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The role of familial conflict in home range settlement and fitness of a solitary mammal

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Familial conflict, including parent–offspring conflict (POC) and sibling competition (SC), occurs when an individual maximizes its access to a limiting resource at the expense of a related individual. The role of familial conflict for competition over space as a limited resource remains relatively unexplored. In this study, we examined how familial conflict affects natal dispersal and settlement decisions of a solitary mammal, the brown bear, *Ursus arctos*, and tested whether these settlement patterns covary with fitness. First, we tested whether the distance settled from the natal range was affected by aspects of POC (litter type: single versus multiple; mother's age; mother's living status) and SC (settled near versus far from the natal home range, body size). We then modelled how distance settled from the natal range influenced three measures of fitness: survival to reproduction, lifetime reproductive success and lifetime survival. In line with POC, we found that daughters settled twice as far from the natal range when their mother was alive than when she was dead. We found strong evidence for SC where in sibling pairs, the 'near' sister settled nearly three times closer to the natal range than her sibling. We found contradictory patterns in fitness outcomes based on settlement distance, such that females settling closer to the natal range had higher lifetime survival but were less likely to successfully wean at least one offspring. Despite survival advantages gained by settling closer to the natal range, there was no evidence that settlement distance influenced lifetime reproductive success. Fitness outcomes in this population may be influenced more by factors related to annual hunting than by familial conflict or proximity to the natal range.

When an individual reaches independence, one of the most important decisions it can make is where to settle on the landscape prior to breeding (Bowler & Benton, 2005), often referred to as natal dispersal (Clobert et al., 2001). During the process of establishing their own home range, individuals face competition over space use, including competition with their relatives (Fattebert et al., 2015; Clutton-Brock et al., 1982). Parent–offspring conflict (POC), the difference in optimal strategies for maximizing fitness for parents and their offspring (Trivers, 1974), may arise among mothers and their independent offspring during the process of home range establishment. In species with only maternal care, a mother is expected to optimize her individual fitness by dividing parental investment equitably among her offspring, who are all equally related to her (Parker et al., 2002). However, her offspring are expected to exhibit selfishness and extract more of a given parental resource as they have more to gain from being selfish than from consigning limited resources to relatives (Kilner & Hinde, 2012). Further factors contribute to higher levels of POC, including promiscuity (Macnair & Parker, 1978), larger litter sizes (Godfray & Parker, 1992), greater number of litters in a lifetime (Parker et al., 2002), younger mothers (Delaney & Janzen, 2020) and philopatry (Kuijper & Johnstone, 2012). For example, older mothers generally have less residual reproductive value and are expected to provide greater parental resources to offspring than younger mothers (Ronce et al., 1998; Descamps et al., 2007). For promiscuous species, POC is exacerbated by the potential for

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multiple paternity which reduces the degree of relatedness among siblings (Macnair & Parker, 1978) and introduces an additional type of conflict.

Sibling competition (SC) is a form of POC that may occur within or across litters (Parker et al., 2002) whereby one sibling attempts to gain a greater amount of parental investment/resources than their sibling(s) (Kilner & Hinde, 2008). This selfishness of offspring comes at the expense of their full or half-siblings (Godfray, 1995). It is usually assumed that the larger offspring acts as the dominant sibling and acquires more parental resources (Parker et al., 1989). Inherent in SC is a limited parental resource over which siblings are in competition, with or without a parent present (Parker et al., 2002). Limiting resources may include food and shelter or features familiar from the natal range (Lawson Handley & Perrin, 2007). In mammal species that exhibit home range overlap, natal range sharing may be another type of parental resource over which POC and SC may arise (Waser & Jones, 1983; Lutermann et al., 2006).

In solitary mammals, dispersal is typically sex biased with males dispersing away from the natal range and philopatric females settling in areas overlapping the natal range (Greenwood, 1980). Female mammals are not strictly philopatric, however, and many species vary in rates of philopatry and dispersal (Karlin & Chadwick, 2012; Denomme-Brown et al., 2020; Ducros et al., 2020). In more philopatric species, a clustered grouping of related females may occur, a so-called matrilineal assemblage, for example in Columbian ground squirrels, *Urocitellus columbianus* (Arnaud et al., 2012) and fissiped carnivores (Holekamp & Sawdy, 2019). This emergent pattern creates conditions where conflict and competition for space use can arise between parent and offspring and among siblings in settlement following independence (Kuijper & Johnstone, 2012).

Space use conflict generally arises in POC and SC for access to resources available in the natal range (Starrfelt & Kokko, 2010; Kuijper & Johnstone, 2012). The resident fitness hypothesis suggests that resident females enjoy greater fitness than females that disperse due to the familiar resources within their natal site (Anderson, 1989), including but not limited to known features such as refuges, foraging patches and familiarity with neighbours (Harris & Murie, 1984; Piper, 2011; Ratnayeke et al., 2002). However, resident females also compete with their mothers and sisters for limited resources (Wiggett & Boag, 1992; Le Galliard et al., 2003), contributing to POC. The success of a mother's independent offspring increases her inclusive fitness (Hamilton, 1964). Allowing them to settle in or near the natal range is beneficial to them; however, it also leads to competition for her and her future offspring (Waser & Jones, 1983; Kuijper & Johnstone, 2012). Alternatively, inducing dispersal, an inherently risky process, may increase her offspring's mortality risk (Bonte et al., 2012) and ultimately reduce the mother's own inclusive fitness.

Previous studies examining POC and SC typically focused on prenatal and natal periods (Hudson & Trillmich, 2008; Roulin & Dreiss, 2012) and there is a need to better understand how familial conflict might influence postnatal processes such as dispersal and settlement. Mixed patterns of female philopatry and dispersal have been found in bears, including American black bear, *Ursus americanus* (Kristensen et al., 2018; Moore et al., 2014) and brown bear, *Ursus arctos* (Jerina & Adamič, 2008; Karamanlidis et al., 2021) populations. The drivers behind these patterns have not yet been identified and it is possible that POC and SC may partially explain variation in female settlement distance in the postnatal period. We used data from an individual-based study running more than 30 years, and including multiple generations of mothers and daughters, to investigate POC and SC in a solitary range-resident mammal, the brown bear. Our study population lives in a human-dominated landscape, and we investigated POC and SC in the postnatal period and how it may relate to fitness outcomes. The brown bear serves as an ideal model organism for studying POC and SC for several reasons: (1) they are long lived and females can give birth to many litters in a lifetime; (2) litters may contain single or multiple female offspring; (3) settlement distances of females vary considerably (Zedrosser et al., 2007); and (4) there is a considerable amount of home range overlap among females, including mothers and their independent daughters. Previous research on female brown bears found that independent daughters had greater overlap of their mother's home range after she had died, indicating the potential for POC to occur in this species (Hansen et al., 2022).

