Title: Proximity to humans is associated with longer maternal care in brown bears

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Abstract

In the sexual conflict over the duration of maternal care, male mammals may improve their reproductive success by forcing early mother-offspring separation in species where lactation supresses estrus. However, when individual females benefit from continuing to care for their current offspring, they should adopt counter-strategies to avoid separation from offspring. Here, we tested whether spatial segregation from adult males and proximity to humans during the mating season could be associated with longer maternal care in the Scandinavian brown bear (*Ursus arctos*). Using Resource Selection Functions (RSFs), we contrasted habitat selection patterns of adult males and those of adult females with yearlings that either provided 1.5 years of maternal care ("short-care females") or continued care for an additional year ("long-care females") during the mating season, the period when family break-ups typically occur. Males and short-care females had similar habitat selection patterns during the mating season. In contrast, habitat selection patterns differed between males and long-care females, suggesting spatial segregation between the two groups. In particular, long-care females used areas closer to human habitations compared to random locations (defined here as selection), whereas males used areas further to human habitations compared to random locations (defined here as avoidance). Our results show a correlation between habitat selection behavior and the duration of maternal care. We suggest that proximity to humans during the mating season may represent a female tactic to avoid adverse interactions with males that may lead to early weaning of offspring.

Significance Statement: In mammalian species where lactation supresses ovulation, males may gain a reproductive advantage by forcing early mother-offspring separation, however females can respond through behavioral tactics. We show that female brown bears with yearling cubs can spatially segregate from males during the mating season and that this behavior is associated with

longer maternal care. Females selecting areas close to human habitations tend to keep their yearlings for an additional year, suggesting that human presence could have a shielding effect from males. Our study is among the few to explore sexual conflicts over the duration of maternal care close to weaning and shows that animals have the potential to adjust their behavioral tactics to make use of human-dominated landscapes.

Keywords: Sexual conflict, maternal care, spatial segregation, brown bear.

Introduction

Interest in reproduction differs between the sexes, mainly in terms of number of mating opportunities, leading to sexual conflicts (Arnqvist and Rowe 2005). Sexual traits favoring the interests of one sex will be under selective pressure, sometimes at the expense of the other sex. However, the evolution of sexual traits is not independent between the sexes (Chapman et al. 2003; Arnqvist and Rowe 2005). Indeed, the sex incurring the costs imposed by a behavior of the other sex may respond by adopting counter-strategies (Lessels 2012). For example, female European starlings (*Sturnus vulgaris*) coerce males into providing more parental investment by preventing them from mating with other females (Sandell and Smith 1996). In biparental care systems, the level of care provided by each parent is a common source of sexual conflicts, with several examples across birds and mammals (Arnqvist and Rowe 2005).

Parental care and its duration can limit reproductive opportunities for both sexes, leading to a sexual conflict over the duration of those care, even in species where care is provided by one sex only. Yet, this type of conflict has received little attention. In 90% of mammals, females are the sole providers of parental care (Clutton-Brock 1991). During the period of maternal care, lactation can hormonally supress estrus (Spady et al. 2007), leaving females unavailable for mating and to produce and/or care for new offspring (Tarwater and Brawn 2010; Balme et al. 2017). Early separation from offspring can thus allow females to mate again rapidly, increasing their reproductive success. Because continued maternal care implies a loss of reproductive opportunities for females, it follows that it should be provided only as long as the net benefits exceed the benefits accrued from future reproduction (Williams 1966). However, longer maternal care can be beneficial under some circumstances, as flexibility in the duration of maternal care is observed in several mammalian species (Lee et al. 1991). Despite our limited knowledge of the factors influencing the duration of maternal care and the dynamics of mother-offspring separation (including mother-offspring conflict; Trivers 1974), there is a general tendency across mammals for females to wean offspring once the latter have reached a critical body mass (Lee et al. 1991). Females rearing smaller offspring tend to prolong maternal care (Lee et al. 1991; Dahle and Swenson 2003a) to improve the survival prospects of their progeny. Delayed dispersal of offspring can be favored when dispersal success is low (Boyce 1981) and maternal care can be extended to buffer the effect of adverse environmental conditions (Grüebler and Naef-Daenzer 2008). For example, some female leopards (*Panthera pardus*) continue care of cubs during periods of prey scarcity, which greatly improves their survival chances (Balme et al. 2017). In brown bears (*Ursus arctos*), although short maternal care improves reproductive success of females, the gain in current offspring survival from continued maternal care can compensate for reduced reproductive opportunities, leading to similar fitness output for short- and long-caring females (Van de Walle et al. 2018). The reproductive success of males, however, is affected almost exclusively by the number of successful copulations they can achieve (Bateman 1948). Thus, because continued maternal care reduces female availability for reproduction, it likely has a greater effect on the reproductive success of males, compared to that of females. Most importantly, longer maternal care reduces the number of females available for reproduction at the population level, with potential consequences for the operational sex ratio and selection on male sexual behaviors (Shuster and Wade 2003).

