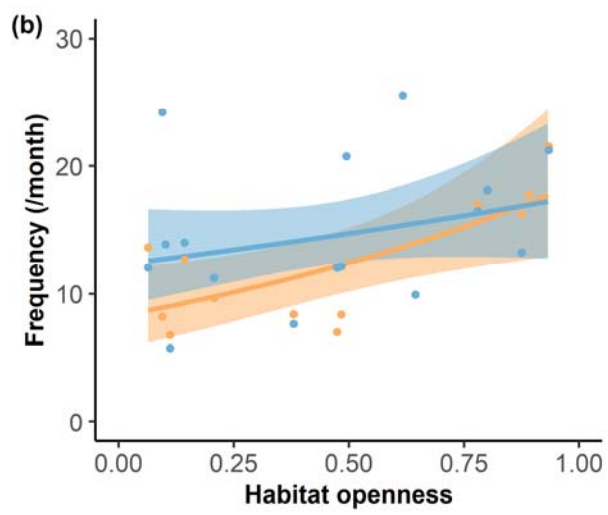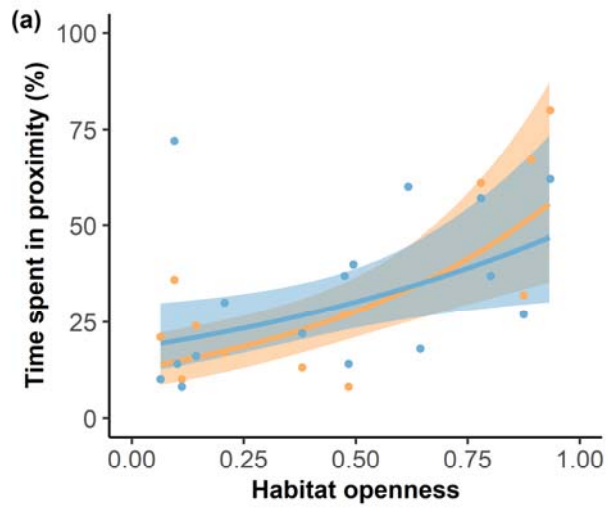
Figure 1. Effects of the presence of cubs in the pride and, for males, of proximity to females, on female and male lion habitat selection. Figures show how the female (a-b-c) and male (d-e-f) selection ratio varies with (a-d) the distance to the home range centroid, (b-e) the distance to the closest waterhole, and (c-f) the habitat openness, according to the absence (orange) or presence (blue) of cubs within the pride and, for males, to

whether females were close by (<1km, solid symbols) or further away (dotted symbols). The dotted horizontal line corresponds to a selection ratio of one, i.e., habitat use proportional to habitat availability. Ribbon extremities show 95% confidence interval, whereas lines show the mean value of selection ratio. Vertical bars at the bottom of each panel show the distance to home range centroid (a-d), the distance to waterholes (b-e) and the habitat openness (c-f) of the available locations (subsampled to the same number of used locations).

and this tendency was more marked at times when cubs were present in the pride (Fig. 1d). Furthermore, when moving away from their pride, males weakened the strength of their selection for waterholes when there were no cubs in the pride, while they maintained the same strength of selection for waterholes during periods when cubs were present (Fig. 1e). We could not detect an influence of the presence of cubs on the male selection of open habitats when they were away from their pride (Fig. 1f).