Our first objective was to look for evidence of POC in the distance a female brown bear settles from the natal range. According to POC theory, we expected the following patterns to emerge. Mothers that had more than one female offspring in the same litter would experience higher conflict due to increased demands from multiple daughters. Therefore, we predicted (P1a) that female offspring from a litter with multiple females would settle on average further from the natal range than those that were the sole female in a litter. Additionally, younger mothers would be expected to have greater conflict with their female offspring due to their higher residual reproductive value compared with older mothers (Descamps et al., 2007). As such, we predicted (P1b) that female offspring with younger mothers would settle further from the natal range than those with older mothers. Lastly, POC ceases when the parent (mother) dies. It follows that (P1c) female offspring with living mothers would settle further from the natal range than those whose mothers had died prior to settlement (i.e. resulting in a home range opening for settlement that would otherwise be occupied).

Our second objective was to look for evidence of SC in female brown bear settlement. We expected two patterns to emerge if SC for space use occurred in this system: one of the sisters in a pair would (1) have a larger body size and (2) would settle closer to the natal range than the other. We predicted (P2) that in a female sibling pair, one sister would settle closer to the natal range and that this would be the larger sister.

Our third objective was to determine whether settling closer to the natal range is associated with increased fitness in female offspring, as suggested in the resident fitness hypothesis (Anderson, 1989). Given that home range overlap is a cost incurred by the mother, we expected that her female offspring would have higher survival and reproduction as a result (thereby increasing the mother's inclusive fitness). We therefore predicted that female offspring that settled closer to the natal range would (P3a) survive to reproduction, (P3b) have greater lifetime reproductive success, and (P3c) have higher lifetime survival.

See Fig. 1 for a visual description of these predictions.

METHODS

Study Area and Population

The study area covers approximately 13 000 km^2 of south-central Sweden in the counties of Gävleborg and Dalarna (61°N, 14°E). Topography in the area is hilly with more rugged terrain in the northwest. The landscape is primarily covered by mixed-age stands of managed forest dominated by Scots pine, *Pinus sylvestris*, and Norway spruce, *Picea abies*. Small farms, lakes and bogs occur throughout the study area. The human population is sparse (8.64 inhabitants/km^2), but an extensive forestry road network runs through the area (Ordiz et al., 2014). See Appendix Fig. A1 for a map of the study area.

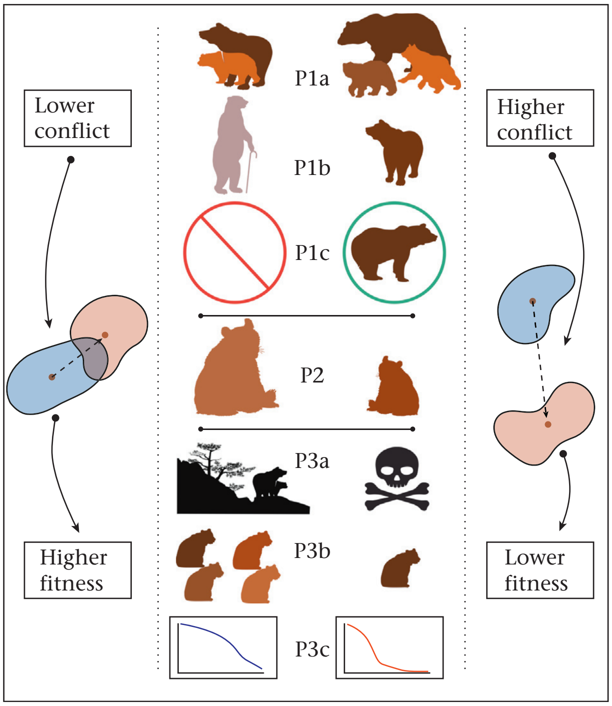

Figure 1. Diagram depicting predictions for three objectives in a study of space use and fitness in relation to parent–offspring conflict and sibling competition for female brown bears, *Ursus arctos*, in Scandinavia from 1989 to 2020. A female's natal range is represented in blue and her settlement range in beige. Objective 1 was to investigate the effect of potential parent–offspring conflict on settlement distance from the natal range: (prediction P1a) individuals from a litter with multiple females will settle further from the natal range than those that were the sole female in the litter; (prediction P1b) female offspring with younger mothers will settle further from the natal range than those with older mothers; and (prediction P1c) female offspring with living mothers will settle further from the natal range than those whose mothers had died prior to settlement. Objective 2 was to look at the effect of sibling competition on distance settled from the natal range. In a female sibling pair (prediction P2) one sister in the pair will settle in a home range significantly closer to the natal range and this will be the larger sister. Objective 3 concerned resident fitness: females settling closer to the natal range will (prediction P3a) be more likely to survive to reproduction, (prediction P3b) have greater lifetime reproductive success and (prediction P3c) have higher lifetime survival.

Brown bears are found across North America, Europe and Asia, and live solitarily aside from mating or rearing offspring (Steyaert et al., 2012). Female bears in the Scandinavian population typically begin mating around 5 years of age (Zedrosser et al., 2009) and may mate with multiple males during the breeding season (Bellemain et al., 2006). Offspring remain with their mother for either 1.5 or 2.5 years (Van de Walle et al., 2018). Following family breakup, independent offspring settle in their own home ranges (Hansen et al., 2022). Virtually all male offspring disperse (Zedrosser et al., 2007) but rates of dispersal vary for female offspring (Støen, Zedrosser, Sæbø et al., 2006). Dispersal for female bears can occur over 2–3 years (Støen, Zedrosser, Sæbø et al., 2006) and concludes when a female settles and begins to breed. Female bears in Scandinavia commonly settle in a home range overlapping their natal range (philopatry), but occasionally settle far (up to 90 km) from the natal range (Støen, Zedrosser, Sæbø et al., 2006). Females in this population are primiparous at approximately 5 years of age (Zedrosser et al., 2009). The greatest source of mortality in the adult population is legal hunting (Bischof et al., 2009). The study population of brown bears has been continuously monitored by the Scandinavian Brown Bear Research Project since 1985. We included marked female bears with known identities and birth/death years in this study, with associated reproduction data from 1986 to 2020. Only the females in any given litter are included in the study, as male offspring disperse on average 119 km from the natal range (Støen, Zedrosser, Sæbø et al., 2006) and do not compete for space with their mother or female siblings.