Males may improve their reproductive success by shortening the duration of maternal care, thereby inducing estrus in females (Lessels 1999). This scenario gives rise to an extreme form of sexual conflict, sexually selected infanticide (SSI), where a male kills unrelated offspring to then mate with the victimized female (Hrdy 1979; Lukas and Huchard 2014). For example, when male African lions (*Panthera leo*) take over a new pride, they typically kill the dependent cubs, after which the victimized mothers rapidly enter estrus and mate with the perpetrators (Loveridge et al. 2007). SSI has been shown to efficiently shorten inter-birth intervals in several carnivores and primates (Smuts and Smuts 1993; Bellemain et al. 2006; Zhao et al. 2011; Balme and Hunter 2013). There are other mechanisms allowing males to shorten inter-birth intervals, without directly killing dependent offspring. For instance, males may force the early termination of maternal care by inducing either abortion or early weaning of offspring (Bruce 1959; Elliot et al. 2014). In lions, males taking over a pride also force the premature dispersal of cubs that would have otherwise received several additional months of maternal care (Elliot et al. 2014). Male-induced separation of mother and offspring may be an important mechanism for males to acquire mating opportunities (Dahle and Swenson 2003b), especially when offspring are older and harder to kill.

Counter-strategies can be adopted by females to avoid adverse interactions with males (Agrell et al. 1998). For example, spatial segregation from males is a tactic employed by females with young to avoid the risk of aggressive encounters in several species (e.g. Smultea 1994, Ben-David et al. 2004, Martin and da Silva 2004, Libal et al. 2011). In brown bears, female with cubs-of-the-year can alter their habitat and daybed selection patterns (Suring et al. 2007; Steyaert et al. 2013a; Elfström et al. 2014b; Skuban et al. 2018) to avoid dominant adult males during the spring and early summer, i.e. the period of high risk for sexually selected infanticide (Gosselin et al. 2017). In some populations, females even have been reported to use human presence as a shelter against males (Steyaert et al. 2016; Skuban et al. 2018). However, studies on spatial segregation from males have mainly focused on the period when females are accompanied by cubs-of-the-year. Whether females can also use this counter-strategy when with older offspring to avoid early weaning, i.e., if spatial segregation from males could favor continued maternal care, remains unknown.

Compared to gestation time (0.5 years; Steyaert et al. 2012), the period of maternal care is long in brown bears (between 1.5 and 2.5 years in Sweden; Dahle and Swenson 2003a). Despite reducing reproductive rates, longer maternal care has been associated with improved survival prospects for both adult females and yearlings (i.e. 1 year-old cubs) in Sweden, due to a hunting regulation protecting family groups. The gain in survival from longer maternal care can compensate for reduced reproductive success in this population, and both maternal care tactics (short- and long-care females) yield similar fitness output under average hunting pressure (Van de Walle et al. 2018). However, longer maternal care can limit male reproductive opportunities, because females in lactational anestrus will not mate until they have separated from their current litter (Dahle and Swenson 2003b; Spady et al. 2007). Therefore, a female providing 2.5 years of maternal care will be available for mating only once every three years. In contrast, a female that separates from her offspring after 1.5 years of maternal care will be available for mating one year earlier. Because females may re-enter estrus after 2-7 days following cub loss during the mating season (Bellemain et al. 2006; Steyaert et al. 2012, 2014), there should be strong incentive for males to force the separation of females from yearling offspring to gain mating opportunities. Killing of yearlings by males has been reported, but whether this behavior is sexually selected has not been investigated (Swenson et al. 2001). However, in most documented cases of family break-ups, males were observed in the vicinity (Dahle and Swenson 2003b). This suggests that males may play a role in the termination of maternal care, such as inducing early weaning.

Our main objective was to evaluate whether females with yearlings spatially segregate from males during the mating season and if this behavior is associated with longer maternal care. We contrasted habitat selection behavior of adult (≥ 5 years-old) males with that of adult females with dependent yearlings during the mating season. Females with yearlings were classified according to whether they had provided 1.5 years of maternal care (hereafter termed “short-care females”) or continued maternal care for an additional year (hereafter termed “long-care females”). We focused on the period from den emergence until the season of family break-up, which also corresponds to the mating season. First, because of the potential role of males in the termination of maternal care (Dahle and Swenson 2003b), we predicted that short-care females would show a habitat selection behavior similar to males during the mating season. Second, we predicted that long-care females would use different habitats than males during the mating season. Third, in line with previous work showing that females with cubs-of-the-year can use human presence as a shield against males (Steyaert et al. 2016), we further predicted that long-care females would use habitats closer to human presence.

