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Livin' on the edge: reducing infanticide risk by maintaining proximity to potentially less infanticidal males

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Infanticide is a significant evolutionary force influencing carnivore behaviours, as it is one of the primary contributors to offspring mortality. Female multimale mating, which creates paternal uncertainty, is known to reduce infanticide. We propose that two crucial steps are needed for this strategy to work in solitary species like brown bears, *Ursus arctos*. First, after mating, females should choose dens within their mating area (step 1), boosting the chances of encountering potential fathers of cub(s) after den emergence in spring. However, the efficacy of this strategy hinges on males' fidelity to the same mating areas from one year to the next (step 2). Our study confirmed that pregnant females consistently selected dens within their mating areas, with significant overlap (around 90%) between areas used by females with cubs and their mating zones. Males also demonstrated fidelity (over 65%) to mating areas over 2 consecutive years. Infanticide significantly shapes the sociospatial ecology of female brown bears, a phenomenon that can carry nutritional costs for females with cubs, and influence settlement patterns near human shields to increase reproductive success. Additionally, in hunted populations, removing resident males can trigger an influx of potentially infanticidal bears from elsewhere.

Sexual selection is a critical evolutionary process through which certain traits enhance an individual's chances of successfully reproducing. This process often leads to the development of elaborate physical characteristics, behaviours, or other traits that confer advantages in terms of reproduction (Goodenough et al., 2009). Among the adaptive behavioural strategies aimed at increasing the fitness of one sex, infanticide refers to the killing of offspring by males of the same species, particularly observed in species where males invest less in parental care (Goodenough et al., 2009; Hausfater & Blaffer Hrdy, 1984). It is also prevalent in species with longer lactation periods than gestation and where females experience lactational amenorrhea, preventing postpartum mating (Palombit, 2015; van Schaik & Janson, 2000). Infanticide benefits a male if he can mate with a female after killing her offspring and has the opportunity to sire her subsequent offspring, aligning with the sexual selection hypothesis (Ebensperger, 1998; Hrdy, 1979). A common scenario involves a new male taking over a group or territory and eliminating existing offspring to induce females to return to oestrus sooner, allowing him to father his own offspring. This behaviour can serve an evolutionary purpose for the new male, as it maximizes his reproductive success by eliminating potential competitors and increasing his own genetic representation in the

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population (Goodenough et al., 2009; Hausfater & Blaffer Hrdy, 1984; Lukas & Huchard, 2014; Palombit, 2015).

Together with the order Primates (Lowe et al., 2018), Carnivora is the mammalian order in which male infanticide is most frequently described in the wild (Ebensperger, 1998; Harano & Kutsukake, 2018). Because infanticide can represent one of the main causes of offspring mortality in both social and solitary carnivores, including species such as spotted hyaenas, *Crocuta crocuta*, African lions, *Panthera leo*, leopards, *Panthera pardus*, pumas, *Puma concolor*, and brown bears, *Ursus arctos* (Balme & Hunter, 2013; Brown et al., 2021; Harano & Kutsukake, 2018; Lukas & Huchard, 2014; Palombit, 2015; Rosenbaum et al., 2016), infanticide can exert a powerful evolutionary force (Agrell et al., 1998; van Schaik & Janson, 2000), influencing carnivore population density, demography and behaviour, with potentially dramatic costs for female reproductive success. Although the primary female counterstrategy against infanticide is offspring defence (Agrell et al., 1998; Palombit, 2015; Teichroeb et al., 2012), natural selection has favoured several behavioural counterstrategies in females (Ebensperger, 1998; Harano & Kutsukake, 2018). One such strategy is the dilution effect (Agrell et al., 1998; Lukas & Huchard, 2014; Palombit, 2015), where potential mates live in close proximity to each other. This makes it challenging for a new male entering the group or territory to eliminate all existing offspring at once. Group protection (Agrell et al., 1998; Palombit, 2015; Teichroeb et al., 2012) is another counterstrategy, as living in cohesive social groups can collectively defend against infanticidal males. Additionally, multimale mating, which creates paternal uncertainty, has been effective in reducing infanticide (Agrell et al., 1998; Palombit, 2015; Rosenbaum et al., 2016; Teichroeb et al., 2012). The possibility that a male might not be certain of parentage can deter infanticidal behaviour. Indeed, DNA analysis in various species has shown that infanticidal males rarely attack their own offspring, with most having not mated with the mother during the previous mating season (Balme & Hunter, 2013; Beaudrot et al., 2009; Bellemain, Swenson, et al., 2006; Bellemain; Zedrosser, et al., 2006; Davoli et al., 2018; Ebensperger, 1998; Palombit, 2015; Soltis et al., 2000; van Schaik, Hodges et al., 2000; Wolff & MacDonald, 2004). Therefore, mothers should adjust their infants' exposure to potentially infanticidal males, and residing close to their mates should increase the males' likelihood of security about parentage, potentially deterring infanticidal behaviour. Thus, the effectiveness of this strategy should rely on the permanence of females within the mating areas of their mates after giving birth and during postnatal development.