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

On average, male lions spent 33% of their time within 1 km of the collared female of their pride [quartile 1 = 18%; median = 29%; quartile 3 = 41%], resulting from 14 distinct proximity events per month [q1 = 7; med = 13; q3 = 17] lasting 18 hours each [q1 = 3; med = 9; q3 = 23]. However, the percentage of time spent in proximity of females varied greatly between males, ranging from 10% (averaged over 14 months) to 68% (averaged over 5 months). Contrary to our predictions, we found no evidence that pride males would spend longer periods close to females to protect cubs (Fig. 2; Table S3.3 in Appendix S3). However, pride males were more likely to be in proximity of pride females when the mean habitat openness within the core of the pride's territory was high (Fig. 2a), a result arising from more frequent (Fig. 2b) and similarly long (Fig. 2c) proximity events.
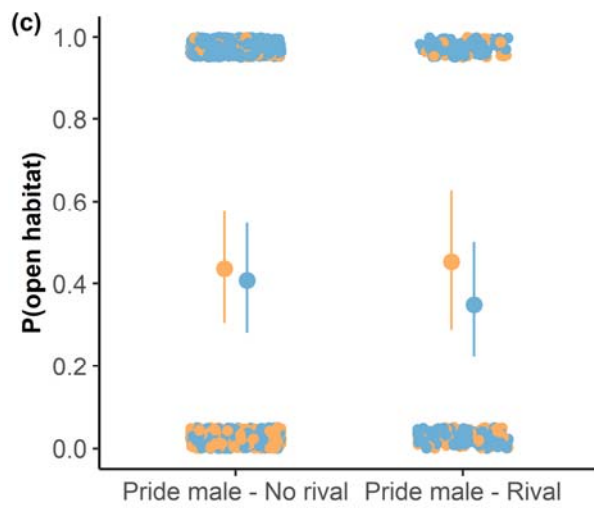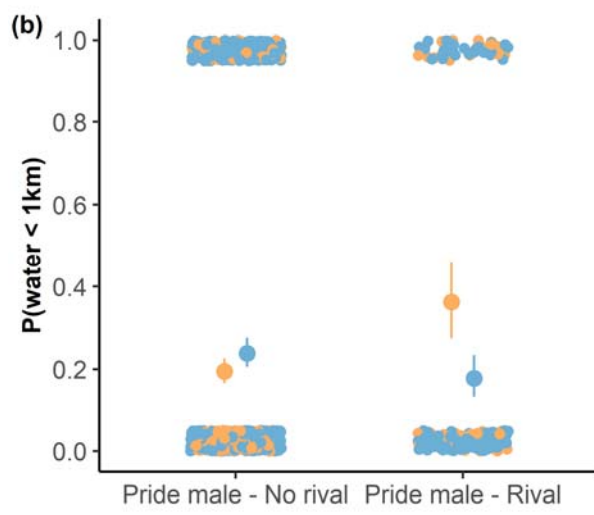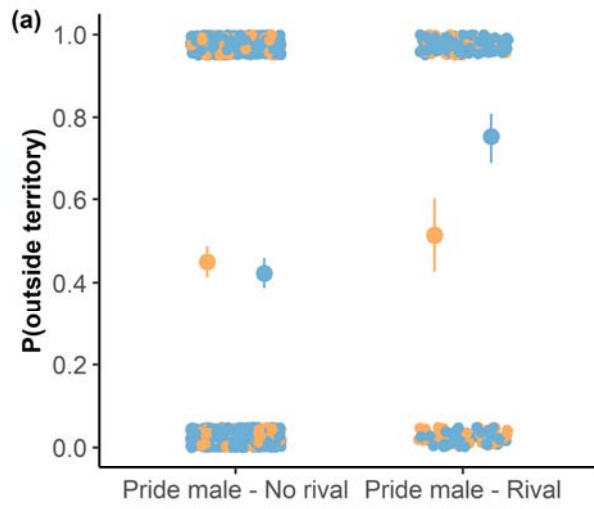
Female reproductive status

Cub absence

Cub presence

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

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

Pride males were in proximity to a collared rival on average 0.8 times a month [q1 = 0; med = 0.4; q3 = 0.9] for a mean duration of 3.2 hours [q1 = 1.0; med = 2.0; q3 = 3.0]. These results are for one male-male dyad and do not consider the fact that a male may have several potential rival males in surrounding territories. As expected, pride males were more frequently in the proximity of rival males whose home range overlapped more (Figure S4.2; Table S4.1 in Appendix S4). The presence of cubs in the pride did not influence the frequency of proximity events between pride and rival males but influenced where proximity events occurred (Fig. 3; Table S4.2 in Appendix S4). When pride males had no cubs, habitats in which pride males were observed close to competitors did not differ from habitats in which pride males were away from competitors, neither relatively to their location inside or outside the male home range core (Fig. 3a) nor to their openness (Fig. 3c), but they differed by being closer to waterholes (Fig. 3b). However, this waterhole-proximity difference did not hold when the pride had cubs, and in these cases habitats in which pride males were observed close to competitors were more likely to be outside the male home range core. Furthermore, we did not find any influence of the presence of cubs on the probability that pride males would initiate a proximity event with rival males (Table S4.3 in Appendix S4). However, rival males moved farther away after a proximity event with pride males when the pride had cubs. For illustration, 12 hours after the

(a)

P(outside territory)

Pride male - No rival   Pride male - Rival

(b)

P(water < 1km)

Pride male - No rival   Pride male - Rival

(c)

P(open habitat)

Pride male - No rival   Pride male - Rival

Female reproductive status

- Cub absence
- Cub presence

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

proximity event, rival males were on average 2.4 km away from the proximity event site when the pride had cubs and 1.5 km away when the pride had no cubs.

4. DISCUSSION

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

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

We showed intersexual differences in the spatial responses of lions to the presence of cubs. Females with cubs were less likely than those without cubs to select areas close to waterholes and territory peripheries, i.e., areas characterized by a high risk of encountering other carnivores in general (i.e., risk of predation) and other lions and rival males in particular (i.e., risk of infanticide). On the contrary, these features were more frequently selected by pride males that moved away from females at times when there were cubs in the pride.