Methods

Study area

The study area is located in south-central Sweden (approximately 61° N, 15° E) and encompasses approximately 13,000 km^2 of rolling landscape dominated by intensively managed forests of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and birch (*Betula* spp.). Age of forest stands ranges from recent clear-cuts to old plantations (90-100 years). Apart from forest stands, the landscape is also largely composed of bogs and lakes. Elevation ranges from 150-810 m asl. The landscape is dominated by human presence, with a dense network of gravel and paved roads used for forestry activities (0.7 km/km^2) and access to private properties (0.3 km/km^2). There are few main public roads with high-traffic volume (0.14 km/km^2) in the area (Steyaert et al. 2016).

Apart from small villages (≥ 200 inhabitants) in the north and in the south, the study area contains only small settlements (< 200 inhabitants) and recreational cabins distributed rather homogeneously throughout (Steyaert et al. 2016). Brown bear population density was estimated in 2002 at 20 bears/1000 km^2 in the area (Solberg et al. 2006). Hunting of bears is allowed throughout the study area in the fall and hunters can shoot any bear, regardless of age or sex, except members of family groups (females with their dependent cubs of any age).

Animal captures and monitoring

As part of an individual-based, long-term monitoring program in south-central Sweden, bears are captured in the spring soon after den emergence (late April) from a helicopter by darting (Dan-Inject, Børkop, Denmark) with an immobilizing drug. Captured bears are equipped with a GPS collar (GPS Plus; Vectronic Aerospace, Germany). We located collared females and counted their cubs from the ground or a helicopter a minimum of three times during the non-denning period: at den emergence, after the mating season and before den entry. We captured collared females and their yearlings. At this time, we weighed all the bears and determined the sex of the yearlings. Yearlings were not GPS-collared, because of their rapid growth. Instead, yearlings were equipped with a VHF transmitter (Telonics, model IMP/400/L HC) implanted in the peritoneal cavity. Although the monitoring of females is the primary objective of the program, males were also monitored, but more opportunistically. Most bears were captured as yearlings with their respective family groups and consequently their year of birth was known. For bears not followed from birth, a premolar tooth was extracted for age determination (Matson et al. 1993). See Arnemo et al. (2011) for further details on capture and handling. All captures and handling were approved by the appropriate authority and ethical committee (Djuretiska nämden i

Uppsala, Sweden). Because our study involved focal animals, it was not possible to record data blind.

Spatial and statistical analyses

The GPS collars were programed to deliver a position every 1 hour. We removed positions with dilution of precision > 10 to improve spatial accuracy (Lewis et al. 2007). GPS data were collected during the period between den emergence and family break-up for the three classes of bears (i.e. males, long-care females, and short-care females), but for long-care females and short-care females, we only used the year they were accompanied by yearlings in our analyses (Fig. 1). For every bear-year, we considered the date of den emergence as the first date when available GPS data showed movements away from the denning site. For short-care females, we considered that family break-up occurred between the last date the female was observed with her yearlings and the first date the female was observed alone. However, because females show drastic and rapid changes in behavior and movement patterns after separating with cubs (Steyaert et al. 2014), we only used GPS relocations until the date of the last observation of the female with her yearlings, which represents a conservative date of family break-up. To keep the period during which we collected GPS data and assessed habitat selection of long-care females, short-care females, and adult males comparable, we randomly assigned an end date for each long-care female and adult male according to the density distribution of family break-ups obtained for short-care females (Online Resource 1: Table S1). We contrasted habitat selection of males, long-care females, and short-care females using a resource selection approach, where GPS locations represented resource use and random locations represented resource availability (Lele et al. 2013). For every bear-year, we evaluated home range as a 100% minimum convex polygon (Mohr 1947). Availability was determined by drawing a random sample of locations within the home range in equal number to the GPS locations recorded for every bear-year (third order of selection; *sensu* Johnson 1980). We extracted land cover types (old-forest, mid-aged forest, young forest, clear-cut and bogs) and distance to human footprint (road, human habitation) variables known or expected to affect the probability of occurrence of males and females with dependent cubs (Steyaert et al. 2013a, 2016). For land cover type variables, we reclassified the Swedish land cover map (Svenska Marktäckedata, © Naturvårdsverket 2014) into water, bog, clear-cut, young forest (tree height < 7 m, >7 years old), mid-aged forest (tree height 7-15 m), old forest (tree height >15 m), and updated the maps annually for new clear-cuts, based on logging data obtained from the Swedish Forestry Agency (www.skogsstyrelsen.se). We used the Swedish National Road Database from the Swedish Transport Administration (© Trafikverket) to extract distance to the nearest road. We updated the road network annually by digitizing new logging roads, based on satellite image mosaics obtained from the Swedish Mapping, Cadastral and Land Registration Authority (© Lantmäteriet). Because of image quality and availability, the years 2006, 2015, and 2016 were not updated. For those years, we used the maps that were closest in time to the GPS data for extraction. We used the Real Property Register from the Swedish Mapping, Cadastral and Land Registration Authority (© Lantmäteriet) to extract Eucledian distance to the nearest human habitation, annually updated for new buildings. Human habitations are found at various distances in the home ranges of all individuals from the two female groups (Online Resource 1: Fig. S1).