Infanticide exerts significant selective pressure on brown bears (Bellemain, Swenson et al., 2006), as has been well documented (Dahle & Swenson, 2003a; Swenson et al., 1997). In fact, infanticide stands out as one of the primary sources of cub mortality (Gonzalez et al., 2012; Steyaert et al., 2012; Swenson et al., 1997, 2001) and infanticidal males are typically not related to the cubs they kill (Bellemain, Swenson, et al., 2006; Bellemain, Zedrosser et al., 2006). Male brown bears seem capable of distinguishing their own cubs from unrelated ones, possibly by recognizing the females they mated with in the previous year (Bellemain, Swenson, et al., 2006; Bellemain, Zedrosser et al., 2006). It is well established that female brown bears engage in promiscuous mating behaviour, although they do not mate while caring for their cubs, and that multiple paternities within the same litter are common (Swenson et al., 2021). For example, in Scandinavia, Bellemain, Zedrosser et al. (2006) observed that 14.5% of 69 litters with two or more cubs and 28% of 32 litters with three or more cubs exhibited multiple paternities. During the mating season, females can be seen with multiple males simultaneously or encountering potential mates sequentially (Bellemain, Zedrosser et al., 2006; Fernández-Gil et al., 2006). In fact, a substantial portion, around 54%, of females were observed with more than one male during their mating season (Bellemain, Zedrosser et al., 2006). Additionally, infanticide serves to shorten the time until the mother's next oestrus, increasing the infanticidal male's opportunity to mate with her. This is because during the breeding period, females become receptive again within 2–4 days after losing cubs (Swenson et al., 2021).

In this study, we investigated the behavioural components required to optimize the effectiveness of the multimale mating strategy in mitigating the risk of infanticide by male brown bears, *Ursus arctos*. To reduce the likelihood of infanticide, brown bear females typically engage in mating with multiple different males during the main mating period, which occurs from April to June (Swenson et al., 2021). This strategic behaviour increases the likelihood that, when females emerge from their dens with cubs the following year, they will encounter one or more of the potential male parents. Such encounters deter the threat of infanticide, as these males are less likely to harm cubs that could be their offspring. However, for this strategy to be effective, two critical behavioural steps must take place, steps that, to our knowledge, have not been empirically tested yet. We hypothesized that, following copulations, pregnant females should select reproductive dens near or in close proximity to the mating area (step 1). This choice increases the probability of encountering males with which they have mated the previous spring when they emerge with cubs, and that are potential fathers of the cubs. Nevertheless, this strategy only works if males also display a high level of fidelity in returning to the same mating areas from one year to the next (step 2). In other words, when females that have mated with males in a specific mating area roam that same area with their cubs (females with cubs, FWCs) because they have chosen a birth den within this mating area, potential fathers should also frequent this same area simultaneously. This is likely to occur if males return to the same mating area in the year following their previous copulations. In essence, if the mating and FWC areas overlap, it is within this overlap that the risk of infanticide is most significantly reduced, provided that males continue to prospect the same mating areas in successive years.

METHODS

Data Collection

General information

We collected GPS data from a total of 43 collared bears, comprising 25 males and 18 females, for this study. Upon capture, we determined the sex of each bear, weighed them, and classified them as adults if they were older than 5 years (Craighead et al., 1970; Støen et al., 2006; Zedrosser et al., 2007). To test our hypotheses, we extracted the following information from GPS location data for each collared female bear: (1) the entire area frequented by the female during the main mating period, spanning from 1 April to 30 June (Swenson et al., 2021); (2) the position of the birth den; and (3) the complete area frequented by the female with cubs (FWC) from den exit (April or May) until 30 June, covering the entire duration of the main mating period, when the infanticide risk is highest (Bellemain, Swenson, et al., 2006; Steyaert et al., 2012; Swenson et al., 2021). For each collared male bear, we extracted data regarding the areas they explored during the main mating period for a given year (year$_x$) and the following year (year$_{x+1}$), providing insight into male fidelity to a mating area across 2 consecutive years.