Our capture and collaring procedures are as follows. Each spring after den emergence, bears are located via helicopter surveys and remotely tranquillized from the helicopter via darts containing a mixture of medetomidine and tiletamine-zolazepam (Dan-Inject; Fahlman et al., 2011). Bears captured for the first time are given a unique tattoo inside their lip, sexed, measured, fitted with a radiocollar of no more than 2% of body weight (Ordiz et al., 2012) and a VHF implant is inserted subdermally near the perineum by a qualified veterinarian. They may also have one premolar removed to assess age, if unknown. Females with cubs-of-the-year are not captured and yearlings are fitted with 'drop-off' collars to accommodate their growth. Collared bears are typically recaptured every other year to replace collars or batteries. Because the goal is to collar bears over their life span, collars are recovered following drop off or after the animal dies. Handling teams leave the anaesthetized bear before the tranquillizer wears off or an antidote to the anaesthetic is given, approximately 1–1.5 h after initial anaesthesia. Further details of the capture and collaring procedure can be found in Arnemo and Evans (2017).

Ethical Note

We have never found evidence of behavioural or detrimental effects of collars in this population. All aspects of animal capture and handling were approved under an ethical permit by Uppsala Ethical Committee on Animal Experiments (Dnr 5.8.18-03376/2020). Our capture permit was provided by the Swedish Environmental Protection Agency (NV-01278-22).

Home Range and Density Estimation and Settlement Distance

Radiocollar data from female brown bears were obtained from 1989 to 2020 and comprise both VHF and GPS locations. Geolocations from VHF were collected once a week and from GPS they were recorded hourly. Both VHF and GPS were filtered by retaining only positions with a dilution of precision (DOP) $\leq$ 10 and were visually inspected for outliers prior to home range estimation. We estimated 95% kernel density annual home ranges for study females and their mothers with the KDE function in the adehabitatHR library (Calenge, 2006), using the reference (href) smoothing parameter, a grid size of 800 and a bivariate normal kernel. We then obtained the centroid location of the estimated home range. To control for slight shifts in home ranges that occur each year, we selected the home range for a single year. Natal range centroids for study females were obtained from their mother's home range in the focal female's natal year. Settlement home range centroids were from the study female's home range at 4 years of age, before females typically begin breeding in the study area (Zedrosser et al., 2009). We then measured distance settled from the natal range (km) as the straight-line distance between a study female's natal and settlement home range centroids. We used distance as a proxy for natal range overlap, as the two metrics are highly correlated ($r = -0.81$, $N = 48$, $P < 0.001$) in our study population (for details see the Appendix). Because density of individuals varies across the landscape, we obtained annual bear density rasters from between 1998 and 2015 derived from noninvasive genetic sampling and the large carnivore observation index (LCOI), described in Frank et al. (2018) to account for that variation. We overlaid the study female's settlement range over the density rasters and summarized the average bear density over that area.

From the reproductive data, we assigned a unique identifier (litter ID) for the litter a study female belonged to. Each litter was then designated as containing a sole female or multiple females (litter type). The mother was identified for each litter (mother ID) as well as her age at the birth of the litter (mother's age). We then determined whether the study female's mother was alive or dead in the year prior to settlement (mother's status). From the litters with multiple females, we excluded those with three or more female offspring and retained pairs of female siblings, assigning each a class, ‘settled closer’ or ‘settled further’, based on the distance settled from the natal range (settlement class). We had no a priori knowledge on the magnitude of difference in distance settled between pairs of female siblings (i.e. it could be small or large) and settlement class was thus simply used as a means of classifying pairs of sisters. We measured head circumference (cm) of yearling females to represent their body size (Zedrosser et al., 2007).

Survival and Reproduction

For all study females, we determined whether they survived to reproduction (successfully weaned at least one offspring) and, if applicable, the total number of offspring that were successfully weaned. For each female that survived to reproduction, we used the total number of offspring weaned to represent their lifetime reproductive success. We created a lifetime survival data set for study females which contained their age at death or oldest known age for right-censored living females and the distance settled from the natal range. In addition, we created a survival data set to get baseline survival information for the entire marked female population.

Statistical Analyses

Prior to analysis, all continuous predictor variables were tested for collinearity and all had a variance inflation factor < 2 (Zuur et al., 2010). All categorical variables were assessed visually with continuous variables for possible collinear relationships. Additionally, continuous predictor variables were scaled by subtracting the mean and dividing by one standard deviation. To investigate potential POC in settlement distances (P1a-c), we fitted a single generalized linear mixed-effect model (GLMM) with distance settled from the natal range (km) as the gamma-distributed response variable and litter type (sole/multiple females), mother's age and mother's status (dead/alive) as predictor variables, while controlling for body size.

To investigate the effect of SC on settlement distance (P2), we constructed a three-level settlement class variable, with ‘sole,’ ‘closer’ and ‘further’ as levels in an analysis of variance (ANOVA). Sole females were included in the analysis to establish whether the closer female siblings' settlement distances differed significantly from those born in sole female litters. Distance settled from the natal range was used as the comparison variable in the ANOVA. From the ANOVA output, we assigned the closer sibling as 1 and the further sibling as 0 as a binomial response variable to assess body size in sibling pairs. For the predictor variable, each sister in a sibling pair was assigned as ‘heavier’ or ‘lighter’ in a body size class.