Resource selection at the population level

We used logistic generalized linear mixed effects models (R package “lme4”; Bates et al. 2015) to estimate resource selection functions and habitat selection coefficients (Johnson et al. 2006; Lele et al. 2013). We compared resource use with resource availability and we defined the use of a resource in a larger proportion compared to its availability as selection, and the use of a resource in a lesser proportion compared to its availability as avoidance (Lele et al. 2013). Resource use (coded “1”) and resource availability (coded “0”) were set as the response variable, bear-year nested in bear identity as a random intercept, and distance to human footprint (roads, habitations) and land cover types (old-forest, mid-aged forest, young forest, clear-cut and bogs) as fixed effects. Land cover types were included as dummy variables (Boyce et al. 2002) and continuous “distance to” variables were scaled prior to analysis. Water was not included as a potential land cover type in our models. Also, due to variance inflation issues in our complete model, we removed one forest-type variable. Removing young forest resulted in a better model fit (lower Akaike Information Criterion, AIC), compared to model without old forest and model without mid-aged forest by 76.0 and 143.3, respectively. Therefore, we decided to remove young forest from our analysis, which resulted in a model with 4 land cover types (“mid-aged forest”, “old forest”, “clear-cut” and “bog”). We constructed three biologically plausible models to determine the relative importance of the human footprint and land cover type variables to explain resource selection by bears and three additional models using the same effect structure, but adding an interaction term with “group” (3 levels factor: “male”, “long-care female”, “short-care female”) to each fixed effect (Table 1). Adding the interaction term allowed testing the importance of between-group differences in resource selection. Model selection was based on AIC and AIC weights ($\mathrm{AIC}w_{\mathrm{i}}$). We reversed the signs of coefficients of selection related to “distance to” variables for ease of interpretation. As a proxy for relative differences in habitat selection between the three groups, we calculated the sum of absolute differences in the coefficient of selection for each variable tested between males and long-care females, males and short-care females, and the two female groups. Large values would indicate large overall dissimilarities, whereas small values would indicate similarities in habitat selection patterns. Following Steyaert et al. (2016), we quantified the relative importance of each variable in explaining between-group differences in resource selection by removing one interaction term at a time from the best performing model and compared AIC between the reduced model and the best performing model. All Variance Inflated Factors (VIF) were < 3 (Zuur et al. 2009).

Resource selection at the individual level

Although some habitats may be selected or avoided at the "population" or "group" level, variation between individuals within the same group is also expected (Leclerc et al. 2016). To assess the possibility that some individuals may have a disproportional effect on the population-level effect, we also modelled resource selection at the individual level (1 model per bear-year). We used generalized linear models, with the same fixed effect structure as the model selected in the first step, however excluding the interaction terms. Individual selection coefficients were extracted for the 6 variables included in the model. To test the effect of bear group on individual habitat selection patterns, we used a non-parametric multivariate analysis of variance. This approach, based on the comparison of between and among group distances in a multivariate space, allows for a lack of dependence on assumptions about data distribution (Anderson 2001). Individual selection coefficients were put into matrix format (rows = bear-year, columns = coefficient of selection for the 6 variables) and then converted into an Euclidean distance matrix. The distance matrix was used as a response variable in a permutational multivariate analysis of variance (PERMANOVA); with 1000 permutations (Anderson 2001) with the R package "vegan" (Oksanen et al. 2017). We also conducted *post-hoc* pairwise comparisons between the groups by performing multiple PERMANOVAS and applying a Bonferroni correction to adjust P-values (Anderson 2001).

Results

From 2004 to 2016, we obtained GPS positions for 78 bear-years: 52 male bear-years (23 individual males) and 26 bear-years for females with yearlings (from 16 individual females; Online Resource 1: Table S1). We divided female data according to whether or not they became separated from their yearlings in that year, i.e. “short-care females” (14 bear-years from 11 individual females) or kept their yearlings for an additional year, i.e. “long-care females” (12 bear-years from 8 individual females). The two female groups did not differ significantly in terms of age (long-care females: mean = 12.1 years, short-care females: mean = 10.9 years, t = -0.91, df = 24, P = 0.37) or years of GPS data collection (long-care females: mean = 2011, short-care females: mean = 2010, t = -1.27, df = 24, P = 0.22), which suggests that age or temporal effects are not likely to confound the results.