To increase data accuracy, we recorded the positional dilution of precision value for all 3D fixes and the horizontal dilution of precision for 2D fixes. We followed the method developed by D'Eon et al. (2002) to remove 2D fixes, which have higher location error, thus improving data accuracy. Although this data screening reduced the data set, it allowed us to detect a significant percentage of large location errors (Bjørneraas et al., 2010). Using the R software package adehabitat (version 0.4.15; Calenge, 2006), we estimated the size (in square kilometres) of the entire area where both adult males and adult females moved during the 3-month period from 1 April to 30 June. This period encompasses the main mating season for adult males and females and is also the riskiest time for infanticide involving females with cubs. We employed the local convex hull (LoCoH) method (Getz et al., 2007; Getz & Wilmers, 2004) to construct these areas. Specifically, we applied the fixed number of points procedure, subsampling days with at least eight locations, and determined that $k = 7$ was the optimal parameter value for constructing the LoCoH with our data set (for more details of this method, see Getz et al., 2007). We calculated the LoCoH area from GPS locations for each individual in each mating season of a given year and the consecutive year. Subsequently, we assessed the overlap between these areas for (1) the same female in mating in year$_x$ and when with cubs in year$_{x+1}$ and (2) the same male during mating in year$_x$ and year$_{x+1}$.

Finland

We used data from 27 radiocollared brown bears (17 males and 10 females, from 2002 to 2013) inhabiting southern and central Finland and Russian Karelia (for more details on the study area, see Olejarz et al., 2022; Penteriani et al., 2021, 2022). Owing to changes in bear physiology and body fat levels, sedative doses were adjusted according to the season, and bears were darted from blinds at temporary baits. Drug dosages followed the protocol by Jalanka and Roeken (1990). The tranquillizer contained a mix of medetomidine (50 μg/kg) and ketamine (2 mg/kg), with their proportion adjusted according to the size of the bear (Jalanka & Roeken, 1990). In late summer and early autumn, the spring dosage was increased by 25–50%, and longer needles were used due to increased body fat (Arnemo et al., 2007). When captured, bears were fitted with GPS transmitters (Televilt, Lindesberg, Sweden; Vectronic Aerospace, Berlin, Germany; for more information see Penteriani et al., 2021) that collected one location every 2 h.

Slovakia

We used data from 12 radiocollared brown bears (seven males and five females, from 2008 to 2015) inhabiting north-central Slovakia (for further information regarding the study area, see Skuban et al., 2018). Upon capture using culvert traps, each bear was equipped with GPS-GSM collars (Vectronic Aerospace, Berlin, Germany), which were programmed to record location fixes at hourly intervals.

Romania

We used data from four radiocollared brown bears (one male and three females, from 2010 to 2019) inhabiting the eastern and southern part of the Romanian Carpathians (for more details on the study area, see Fedorca et al., 2020; Pop et al., 2012). When captured using culvert traps, bears were fitted with GPS transmitters (GPS 8000 Collars, Lotek Wireless, Canada; Vectronic Aerospace, Berlin, Germany) programmed to collect fixes every 1–2 h.

Ethical Note

Finland

The weight of the collars (ca. 600 g) was less than 1.0–2.0% of the body weight of adult females (mean ± SD = 124.6 ± 27.5 kg) and 0.5–1.0% of adult males (mean ± SD = 212 ± 61.4 kg). All collars were removed before the end of the Finnish project in 2014. Permission to capture and manipulate bears was issued by the County Veterinarian of Oulu and the Regional State Administrative Agency of Lahti (Finland). The capturing of bears met the guidelines issued by the Animal Care and Use Committee at the University of Oulu (OYEKT-6e99), and permits were provided by the provincial government of Oulu (OLH-01951/Ym-23). During bear captures and tracking no adverse effects of manipulations were observed.

Slovakia

The weight of these collars averaged around 600 g, representing approximately 0.4–0.8% of the body weight of adult females (mean ± SD = 107.4 ± 25.1 kg) and 0.2–0.7% of adult males (mean ± SD = 150.9 ± 52.3 kg). All collars were equipped with timer-controlled drop-off mechanisms set to release after 24 months. The Ministry of Environment of the Slovak Republic issued the permit (No. 10155/2010-2.2) for capturing and handling the bears. Because ethical clearance for wildlife research is not required in Slovakia, we adhered to the recommendations outlined in the Scandinavian biomedical protocols for capturing, chemically immobilizing and radiotagging brown bears (Arnemo et al., 2007). There were no adverse incidents or undesirable effects observed during the capture operations and handling of the bears. Owing to drop-off failure, we had to recapture two bears and manually remove the collars.