To investigate the influence of settlement distance on fitness (P3a-c), we fitted a logistic GLMM with the response variable survived to reproduction (yes $= 1$, no $= 0$) and distance settled from the natal range as the sole predictor variable for P3a. We fitted a Poisson GLMM with lifetime reproductive success as the response variable and an offset containing the log-transformed number of breeding attempts a female had (plus one to prevent zeroes) to represent the breeding rate of females for P3b. We included distance settled from the natal range as the sole predictor in the Poisson GLMM. To assess survival, we used our survival data set to fit a Weibull accelerated failure time regression (survival regression) with distance settled from the natal range as the predictor variable and age at death or censoring as the response variable. We initially included the term average density in models for P1a-c, P2 and P3a, b. Adding density only affected one model (lifetime reproductive success), so we dropped it as a predictor from all other models (see Appendix Tables A1 and A2 for results of unused models). A unique mother ID was included as a random effect term in all models and a unique litter ID was included as a random effect in the SC model. We used the R package ‘glmmTMB’ (Brooks et al., 2017) for fitting GLMMs and ‘survival’ (Therneau & Lumley, 2015) to fit the survival regression. We used the R package ‘DHARMa’ (Hartig, 2022) to select model distributions and validate model results by assessing plots of model residuals versus fitted, QQ plots, quantile plots, the deviance value and the Kolmogorov–Smirnov statistic. All data handling and statistical analyses were done using R version 4.1.2 (R Core Team, 2021).

RESULTS

We identified 77 radiocollared females (33 from sole female litters, 44 from multiple female litters) from 35 mothers with sufficient location data to estimate settlement ranges and distance settled from the natal range at 4 years of age to include in POC and fitness models (P1a-c, P3a-c). While the parent–offspring data set included 44 females from multiple litters, we lacked the radiocollar data for several of the siblings from multiple female litters. From that data set, we found 15 female sibling pairs from 12 mothers with adequate data to estimate settlement ranges and distance settled from the natal range at 4 years of age to include in the SC model (P2a, b). Median age of survival was 9 years (95% confidence interval, CI 9–10, range 4–25) for our study population and 6 years (95% CI 5–9, range 0–25) for the general marked population of females. The marked population includes all known females in the population ($N = 202$) with known life history data but lacking the required radiocollar data to be included in the study population. Females in the marked population had a survival probability of 0.603 of living to age 4 (when settlement was measured). Mean age of primiparity in the study population was 5 years. See Appendix Tables A3 for variable descriptions and summary statistics. All reported models were considered valid using our goodness of fit procedure.

Parent–Offspring Conflict and Sibling Competition

The results of our full POC model indicate a significant effect of the mother's status on settlement distance (Table 1). Females whose mother's died prior to the settlement period settled significantly closer to the natal range than those with living mothers (Fig. 2). Neither litter type nor mother's age had a significant influence on settlement distance (Table 1). The results of our SC ANOVA show a significant difference in distances settled from the natal range by settlement class ($F = 6.768$, $P = 0.002$). A post hoc Tukey's test revealed no significant differences between sole females and the closer female sibling (mean $= -2.063$, $P = 0.847$; Fig. 3a). The Tukey's test did show significant differences between sole/further (mean $= 12.36$, $P = 0.005$) and closer/further (mean $= 14.424$, $P = 0.005$). The follow-up binomial regression output indicated a significant difference in body size between settlement classes ($\beta = -2.197$, SE $= 0.943$, $P = 0.02$). Larger females in a sibling pair were more likely to settle closer to the natal range than the smaller sibling (Fig. 3b).

Table 1
Results from the full parent–offspring conflict model on the distance settled from the natal range of female brown bears, *Ursus arctos*, in Scandinavia, from 1989 to 2020

Term	β	SE	P	95% CI
(Intercept)	2.54	0.17	< 0.001	[2.22, 2.87]
Litter type: sole	−0.31	0.20	0.131	[−0.70, 0.09]
Mother's age	−0.13	0.10	0.201	[−0.34, 0.07]
Mother's status: dead	−0.52	0.25	**0.038**	[−1.01, −0.03]
Body size	0.16	0.11	0.150	[−0.06, 0.39]

The response variable is distance settled from the natal range (km) and the predictors are litter type (litter contains either a sole female or multiple females), mother's age and mother's status (mother died prior to settlement or was alive at settlement), controlling for body size (head circumference (cm) as a yearling). Mother's tage and body size were scaled prior to modelling. Test statistics are reported from the output of a gamma generalized linear mixed model. CI: confidence interval. Significant ($P < 0.05$) value is in bold.

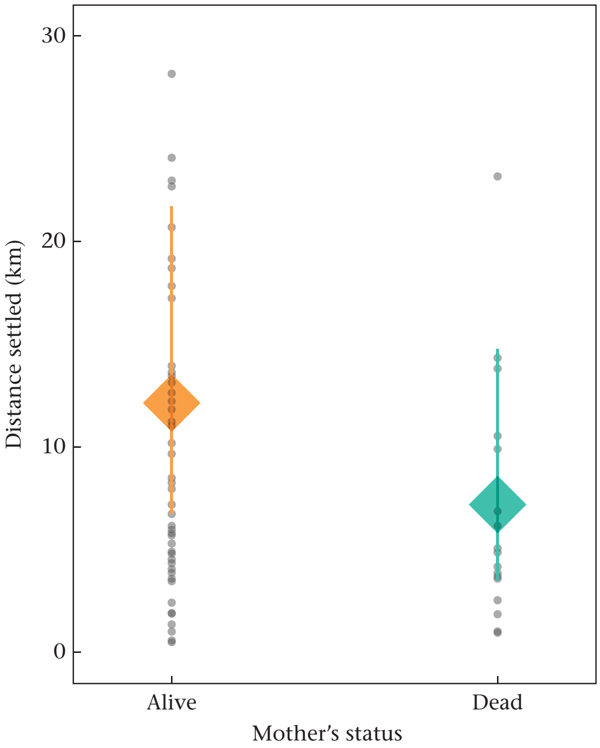

Figure 2. Predicted model of the effect of parent–offspring conflict on the mean distance settled from the natal range (with 95% confidence intervals) by female brown bears when their mother was alive or dead in the year of settlement. Average settlement distance was 11.7 km for females with living mothers and 6.82 km if the mother died prior to settlement.

Fitness

Our fitness model for a female's probability of surviving to reproduce indicated a positive effect of distance settled from the natal range (Fig. 4a; model output: $\beta = 0.586$, 95% CI = 0.033–1.140, $P = 0.038$), contrary to our prediction. Conversely, our survival regression showed that lifetime survival was higher for females that settled closer to the natal range (Fig. 4b; model output: $\beta = -0.010$, 95% CI = −0.020 to −0.0001, $P = 0.033$). Similar to the findings for surviving to reproduction, we found a positive relationship between distance settled from the natal range and lifetime reproductive success (model output: $\beta = 0.445$, 95% CI = 0.053–0.838, $P = 0.026$).