Resource selection at the population level

The best performing model to explain bear resource selection included the interaction term “group” with “distance to” and land cover type variables (Table 1). Based on parameter estimates from the model (Table 2), we calculated the selection coefficient associated with each variable for the three bear groups separately. All bear groups avoided old forests (Fig. 2a; Online Resource 1: Table S2). Males and short-care females showed very similar avoidance of mid-aged forest, old forests, and bogs. In contrast, long-care females and males only showed similar selection coefficients for distance to roads and old forest, but the confidence intervals overlapped only very slightly. The sum of absolute differences in selection coefficients for all variables (our proxy of relative differences in habitat selection between the groups) was greatest between males and long-care females (males *vs* long-care females: 2.23, males *vs* short-care females: 1.08, long-care females *vs* short-care females: 1.20), suggesting that males and long-care females have the most contrasted habitat selection patterns. Long-care females showed selection coefficients for distance to human habitations and bogs that strongly diverged from males and short-care females (Fig. 2a). With the exception of old forest, removing the interaction of all other variables in the selected model with "group" increased AIC values of the reduced models (all ΔAIC > 3; Fig. 2b). Removing the interaction between "habitation" and "group" substantially reduced model fit (ΔAIC = 670), to a greater extent compared to any other variable (all other ΔAIC < 76; Fig. 2b), suggesting that between-group differences in probability of occurrence were mostly explained by distance to human habitations.

Resource selection at the individual level

For four bear-years (1 long-care female and 3 short-care females), the model did not converge, which hindered the proper estimation of individual selection coefficients. We thus removed those bear-years and extracted selection coefficients for the 74 remaining bear-years (52 males, 11 long-care females, and 11 short-care females) to perform the analysis. The three groups differed significantly in their habitat selection patterns (PERMANOVA, $F = 2.66$, $R^2 = 0.07$, $P = 0.02$), indicating more dissimilarities between groups than within groups. *Post-hoc* pairwise comparisons showed that only males and long-care females were statistically dissimilar in their habitat selection patterns (males vs long-care females: $F = 4.38$, $P_{adj} = 0.02$; males vs short-care females: $F = 1.63$, $P_{adj} = 0.47$; long-care females and short-care females: $F = 1.24$, $P_{adj} = 0.77$).

Discussion

Identifying the factors influencing the termination of parental care has interested evolutionary ecologists for decades (Trivers 1972; Martin 1984; Lee et al. 1991). However, data on the timing of weaning are rarely available in wild populations. In this study, we tested whether female brown bears with yearlings could spatially segregate from dominant adult males during the mating season, and if this behavior was associated with longer maternal care. Females that provided short maternal care selected for habitats similar to those selected by males. In contrast, we found significant differences in habitat selection patterns between males and females that kept their yearlings for an additional year. The most striking difference was that long-care females strongly selected for human habitations, whereas males avoided human habitations. We hypothesize that by reducing the probability of encounters with males, spatial segregation from males through spatial association of females with humans may allow for continued maternal care in brown bears.

Our results showed that short-care females selected habitats similar to those selected by males during the mating season. Females could intentionally seek male habitats to initiate family break-up and secure mating, which would increase their reproductive success. The time distributions of family break-ups and the mating season overlap highly in brown bears (Craighead et al. 1995; Dahle and Swenson 2003b). During this period, there is a high risk of encounters with adult males because males cover considerable distances to gain mating opportunities (Dahle and Swenson 2003c), and females can associate with a large number of males (Steyaert et al. 2012). Encounters with males are also likely to result in mating as 82% of the short-care females included in our study that survived until the next year (n = 11) gave birth to a new litter, indicating that they encountered and mated with at least one male during the mating season.

Alternatively, unintentional selection of male habitats could increase the probability of encounters with males, which could lead to the separation of the family group. For many species, we know very little about male-female interactions around the time offspring are weaned. Direct observations in the wild are needed to confirm the respective roles of males and females in the termination of maternal care. However, we know that males pose a threat to yearlings in brown bears (Swenson et al. 2001). Because of sexual dimorphism in this species (Swenson et al. 2007; Steyaert et al. 2012), there is a risk of injuries and death associated with aggressive encounters with males (McLellan 1994; Craighead et al. 1995). The risk of SSI is usually considered to be only applicable for young offspring (Hrdy 1979). Yet, whether it is sexually selected or not, intraspecific killing by males is an important cause of mortality for brown bear yearlings (McLellan 1994; Swenson et al. 2001; Bischof et al. 2009). Swenson et al. (2001) estimated annual mortality of yearlings due to intraspecific killing by males at between 3-16% in south-central Sweden, suggesting that adult males pose a significant threat to yearlings. The cause of yearling killing by males remains unclear, but considering the significance of this threat, we suggest that an encounter with males should lead females to adopt risk minimizing tactics and be more prone to chase the yearlings away to minimize risk. In several primate species where males pose a threat to offspring, the arrival of a new male in a group has been associated with abrupt weaning and/or maternal rejection, irrespective of the age of the infant and even in the absence of aggressions (Fairbanks and McGuire 1987; Zhao et al. 2011; Morino and Borries 2017). For instance, in captive vervet monkeys (*Cercopithecus aethiops sabaeu*), females placed with a new male reject their infant more frequently near the expected weaning age, even without being harassed, compared to when placed with a resident male (Fairbanks and McGuire 1987).