Romania

The weight of the collars (ca. 1200 g) was less than 1.0% and 0.5% of the body weight of adult females and of the adult male, respectively. The duration of radiotracking after the capture was restricted to a maximum of 2.5 years. Collars equipped with a drop-off system were removed when malfunctioning or data reception errors were detected. Permission to capture and manipulate bears was issued by the Ministry of Environment, Waters and Forests of Romania. These bears were collared for research purposes, specifically either as individuals rescued from illegal traps and subsequently released and relocated, or as bears captured and relocated due to their presence and problematic activities in urban areas. The capturing of bears met the guidelines issued by the National Institute for Research and Development in Forestry Marin Dracea, INCDS (see technical reports of the project LIFE FOR BEAR—Project LIFE 13 NAT/RO/001154; http://www.forbear.icaswildlife.ro/en/), and permits were provided by the hunting associations (state or private) where the capture took place. No negative effects were observed during bear captures and tracking procedures.

Statistical Analyses

To address the predictions of our hypotheses, we conducted comparisons of percentage overlaps in the following scenarios: (1) between the area inhabited by each FWC after den emergence and the area she roamed during the mating period ($N = 27$ overlaps: 12 for Finland, 12 for Slovakia and three for Romania); and (2) by individual males during the mating period in year$_x$ versus the subsequent year$_{x+1}$ ($N = 26$ overlaps: 17 for Finland and nine for Slovakia), serving as a proxy for assessing male fidelity to a mating area over 2 consecutive years. In addition, we pinpointed the location of each birth den of FWCs in relation to the mating area of each of them ($N = 16$ breeding den locations: eight for Finland, five for Slovakia and three for Romania).

We built two separate models to compare the extent to which the size of the area covered during the mating period and the percentage of overlap varied according to the above-mentioned scenarios, across the study areas. As the size of the area had a skewed distribution, we log-transformed this response variable