DISCUSSION

Our results indicated support for our predictions that female offspring settle closer to the natal range when their mother dies prior to settlement, that one sister in a sibling pair will settle closer to the natal range and that larger females settle closer to the natal range. Additionally, we found that females settling closer to the natal range had higher lifetime survival. We failed to find support for the predictions that sole female offspring settle closer to the natal range than those from multiple female litters or that females with older mothers settle closer to the natal range than those with younger mothers. Lastly, we found contrary evidence for our prediction on probability of surviving to reproduce: females settling closer to the natal range were less likely to survive to reproduction and had lower lifetime reproductive success.

Familial Conflict in Space Use

We found evidence for POC in female brown bear settlement, that is, female offspring settled closer to the natal range if their mother died prior to settlement. This suggests that the death of a mother releases her female offspring from conflict or competition with her (Starrfelt & Kokko, 2010). Females of other species have shown similar patterns in settlement. For example, Columbian ground squirrels settled within their mother's home range when her death preceded settlement (Arnaud et al., 2012), Amur tigers, *Panthera tigris altaica*, may take over the natal range if their mother dies (Goodrich et al., 2010), and common lizards, *Lacerta vivipara*, disperse more often when their mother is present than when she is absent (Le Galliard et al., 2003). Previous research on our study population also showed greater overlap with the mother's range if she died prior to settlement (Hansen et al., 2022). We did not find evidence that female offspring from older mothers would settle closer to the natal range. A possible reason for this is that annual hunting has resulted in a population skewed towards younger mothers on the landscape (Frank et al., 2018), potentially disrupting any patterns with age that might otherwise exist. A similar pattern was found in a study of American black bear, where hunting led to a younger population of mothers thereby confounding a potential link between maternal age and dispersal probability (Moore et al., 2014). Thus, while it is possible that older mothers may exhibit lower conflict over space use with their independent female offspring, such patterns are not possible to detect in populations where most females are killed prior to attaining an advanced reproductive age (Zedrosser et al., 2013; McLellan, 2015). Our failure to find evidence of POC in sole versus multiple litters may be partially due to greater variation around distance settled in ‘multiple’ siblings than with ‘sole’ individuals, that is, the span of distances settled in individuals from multiple female litters was much greater. A visual comparison (Fig. 3b) indicates that sole females settled similar distances to the ‘closer’ sister in sibling pairs, which may help explain the results of our POC models. Other factors in addition to POC may influence female brown bear settlement patterns. For example, neighbouring females on the landscape (the social environment) might exert pressure on settling individuals (Støen et al., 2005; Hansen et al., 2022).

In this population, SC seems to have a clearer influence on settlement distances than POC. We found support for our predictions that between a pair of female siblings, one would settle significantly closer to the natal range. Furthermore, the closer sibling settled at a distance similar to individuals from sole female litters, while her sister settled significantly further than both groups. Our finding that the larger sibling was more likely to be the closer settling sibling indicates that body size was influential in settlement. Many studies looking at sibling size and dispersal distances

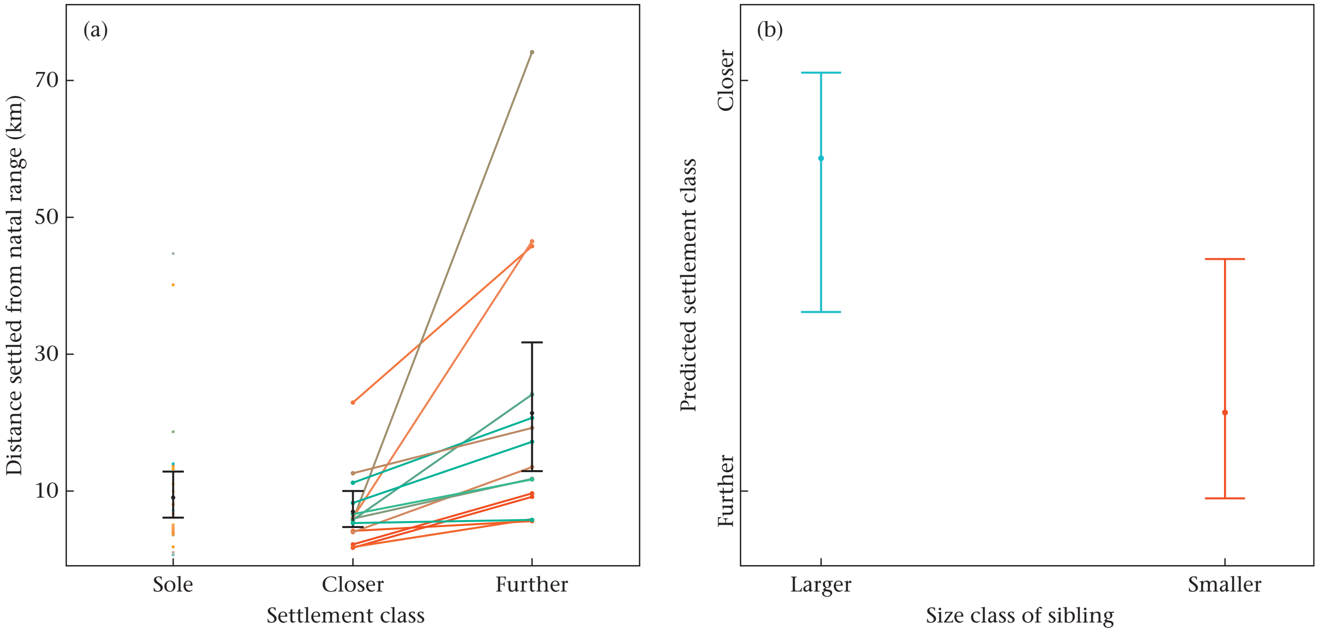

Figure 3. Results from a sibling competition analysis on female brown bears. (a) Mean (closer = 6.92 km, further = 21.3 km) and 95% confidence intervals of distance settled from the natal range of pairs of female siblings (represented here with different colours) classified as settling further or closer from the natal range. Values of females without a sister (sole, mean = 8.98 km) are shown for comparison. (b) Predicted model mean settlement class ('closer'/'further') with 95% confidence intervals from a binomial model containing a predictor for the size class of siblings within a pair.