We documented spatial segregation between brown bear females that kept their yearlings for an additional year and adult males during the mating season, both at the group and the individual levels. Whether the selection of habitats different than those of adult males arises from an active female-based decision to continue maternal care is difficult to ascertain. Habitat selection patterns may vary according to differences in physiology, energy needs, and individual preferences (Main et al. 1996; Leclerc et al. 2016; Hertel et al. 2019) and these factors could explain why long-care females select habitats similar to those of males, whereas short-care females do not. We also hypothesize that such segregation by long-care females represents a risk-minimizing tactic of male-avoidance. To avoid interactions with dominant conspecifics, the most vulnerable individuals (usually sub-adults and females with dependent offspring) can adopt spatial avoidance as a risk-minimizing tactic (Hrdy 1979; Elfström et al. 2014b). By selecting different habitats than males, females may avoid risky encounters that could lead to either offspring mortality or separation. Spatial segregation from males by females with dependent offspring is a tactic commonly found in other mammalian species where males are a threat to offspring and females (Hrdy 1979; Smultea 1994; Martin and da Silva 2004; Rode et al. 2006; Loseto et al. 2006). Our results are also in line with previous studies on brown bears, showing that spatial segregation of females with cubs-of-the-year (the most vulnerable group to SSI) from adult males during the mating season can be a female tactic to reduce the risk of cub mortality and mitigate sexual conflict (Steyaert et al. 2013a, 2016). Here, we build upon this previous result and show that females with yearlings can also segregate spatially from males and that this segregation is associated with a higher probability of keeping the yearlings for an additional year. However, the correlative nature of our results does not allow us to infer causation.

Distance to human habitations was the most important factor explaining differences in habitat selection patterns between bear groups, with long-care females strongly selecting proximity to human habitations and adult males showing the opposite pattern. In Sweden, food-search does not explain the occurrence of brown bears close to human habitations as bears near human settlements do not have a superior diet than those in remote areas (Elfström et al. 2014a).

Therefore, we do not think that long-care females select areas close to human habitations to access food. Also, it has been shown that continued maternal care compensates for lower offspring mass (Lee et al. 1991; Dahle and Swenson 2003a) in several mammals, such as brown bears. It could thus be argued that the distinct habitat selection pattern of long-care females results from females selecting for higher quality habitats to obtain high-energy foods to increase offspring mass. However, in our study, mean yearling mass was comparable between litters of long-care females (mean = 18.8 kg, SD = 4.0, n = 11) and short-care females (mean = 16.4 kg, SD = 5.1; t = -1.23, df = 22, P = 0.23, n = 13).

According to the despotic distribution hypothesis (Fretwell and Lucas 1969), the most vulnerable individuals may be forced into suboptimal habitats. In brown bears, sexual segregation from dominant adult males by vulnerable females with young can entail a risk in terms of nutrition (Steyaert et al. 2013b) and disturbance by humans (Rode et al. 2006). Hunting is the main cause of mortality for brown bears in Sweden, affecting their natural mortality patterns, life histories, and behaviors (Ordiz et al. 2012; Zedrosser et al. 2013; Bischof et al. 2018; Van de Walle et al. 2018). Because of this and considering the importance of other human-related sources of mortality in brown bears (Bischof et al. 2009), humans can be perceived as a threat, which could explain why brown bears generally avoid human activity (Støen et al. 2015). However, there is a tendency for young individuals and females with cubs to come closer to human settlements than solitary adult females and adult males (Steyaert et al. 2013a; Elfström et al. 2014b; Skuban et al. 2018), which is interpreted as a safety-search tactic (Elfström et al. 2014b). For females with offspring, the risk of living in close proximity to humans appears to be outweighed by its fitness benefits. Indeed, cub survival is improved when Scandinavian brown bear females with cubs-of-the-year employ such a safety-search tactic and use humans habitations as shields against males

(Steyaert et al. 2016). Moreover, females can alter their habitat selection behavior post-mating, allowing for a compensation of the nutritive cost of living in proximity to human habitations during the mating season (Steyaert et al. 2013b).

We propose that some females actively decide to avoid males during the mating season when accompanied by yearling offspring to avoid early family break-up. Accordingly, the following year, when they will separate from their 2-year-olds (maternal care does not exceed 2.5 years in this population; Dahle and Swenson 2003a) they would then alter their habitat selection pattern towards adult male habitats to initiate family break-up. Indeed, a *post-hoc* analysis showed that long-care females switched habitat selection from strong selection when with yearling cubs to a tendency to avoid human habitations when with 2-year-old cubs (Online Resource 2: Table S3 & Fig. S2-S5). Although based on a small sample size, this suggests that some females may decide to remain closer to human habitations temporarily during the mating season, increasing their probability of keeping their yearlings for an additional year. This is in line with a previous study showing that females with cubs-of-the-year alter their habitat selection patterns towards human habitations only during the mating season (Steyaert et al. 2013b). Evaluating intra-individual changes in habitat selection behavior according to female reproductive state and relative fitness outcome would be helpful to infer causality, but this goes beyond the scope of this study.