The preference shown by females with cubs for safer habitats (i.e., territory core, far from waterhole) is consistent with the pressure to protect cubs from infanticidal rival males that are more likely to be near the territory edge and close to water sources (Mosser & Packer, 2009; Valeix et al.,

2010) representing a threat for cub survival (Packer & Pusey, 1983). This selection of areas far from waterholes may also be explained by the need to minimize the risk of intraguild predation, particularly from spotted hyaenas, which pose a threat to the survival of lion cubs (Curveira-Santos et al., 2022; Schaller, 1972). Reduced movement abilities of young cubs (i.e., < 2 months) (see (Laurenson, 1994) for cheetahs *Acinonyx jubatus*) may also explain the increased use of the cores of female home ranges. This reduction of female movements within their home range core in response to offspring presence is consistent with studies on other species, such as Louisiana black bears (*Ursus americanus luteolus*; (Benson & Chamberlain, 2007)), Amur tigers (*Panthera tigris altaica*; (Klevtcova et al., 2021)), spotted hyaenas (*Crocuta crocuta*; (Boydston et al., 2003)), or red foxes (*Vulpes vulpes*; (Henry et al., 2005)).

Previous studies documented examples of paternal care, such as male brown hyaenas (*Parahyaena brunnea*) bringing food to cubs (Mills, 1990) or bushbuck (*Tragelaphus scriptus*) protecting calves (Wronski et al., 2006). However, studies investigating the strategies used by males to avoid infanticide by rivals or intraguild predation on offspring are rare. Although females with cubs avoided riskier locations, males showed stronger preferences for these places when they moved away from their pride, possibly because they invested more in territorial defence directed toward potential intraspecific competitors. This result is in line with the territorial-defence hypothesis, when males indirectly prevent intrusion from rivals by patrolling, scent-marking, and roaring throughout their territory (McLean, 1983). However, using only GPS-data, we cannot test whether male lions marked their territory more intensely or more frequently when patrolling (e.g. through more frequent vocalizations) when there are cubs in their pride. This question could be investigated in the future using acoustic loggers, as was recently done on the influence of spatial features on lions' vocalization (Wijers et al., 2021).

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

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

We predicted that males would be with females more frequently and over longer periods to reduce the risk of infanticide when cubs are present (i.e., in accordance with the infant-defence hypothesis), such as observed among primate societies (Van Schaik & Kappeler, 1997), or to reduce the risk of intraguild predation on offspring. Our results provide little support for this prediction. Perhaps the need for pride males to maintain the integrity of their territory by patrolling can limit the time they have to be close to females. Habitat structure shapes social interactions by modifying patterns of animal space use (He et al., 2019), similarly, the need for territorial animals to patrol throughout their territories can shape/constrain their social interactions with groupmates and rivals. Overall, the formation of nursery groups by females (Packer et al., 1990; Packer & Pusey, 1983) may be sufficient to protect pride cubs against neighbouring infanticidal males, especially when males prevent intrusion from rivals.

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

presence of cubs by investing more heavily in preventing the intrusion of rivals within the territory core, which supports the territorial-defence hypothesis.

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

The structure of vegetation in a lion's territory core largely explained the variability in male-female association rates. Similarly, Funston et al. (1998) investigated (in a cross-site review) the ecological factors likely to impact the rate of male-female association among lions, finding more frequent male-female association in open ecosystems, which is consistent with our results observed at a finer scale. As discussed by Funston et al. (1998), three hypotheses may explain the variability of male-female association according to the habitat structure: (1) a lower hunting success for males in open areas and hence a greater need to use kills from pride females and/or hunt with females, (2) a greater ease for pride males to detect competitors in open areas reducing the need to patrol, as well as a higher detectability of females and their cubs, resulting in a greater need to accompany them, and (3) a greater need for lions to defend kills from hyaenas in open areas, particularly important when cubs need to be fed. The influence of habitat structure on association between groups (i.e., fission / fusion dynamics) has been investigated, especially in herbivore species, such as plains bison (*Bison bison*; Fortin et al., 2009), roe deer (*Capreolus capreolus*; Pays et al., 2007), and blackbuck antelope (*Antilope cervica*; Isvaran, 2007) with fusion events facilitated by habitat openness. However, it has rarely been explored in carnivore species, whose fission-fusion dynamics and male-female associations have been mainly explored in light of prey availability and size (Chakrabarti et al., 2021; Mbizah et al., 2020).

CONCLUSION

In general, our findings illustrate how the social and spatial behaviours of lions are entwined, with animal movement in relation to the environment being influenced by social context, but also social interactions being shaped by habitat structure and potentially constrained by territoriality. The long-term demographic and spatial monitoring of a lion population allowed us to assess the

counterstrategy of male lions to the risk of infanticide, with support to the territorial-defence hypothesis.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

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

DATA AVAILABILITY STATEMENT

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

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