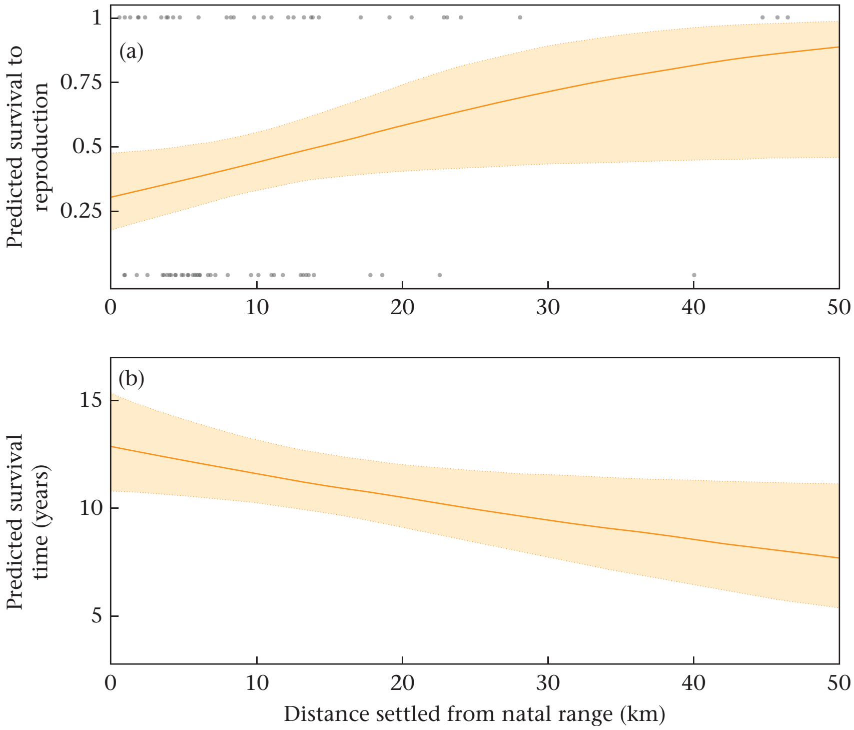

Figure 4. (a) Prediction plot with 95% confidence interval for survival to reproduction (successfully weaned at least one offspring) based on distance settled from the natal range ($N = 76$). Data points are shown in grey. (b) Prediction plot with 95% confidence interval from a Weibull accelerated failure time model for lifetime survival based on distance settled from the natal range ($N = 76$).

show no evidence of body size effects, for example in brook trout, *Salvelinus fontinalis* (Hudy et al., 2010), jacky dragon lizards, *Amphibolurus muricatus* (Warner & Shine, 2008), and house sparrows, *Passer domesticus* (Fleischer et al., 1984). However, a study on white-footed mice, *Peromyscus leucopus*, found that sibling interactions appeared to influence dispersal distances more than conflict with the mother (Jacquot & Vessey, 1995). Aggression from a larger, dominant sibling on a smaller, subordinate sibling was associated with earlier dispersal from the natal nest in a study on cichlids, Variabilichromis moorii (Satoh et al., 2021) *and, similarly,* *in Siberian jays, Perisoreus infaustus, the smaller sibling was forced to disperse before its socially dominant sibling* (Ekman et al., 2002). If a 'dominant' sibling is able to settle near the natal range and her sister is forced to settle further away, it effectively relaxes competition for space use with the mother and potentially increases inclusive fitness (Cote & Clobert, 2010). Viewed from a kin selection perspective, the dispersing sister reduces kin competition by settling away from her philopatric sibling (Cote & Clobert, 2010; Waser et al., 2013); however, kin selection would be lessened in siblings from litters with multiple paternity which can occur in brown bears. Previous research on this study population found that within female sibling pairs, one sibling had closer spatial proximity to the mother in the natal period, which may have secured a more favourable settlement location in the future (Zedrosser et al., 2007). Future research might investigate other mechanisms that might influence dominance in female sibling pairs, such as personality (Hudson et al., 2011) or agonistic interactions (Drummond, 2006).

It is generally thought that dispersal and settlement are driven by multiple factors (Matthysen, 2012) and the results of our study support that premise. We have found evidence that settlement distance is under both maternal and offspring control, with partial support for POC and evidence of SC. Although we did not detect density effects in our study, previous research on this population suggests that settlement is at least partially mediated by neighbouring females on the landscape, through familiarity (Hansen et al., 2022), relatedness and density (Støen et al., 2005). Previous research points to this population as being near or at carrying capacity by 2003 (Zedrosser et al., 2006), but that was prior to an increase in hunting intensity and subsequent population decline starting in 2006 (Gosselin et al., 2015). It is possible that in a population with regular turnover and likely below carrying capacity, conflict and competition for space use are relatively low.

Space Use and Fitness in a Harvested Population

For our third objective, we found mixed evidence for the resident fitness hypothesis in our population of female bears. We discovered that females had a clear survival advantage when settling closer to the natal range. However, that advantage did not equate to higher reproduction, either in survival to reproduction or lifetime reproductive success. How can females live longer and not necessarily have higher reproductive output? Although they had greater survival probability, females that settled closer to the natal range had a lower probability of surviving to reproduction and lower reproductive success, opposite to our predictions. One potential explanation for this phenomenon relates to a pattern described earlier in this population in which females settling closer to their natal range exhibit delayed primiparity (Støen, Zedrosser, Wegge et al., 2006), possibly due to reproductive suppression by dominant neighbouring females (Ordiz et al., 2008). Given the strong mortality pressure exerted by annual harvest (Bischof et al., 2018), female bears that settle further away and reproduce sooner may have a reproductive advantage over those that experience delayed primiparity, selecting for individuals that settle further from the natal range. The latter may have the opportunity to pass on their genes at least once before dying. Because the median age of survival in the female population is only 6 years and the average age of primiparity is 4.8 years, females may only have the opportunity to breed once if at all. Owing to higher cub loss for primiparous females (Zedrosser et al., 2009), females may survive to primiparity without having successfully weaned offspring. A study of multiple populations of American black bears suggested that dispersal may confer fitness benefits and that plasticity in philopatry/dispersal may be adaptive for female bears (Kristensen et al., 2018).