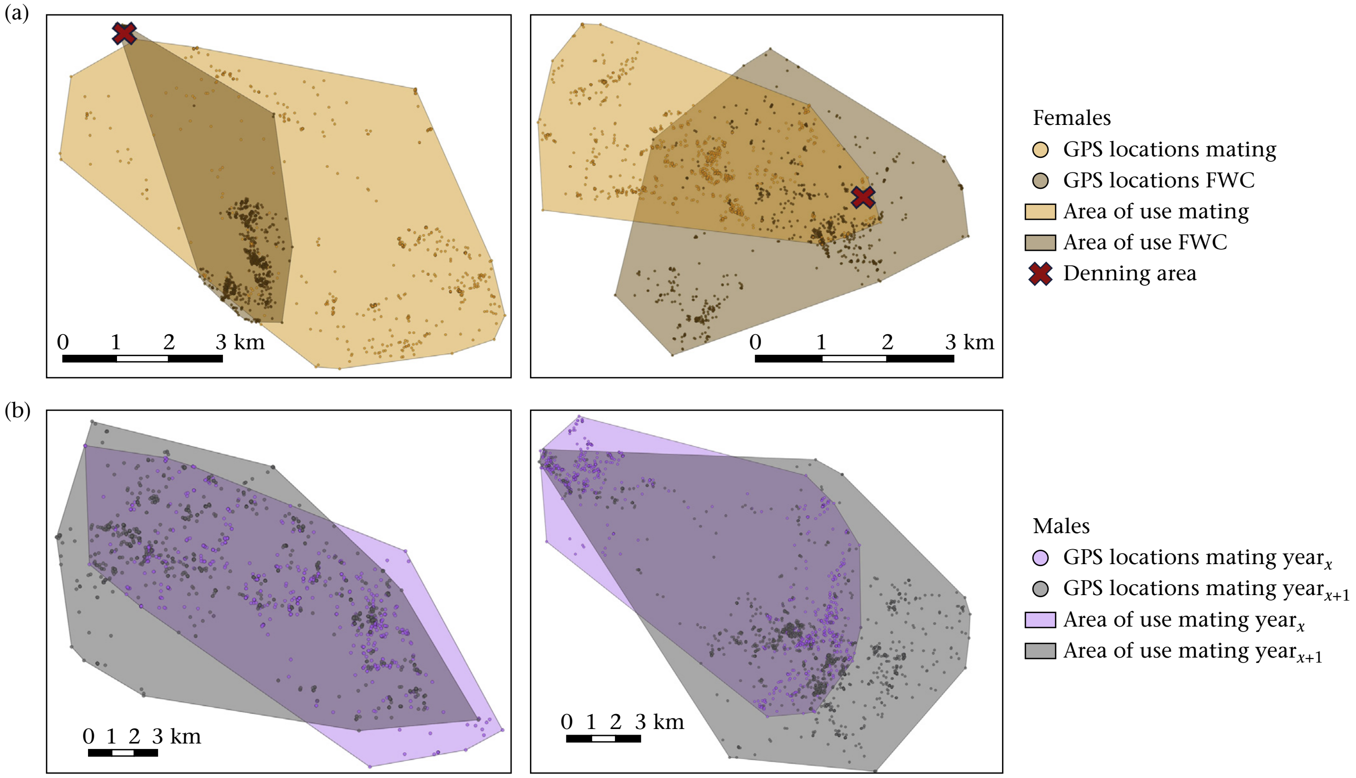

Figure 1. (a) Examples of overlap, for two different females, between areas of use during the mating period (1 April to 30 June) and after den exit with cubs the following year (female with cubs, FWC; orange and brown areas, respectively). (b) Examples of overlap, for two different adult males, between areas of use during the mating period (1 April to 30 June) of a given year and during the same period the following year (violet and grey areas, respectively).

and built a linear regression model using the lme4 R package (Bates, et al., 2015). In the case of the percentage of overlap, we built a beta regression model using the betareg R package (Cribari-Neto & Zeileis, 2010). In both models, the explanatory variables were included as categorical factors. Once we generated the sets of competing models, we employed the Akaike information criterion (AIC), using the values of ΔAIC of less than 2 as the criterion for selecting the most parsimonious model (Burnham & Anderson, 2002). Following standard procedures, we calculated the Akaike weight for each candidate model (*wi*) as the relative strength of evidence (i.e. the probability of model *i* being the best-approximating model from the entire set of candidate models). All analyses were performed using R 4.0.4. (R Development Core Team, 2023).

RESULTS

As expected (step 1), pregnant females consistently chose reproductive dens within their mating areas (Fig. 1), with only one exception found in the case of one Slovakian bear whose den was located 331 m from the nearest edge of her mating area. The overlap between the areas frequented by FWCs and their previous mating areas was substantial, averaging 89.1 ± 18.0% ($N = 20$; Table 1). In most cases, this overlap was nearly complete, with a 100% overlap observed in 30% of the cases, and an overlap in the range of 90%–100% observed in 75% of the cases. In step 2, males also displayed a high level of fidelity to their mating areas from one year to the next, showing a mean overlap of 65.5 ± 26.5% between 2 successive years (Table 1). The percentages of overlap displayed by male and female bears during the mating period were not significantly different (Table 1).

The areas covered by male and female bears during the mating period differed in size (Tables A1 and A2), with males ranging over larger areas (1381.4 ± 1751.6 km^2; $N = 51$) than females (550.9 ± 774.5 km^2; $N = 20$; Table 2). The smallest areas covered during this period were those of the FWCs, with an average of 103.7 ± 136.1 km^2 ($N = 20$; Table 2). The extent of the area covered during the mating period also varied across the various study areas (Tables A1 and A2), being generally larger in Finland (1300.8 ± 1387.0 km^2; $N = 56$) than in Slovakia (84.1 ± 61.9 km^2; $N = 26$) and Romania (38.2 ± 25.7 km^2; $N = 7$).

DISCUSSION

In this study, we found that female brown bears selected a den within their mating area and that, when they emerged from hibernation with their cubs the following year, the area they used as FWCs largely overlapped with the area they used for mating. Our research also revealed that males exhibit a high degree of fidelity between their mating area in one year and their location the following year. These findings provide support for our hypothesis, suggesting that females consistently select similar areas from year to year, perhaps as a strategy to reduce the likelihood of encountering potential infanticidal males. Notably, these results were consistent across brown bear populations studied in different countries.