In a previous study from the same population, we found within-individual consistencies in the duration of maternal care, with two female tactics: short- and long-care females (Van de Walle et al. 2018). The costs and benefits in terms of reproduction and survival are opposed between the two tactics, yielding overall similar fitness output under average hunting pressure. Due to insufficient sample size, we did not test for repeatability of habitat selection behavior here, although it is a reasonable possibility that there are also two distinct female tactics with regard to habitat selection (Leclerc et al. 2016). However, repeatability of maternal care is around 30%, (Van de Walle et al. 2018), which also indicates potential for environmentally-driven intra-individual variation in this trait. Such variation may result from undesirable male intervention, or alternatively, from an active female-based decision to prolong maternal care in response to offspring needs or environmental conditions, with sexual segregation during the mating season as one mechanism to achieve this.

Seldom has sexual conflicts over the duration of maternal care been investigated at later stages of maternal care. This gap in knowledge is surprising, considering the large number of species with variable and long periods of mother-offspring association. As it reduces male reproductive opportunities, long mother-offspring association periods are expected to be fertile grounds for sexual conflicts in polygynous species. Males could thus play an important, and potentially under-appreciated, role in the termination of maternal care, resulting in selective pressures on females to adopt tactics to regain power over their allocation decisions. As such, our study provides a new contribution to our limited understanding of the factors determining the duration of maternal care. Previous studies have shown how human activities can affect animal behaviors (Ciuti et al. 2012) and sexual selection (e.g. Allendorf and Hard 2009). We show that females have the potential to take advantage of a human-dominated landscape to reduce their interactions with males and modulate their maternal investment. Our study reinforces the conclusion that human activities may shape sexual selection and offer a new perspective on how sexual conflicts can be mitigated.

Compliance with ethical standards: Our use of animals followed all applicable national guidelines. Our handling of study animals was approved by the appropriate authorities and ethical committee: the Swedish Board of Agriculture (no. 35-846/03, 31-7885/07, 31-11102/12), the Uppsala Ethical Committee on Animal Experiments (no. C40/3, C47/9, C7/12), and the Swedish Environmental Protection Agency (no. 412-7327-09 Nv).

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Data availability: All data generated or analysed during this study are included as supplementary material.

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Tables

Table 1 Candidate models to evaluate habitat selection of Scandinavian brown bears in south-central Sweden, 2004-2016. All models are logistic regressions with the binomial response variable "used/available" (used=1, available=0) and include bear-year nested in bear identity as a random intercept. When present, the interaction (indicated by a *) term "group" (3 levels variable: "male", "short-care female" and "long-care female") is applied to all variables within the model. Models are listed with their number of parameters (K), the difference in AIC to the best performing model (ΔAIC), and model weight (AICw_i)

Model	Model description	K	ΔAIC	AICw_i
1	Distance to road + Distance to habitation	5	1887.01	0
2	Mid-aged forest + Old forest + Bog + Clear-cut	7	966.40	0
3	Model 1 + Model 2	9	914.20	0
4	Model 1*Group	11	1102.27	0
5	Model 2*Group	17	813.57	0
6	**Model 4 + Model 5**	**23**	**0.00**	**1**

Table 2 Parameter estimates (β) of the most parsimonious model to determine resource selection of brown bears males, females that have separated from their yearlings (“short-care female”) and females keeping their yearlings for an additional year (“long-care female”) in south-central Sweden, 2004-2016. Continuous variables were scaled. The signs of β coefficients for “distance to” variables were reversed for ease of interpretation. Positive coefficients (β > 0) indicate that resources are used in a larger proportion compared to their availability (defined here as selection), negative coefficients (β < 0) indicate that resources are used in a lesser proportion compared to their availability (defined here as avoidance), and null coefficients (95% confidence interval of β includes 0) mean that resources are used in proportion to availability