As predicted, we found that females settling closer to the natal range had higher lifetime survival. Similarly, dispersing yellow-bellied marmots, *Marmota flaviventris*, had higher mortality rates than philopatric individuals (Van Vuren & Armitage, 1994), a pattern also seen in banner-tailed kangaroo rats, *Dipodomys spectabilis* (Jones, 1986). Additionally, in North American red squirrels, *Tamiasciurus hudsonicus*, resident females have greater longevity than immigrant (dispersing) females (Martinig et al., 2020), and in American martens, *Martes americana*, greater dispersal distance is associated with higher mortality (Johnson et al., 2009). The specific mechanisms leading to higher lifetime survival for female bears that settled closer to the natal range were not studied but are likely to be related to familiarity with the landscape. Moving through unfamiliar space was linked to increased risk of predation in ruffed grouse, *Bonansa umbellus* (Yoder et al., 2004), black-tailed deer, *Odocoileus hemionus columbianus* (Forrester et al., 2015), and roe deer, *Capreolus capreolus* (Gehr et al., 2020), indicating that site familiarity provides a survival advantage. We did not look directly at harvest-related risk in our study, but it is possible that settling in unfamiliar areas increases an individual's susceptibility to human-caused mortality, as seen in elk, *Cervus elaphus* (McIntosh et al., 2014) and coyotes, *Canis latrans* (Van Deelen & Gosselink, 2006).

Although longevity in female brown bears has been linked to higher reproductive success (Zedrosser et al., 2013), we did not find support for our prediction that females settling closer to the natal range would have higher lifetime reproductive success. Our finding of the opposite pattern is difficult to interpret. Although females settling further away may receive an initial gain over closer females (as discussed above), there is no reason to expect that closer females should not 'catch them up' over time. The higher longevity in closer-settling females makes this finding especially counterintuitive. One possible reason for this is the prevalence of sexually selected infanticide (SSI) in this study population (Bellemain et al., 2006). When a resident male is harvested from the population, a new male will take over his former range and often kill the cubs of resident females which brings females into oestrus (Gosselin et al., 2017; Leclerc et al., 2017). Although females travelling with offspring have legal protection from hunting (Van de Walle et al., 2018), overlapping males in the area are not, leaving cubs vulnerable to male infanticide. For an individual female bear, this can result in many unsuccessful breeding attempts (Swenson et al., 2001), such that longevity does not necessarily correlate with reproductive success. Harvest-driven SSI has been recorded in other carnivore populations (Frank et al., 2017); for example it is the highest cause of cub mortality in South African leopards, *Panthera pardus*, partially driven by trophy hunting of males (Balme et al., 2013) and as a causal factor for population decline in cougars, *Puma concolor*, exposed to a male-only harvest (Wielgus et al., 2013). Whether from direct hunting mortality or indirect SSI, constant turnover in the population due to the annual harvest could be disrupting evolutionary patterns that would normally govern reproductive success. However, even if SSI is resulting in closer-settling females having lower lifetime reproductive success, it does not explain why females settling further away had higher lifetime reproductive success. More research is needed to understand the mechanism(s) that may be driving this counterintuitive pattern. Given our contradictory findings of how survival and reproductive success relate to settlement patterns, it is likely that predictions for population management and conservation may be challenging (Jonzen et al., 2003). Owing to the relatively high hunting pressure existing in our study system, our results may not be extendable to less intensively hunted populations.

Conclusions

We found limited evidence for POC and strong evidence for SC in female brown bear settlement. The influence of settlement distance on fitness was counterintuitive, in the case of survival to reproduction or inconclusive as in lifetime reproductive success. In human-dominated landscapes, evolutionary processes such as dispersal and reproduction may be disrupted. In this study system, both settlement and fitness may be influenced more by anthropogenic effects than conflict and competition among female bears. The influence of the annual harvest could especially create difficulties in trying to predict aspects of space use, geographical expansion and population growth.

Author Contributions

J.E.H.: Conceptualization, Data curation, Formal analysis, Writing—original draft, Writing – review & editing. **A.G.H.** and **S.C.F.**: Conceptualization, Formal analysis, Writing – review & editing. **J.K.**: Funding acquisition, Project administration, Writing – review & editing. **A.Z.**: Conceptualization, Supervision, Writing – review & editing.

Data Availability

The data that support the findings of this study are available on reasonable request from the corresponding author, J.E.H. The data are not publicly available to protect the locations and status of living animals.

Declaration of Interest

All authors declare that they have no conflicts of interest.

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Appendix

We calculated an index of overlap for a focal female's settlement home range and her natal home range using the following formula: $(O_{ij}/(A_i + A_j)) \times 2$,

where O_{ij} represents the area of overlap between the natal and settlement home ranges, Ai is the total area of the natal range and Aj is the total area of the focal female's settlement range (Støen et al., 2005); overlap index values are between 0 (no overlap) and 1 (complete overlap).

We calculated distance settled from the natal range as the Euclidean distance between the natal range centroid and the settlement range centroid.

Import data:

```
df <- readRDS("Objects/overlapDistDF.rds")
summary(df)

##    focalID              overlap         hrDistance
##  Length:48          Min.   :0.0000   Min.   : 0.6141
##  Class :character   1st Qu.:0.2516   1st Qu.: 3.8959
##  Mode  :character   Median :0.3993   Median : 7.2156
##                     Mean   :0.4078   Mean   :10.1335
##                     3rd Qu.:0.5910   3rd Qu.:12.8559
##                     Max.   :0.8606   Max.   :46.4617
```

Perform Spearman's rank correlation.

```
cor.test(df$overlap, df$hrDistance, method = "spearman")

##
##  Spearman's rank correlation rho
##
## data:  df$overlap and df$hrDistance
## S = 33438, p-value = 1.798e-12
## alternative hypothesis: true rho is not equal to 0
## sample estimates:
##        rho
## -0.8149374
```

Table A1

Results of an alternative full model of parent–offspring conflict (predictions P1a-c) and distance settled from the natal range of female brown bears from 1989 to 2020

Term	β	SE	*P*	95% CI
(Intercept)	2.23	0.16	< 0.001	[1.92, 2.54]
Litter type: sole	−0.01	0.28	0.965	[−0.56, 0.54]
Mother's age	−0.11	0.13	0.388	[−0.36, 0.14]
Mother's status: dead	−0.31	0.28	0.272	[−0.85, 0.24]
Body size	0.23	0.13	0.088	[−0.03, 0.49]
Average density	0.10	0.12	0.403	[−0.13, 0.32]

The original full model reported in the paper does not contain the predictive term average density; we report here the results of the model containing the predictive term average density. Other variables are litter type (litter contains either a sole female or multiple females), mother's age, mother's status (mother was alive or died in year of settlement), while controlling for body size (measured as head circumference as a yearling). All continuous variables are scaled in the model. CI: confidence interval.