While infanticide may confer fitness advantages in males, it can reduce the fitness of victimized females, causing sexual conflict (Palombit, 2015). Sexual selection may consequently favour behavioural adaptations in females to avoid male infanticide, which are maintained when the costs of female resistance to infanticide are lower than the benefits (Yamamura et al., 1990). The persistence of an FWC within the same area she has previously prospected

Table 1

Percentages of overlap between the areas prospected by the same adult female and the same adult male brown bears during the main mating period[a] in a given year, and during the same period in the subsequent year[b]

	Overlaps (%) FWC vs female mating areas				Overlaps (%) male mating areas year$_x$ vs year$_{x+1}$		
	Entire sample ($N = 20$)	Finland ($N = 12$)	Slovakia ($N = 5$)	Romania ($N = 3$)	Entire sample ($N = 26$)	Finland ($N = 17$)	Slovakia ($N = 9$)
Mean	89.1	90.6	79.2	99.7	65.5	61.3	74.4
SD	18.0	17.1	23.0	0.5	26.5	27.7	24.6
Min	44.2	44.2	53.5	99.1	10.4	10.4	17.5
Max	100.0	100.0	99.3	100.0	100.0	100.0	92.0

[a] The main mating period ranged from 1 April to 30 June.

[b] For females, the same period the year after corresponds to the period when she exits the birth den with cubs (FWC) and the infanticide risk is highest. Conversely, for males, the same period the year after serves as a proxy for male fidelity to a mating area across 2 consecutive years.

Table 2

Extent of areas (km^2) prospected by adult males and females during the main mating period[a], and by females with cubs (FWCs) from den exit (April or May) to 30 June, encompassing the entire mating period with the highest infanticide risk

	Female mating area (km^2)				Male mating areas (km^2)				FWC areas (km^2)			
	Entire sample ($N = 20$)	Finland ($N = 12$)	Slovakia ($N = 5$)	Romania ($N = 3$)	Entire sample ($N = 51$)	Finland ($N = 33$)	Slovakia ($N = 16$)	Romania ($N = 2$)	Entire sample ($N = 20$)	Finland ($N = 12$)	Slovakia ($N = 5$)	Romania ($N = 3$)
Mean	550.9	891.3	33.1	52.4	1381.4	2074.2	120.0	41.1	103.7	161.7	20.1	11.4
SD	774.5	848.4	15.3	31.9	1751.6	1841.1	51.8	11.5	136.1	150.9	13.0	4.6
Min	15.5	43.7	15.5	29.3	26.7	26.7	27.3	33.0	6.1	8.0	9.8	6.1
Max	2985.5	2985.5	56.2	88.8	8240.4	8240.4	211.8	49.2	511.4	511.4	42.2	14.8

[a] The main mating period ranged from 1 April to 30 June.

during the mating season, as demonstrated here, may not be excessively costly because she will continue to frequent a familiar area with her cubs. The observed male fidelity to the same mating area for 2 consecutive years also supports the female strategy of remaining within their mating areas during the period of the greatest risk of infanticide after den emergence with cubs. Thus, female selection for reproductive dens within mating areas, which could be considered a by-product (at least partially) of male fidelity to these areas in successive years, may also support the efficacy of promiscuity.

However, the notably smaller areas frequented by FWCs, in comparison to when they are alone searching for mates, suggests that FWCs may employ discreet movement behaviours to further reduce the possibility of risky encounters with males other than potential fathers of the cubs, with which they mated in the previous year. In fact, females tend to roam extensively during the mating season (Dahle & Swenson, 2003c; Penteriani et al., 2022), indicating an active search for mates, possibly to confuse paternities as a strategy to counter infanticides (Bellemain, Zedrosser et al., 2006). In contrast, their movements become limited after den emergence with cubs (Dahle & Swenson, 2003c; Gardner et al., 2014). Our findings thus suggest that (1) infanticide plays a pivotal role in shaping the sociospatial ecology of brown bears; and (2) female counterstrategies encompass a wide range of behaviours, including sexual (e.g. polyandrous mating), individual (e.g. elusive behaviour and maternal aggression of FWCs) and ‘social’ strategies (e.g. remaining in the area of previous mates), as well as habitat selection (e.g. den location and FWC movement areas). The evolutionary significance of infanticide in brown bears thus becomes evident through the diverse array of strategies females employ to reduce the risk of infanticide. In fact, female mammals at risk of infanticide generally rely on a combination of infanticide counterstrategies, rather than a single one (Palombit, 2015).