Table A2
Alternative fitness model results for female brown bears from 1989 to 2020

Model	Term	β	SE	95% CI	*P*
Fitness I: survival to reproduction					
	Intercept	0.145	0.346	−0.534–0.823	0.676
	Distance (km)	0.925	0.571	−0.195–2.044	0.105
	Average density	0.090	0.334	−0.565–0.745	0.788
Fitness II: lifetime reproductive success					
	Intercept	−1.012	0.227	[−1.457, −0.567]	< 0.001
	Distance (km)	−0.032	0.101	[−0.23, 0.167]	0.754

These fitness models (predictions P3a, b) have a different structure from those in the main text. Model P3a: survival to reproduction contains an additional predictor variable, average density, not included in the model reported in the main text. Model P3b: lifetime reproductive success does not contain average density, as that predictor is included in the model reported in the main text. The primary predictor variable is distance settled from the natal range. Both average density and distance settled from the natal range are scaled in the model(s). The response variable in the first model is binomial and represents whether a female survived to wean at least one offspring. The response variable in the second model is the total number of weaned offspring of a female, fitted in a Poisson model with an additional offset containing the log of the number of breeding attempts (+1) included as a predictor to obtain a breeding rate.

Table A3
Description of study variables and summary statistics for the period 1989 to 2020

Variable	Type	Min	Max	Mean	SD	*N*
Litter type: ‘sole’ or ‘sibling’ Sole females are the only female in the litter, sibling females were two females in the litter	Categorical	–	–	–	–	33/44
Mother's age: age of the mother at the birth of a focal female	Discrete	4	23	9.9	4.19	77
Mother's status: ‘alive’ or ‘dead’ status of mother taken in year prior to settlement	Categorical	–	–	–	–	60/17
Settlement class: ‘Near’ or ‘far’ In a pair of female siblings, the near female settled closer to the natal range than the far female	Categorical	–	–	–	–	15/15
Distance settled from the natal range: distance (km) a study female's settlement range was located from their natal range	Continuous	0.614	74.12	11.56	12.4	77
Body size: head circumference (cm) of a study female measured as a yearling	Continuous	34	64	40.4	5.16	77
Average density: density of other bears overlapping the settlement range of a focal bear, averaged over the settlement range	Continuous	0.07	0.69	0.44	0.2	40
Survived to reproduction: whether a focal female survived long enough to wean at least one offspring	Binary	0	1	0.44	0.5	76
Lifetime reproductive success: total number of weaned offspring produced by a focal female divided by the number of breeding attempts	Continuous	0	3	0.49	0.72	76

This study concerned the effects of parent–offspring conflict and sibling competition on the distance settled from the natal range. It also assessed how the distance settled from the natal range influenced fitness variables, such as whether a female survived to successfully wean at least one offspring, lifetime reproductive success and lifetime survival. Lifetime survival is not included in this table, as it does not have associated summary statistics.

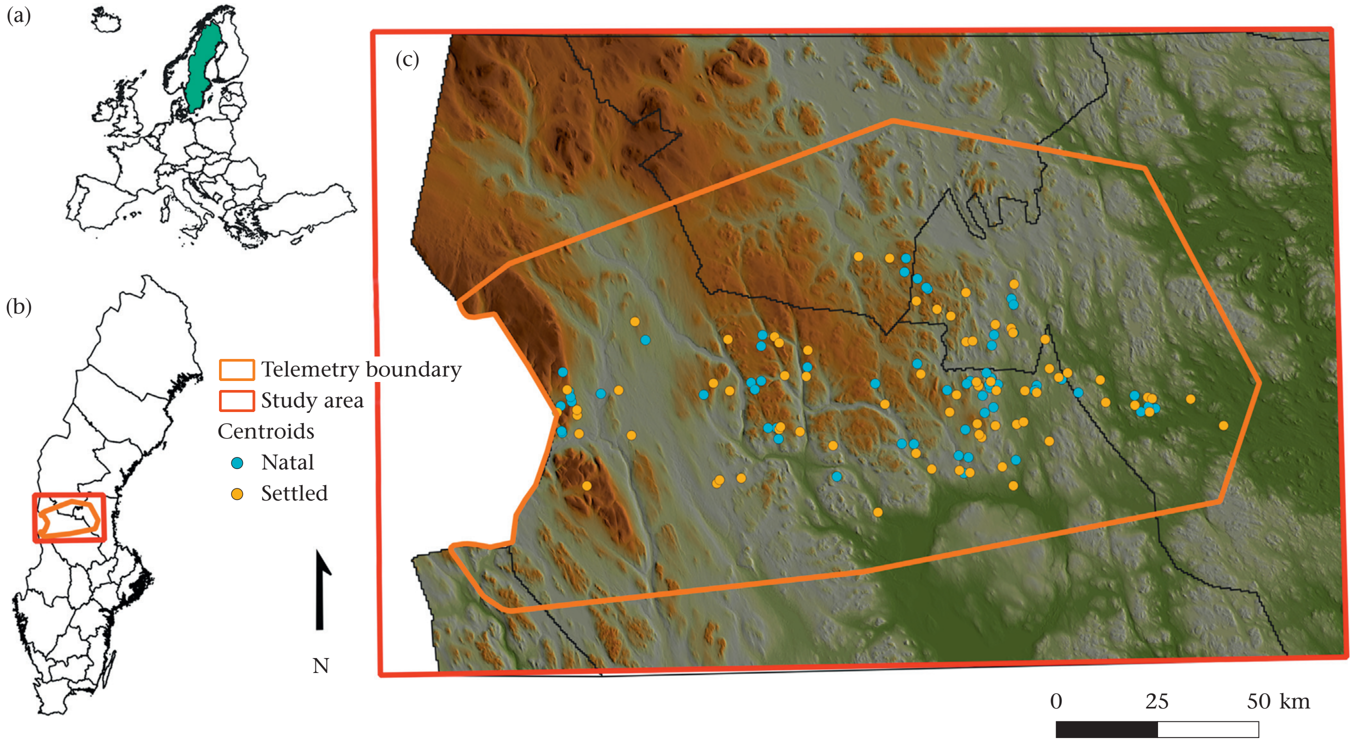

Figure A1. Map depicting the study area in Scandinavia. Map shows (a) the location within Europe, (b) the location in Sweden and (c) the boundary area of the telemetry data with natal and settled home ranges.