The extent of the areas inhabited by female brown bears in the three countries we analysed is comparable to that previously documented for Scandinavian brown bear females (Dahle & Swenson, 2003c). These Scandinavian females utilized larger areas during the mating season, likely to increase their chances of encountering prospective mates, thereby promoting greater mate promiscuity and, consequently, increasing paternal uncertainty. Our results also align with evidence showing that females with cubs occupy smaller ranges than females in oestrus (Dahle & Swenson, 2003c). Notably, the areas frequented by female brown bears with cubs in our three study populations frequently overlapped with or were included within the female mating areas (Fig. 1). While it is agreed that this behaviour could serve as an adaptive female strategy to reduce contacts with potentially infanticidal males (Dahle & Swenson, 2003c), it is crucial to emphasize that most of the FWC area was either within or largely overlapped the female mating area, and potential mates showed fidelity to their mating areas between 2 consecutive years at least. In other words, an effective counterstrategy to infanticide involves not only reducing the movement range of FWCs within a relatively small area, possibly reflecting an elusive lifestyle during the mating season to mitigate infanticide risk (Steyaert, Kindberg et al., 2013), but also ensuring that this area is situated within the mating areas of males that are putative fathers of the cubs. This holds true regardless of whether the smaller FWC movement areas are partly due to the limited mobility of the small cubs during the brown bear mating period (Dahle & Swenson, 2003c).

After emerging from the den with cubs, FWCs face the dual challenge of remaining within or near their mating areas while also limiting their movement as an additional preventive measure to avoid potential infanticidal males. These factors may contribute to the suggested nutritional costs experienced by FWCs, as restricted foraging behaviour can entail nutritional consequences (Steyaert, Reusch, et al., 2013). This phenomenon is not unique to brown bears and is observed in various species where infanticides are a significant source of offspring mortality (Steyaert, Reusch, et al., 2013). In fact, the strategies adopted by females, including multimating, den selection and remaining within the mating area as FWCs, have the potential to influence the multilevel process of female habitat selection. This process begins with the choice of the mating area, extends to the selection of the breeding den, and culminates in the use of the FWC landscape. While we may not fully understand the intricacies of this selection process, it is clear that landscape characteristics of the areas chosen primarily for mating needs and infanticide avoidance can impact female diet, reproductive outcomes and, ultimately, individual fitness. Similar effects have indeed been observed in other carnivorous species (Balme et al., 2012; Keehner et al., 2015; Packer et al., 2009).

During the mating season, FWCs have demonstrated their ability to evade infanticidal males through a variety of strategies, such as avoiding good habitats, moving to rough and higher elevation areas with steep slopes, and selecting habitat in close proximity to human settlements (Dahle & Swenson, 2003b; Gosselin et al., 2015; Libal et al., 2011; Penteriani et al., 2020; Leclerc et al., 2017; Steyaert, Kindberg, et al., 2013). For instance, one significant factor that distinguishes successful from unsuccessful FWCs is their choice to settle near human infrastructure, referred to as 'human shields' (Steyaert, Leclerc et al., 2016). These avoidance strategies for infanticide may complement the two essential steps required to make multimating paternity an effective strategy for reducing the risk of infanticide. We propose that, within the first level of FWC selection, which involves remaining within the mating area, a smaller-scale habitat selection may include the presence of human shields if they are present within the FWC areas. That is, the proximity of FWCs to human shields may more likely be a consequence of the primary selection, which involves denning within the mating area and the near-complete overlap of the ranges of FWCs with the mating areas. Actually, not all FWCs are equally successful in increasing their reproductive success through proximity to human shields (Steyaert, Leclerc et al., 2016), which may depend on whether such human presence is absent or distant from the range of the FWC. However, it is important to remark here that patterns of use of human shields have often been observed in regions with high male densities (Steyaert, Zedrosser et al., 2016), where FWCs may be forced to move away from their mating areas to avoid infanticides, and might be more likely to select peripheral territories close to human shields. Uneven sex ratios, high densities and dominant traits over large, unfragmented territories, intensify the use of human shields within the Romanian brown bear population (García-Sánchez et al., 2022; Popa et al., 2018).

It is interesting to highlight that in harvested brown bear populations, hunting can trigger a trap mechanism that may compromise the effectiveness of the two identified steps necessary to establish multimating paternity as an effective strategy for reducing the risk of infanticide (Balme et al., 2012; Packer et al., 2009). In areas where bear hunting is permitted, FWCs settling within the mating areas of potential fathers of their cubs might face an elevated risk of infanticide. This risk arises from the influx of new males following the removal of resident males due to hunting (Gosselin et al., 2015, 2017; Leclerc et al., 2017; Morales-González et al., 2020; Penteriani et al., 2018). The harvesting of resident males, which were potential mates the previous year before den emergence with cubs, can lead to an increase in the immigration of new males, including potentially infanticidal bears. Consequently, hunting can disrupt the expression of behaviours that have evolved as elaborate strategies to enhance individual reproductive success, such as relying on paternal promiscuity and male fidelity to mating areas to mitigate infanticides (Penteriani et al., 2018). This scenario can also affect species beyond brown bears, as the removal of specific individuals (through hunting or poaching) has been shown to destabilize social structures and have negative consequences on harvested populations of other carnivores (Balme & Hunter, 2013; Keehner et al., 2015; Maletzke et al., 2014; Packer et al., 2009). Furthermore, hunting harvests are typically not evenly distributed across the landscape (Gosselin et al., 2017; Steyaert, Zedrosser et al., 2016), leading to spatial heterogeneity in the removal of males. This spatial heterogeneity can result in sink dynamics with increased infanticide in areas where bear hunting and FWC range overlap (Gosselin et al., 2017; Leclerc et al., 2017). After the removal of males in areas frequented by FWCs, the occurrence of infanticide may not be immediately recorded because it can take 1–2 years for surrounding males to adjust their home ranges following the death of an adjacent male (Gosselin et al., 2017; Leclerc et al., 2017). Thus, the implications of sexually antagonistic coevolution may extend well beyond infanticide and its associated counterstrategies, potentially leading to diverse and far-reaching cascading effects in the context of sexual conflict (Palombit, 2015). To enhance the validation of the findings presented in this work, we strongly recommend that future studies take into account additional factors. These factors include assessing food and habitat availability, as well as considering demographic parameters, all of which have the potential to exert significant influence on bear movement during the mating season across various study areas.

Author Contributions

Vincenzo Penteriani: Conceptualization, Methodology, Formal analysis, Writing (original draft), Funding. **María del Mar Delgado**: Methodology, Data curation, Formal analysis, Writing (review and editing). **Ilpo Kojola**: Investigation, Data curation, Writing (review and editing), Funding. **Samuli Heikkinen**: Investigation, Data curation, Writing (review and editing), Funding. **Slavomír Find'o**: Investigation, Data curation, Writing (review and editing), Funding. **Michaela Skuban**: Investigation, Data curation, Writing (review and editing). **Ancuta Fedorca**: Investigation, Data curation, Writing (review and editing), Funding. **Mihai Fedorca**: Investigation, Data curation, Writing (review and editing). **Pino García-Sánchez**: Writing (review and editing). **Alejandra Zarzo-Arias**: Formal analysis, Writing (review and editing). **Javier Balbontín**: Writing (review and editing).

Data Availability

Owing to the sensitive nature of the bear GPS locations used in this study, we only share data on bear area overlaps and extensions, as well as data used for statistical models. Data are shared as Supplementary material.

Declaration of Interest

The authors have no conflicts of interest to declare.

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Supplementary Material

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Appendix

Table A1

Overlaps of the extent of the areas prospected by brown bears as a function of the different scenarios considered (females with cubs versus mating females; male mating areas in year$_x$ versus year$_{x+1}$) and country

Component models	*df*	logLik	AIC$_c$	Δ	Weight
Country + Type + Country:Type	5	18.39	−25.16	3.64	0.07
Country	3	16.09	−25.57	3.24	0.09
Country + Type	4	17.75	−26.46	2.35	0.14
(Null)	2	16.06	−27.82	0.99	0.27
Type	3	17.71	−28.81	0	0.44

'Type' denotes the values of the interactions between bear sexes and periods.

Table A2

Factors explaining the size of the area prospected by male and female brown bears during the mating season, and by females with cubs (FWCs), as a function of country

Component models	*df*	logLik	AIC$_c$	Δ	Weight
(Null)	2	−177.62	359.37	96.93	0
X	4	−163.92	336.31	73.86	0
Country	4	−151.41	311.29	48.85	0
Country + Bear + Country:Bear	10	−122.33	267.48	5.04	0.07
Country + Bear	6	−124.71	262.44	0	0.93
Explanatory variables		β	SE	*t* value	Pr (>|t|)
Intercept		3.5934	0.4113	8.736	2.01E−13***
Slovakia		0.1946	0.4372	0.445	0.657
Romania		2.5713	0.4108	6.259	1.57E−08***
Female with cubs		−1.3698	0.3245	−4.222	6.11E−05***
Male		0.8928	0.2714	3.29	0.001**

'X' denotes the values of the scenarios under evaluation: i.e. areas prospected by males and females during the mating period, as well as the area frequented by females with cubs. Multiple R-squared: 0.6954, Adjusted R-squared: 0.6809.

**$P = 0.01$; ***$P = 0.001$.