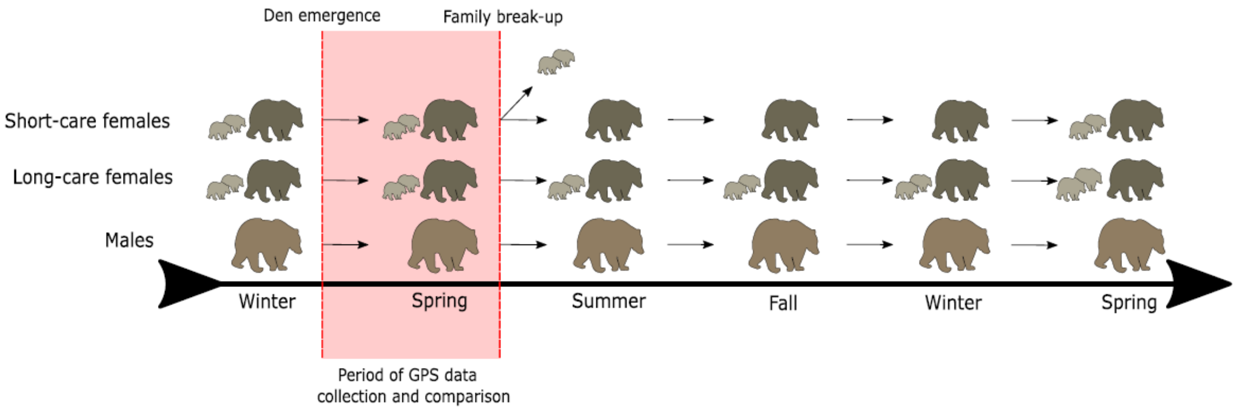
		95% CI	
Model term	β	Lower	Upper
Intercept	0.19	0.15	0.23
Long-care female	-0.08	-0.16	0.01
Short-care female	-0.06	-0.14	0.02
Distance to the nearest road	0.05	0.04	0.07
Distance to the nearest habitation	-0.09	-0.11	-0.08
Old forest (1 vs 0)	-0.23	-0.26	-0.20
Mid-aged forest (1 vs 0)	-0.18	-0.21	-0.15
Bog (1 vs 0)	-0.56	-0.60	-0.51
Clearcut (1 vs 0)	-0.33	-0.39	-0.27
Long-care female * Distance to the nearest road	0.04	0.00	0.07
Short-care female * Distance to the nearest road	-0.12	-0.15	-0.09
Long-care female * Distance to the nearest habitation	0.52	0.48	0.57
Short-care female * Distance to the nearest habitation	0.16	0.13	0.19
Long-care female * Old forest (1 vs 0)	0.09	0.00	0.19
Short-care female * Old forest (1 vs 0)	0.05	-0.03	0.14
Long-care female * Mid-aged forest (1 vs 0)	-0.19	-0.28	-0.10
Short-care female * Mid-aged forest (1 vs 0)	0.08	0.00	0.16
Long-care female * Bog (1 vs 0)	-0.44	-0.58	-0.30
Short-care female * Bog (1 vs 0)	0.00	-0.11	0.10
Long-care female * Clearcut (1 vs 0)	0.34	0.17	0.50
Short-care female * Clearcut (1 vs 0)	0.57	0.41	0.73

Figure captions

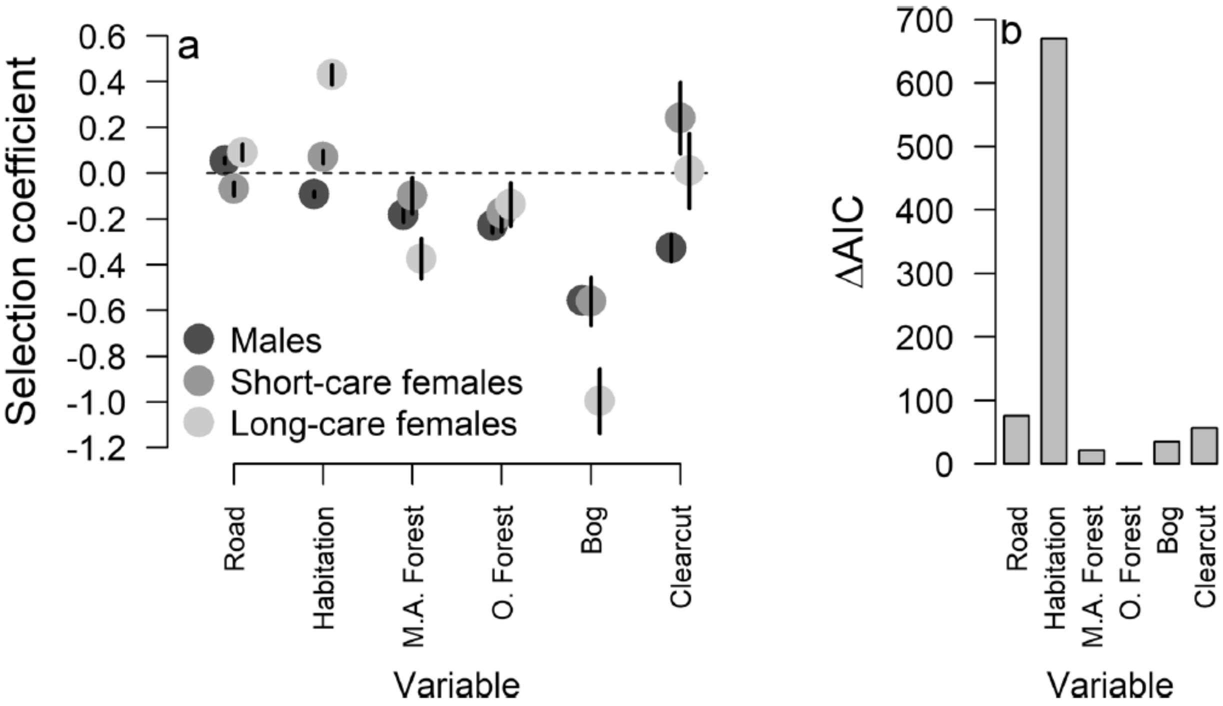
Fig. 1 Timeline showing that GPS data used to compare habitat selection between brown bear short-care females, long-care females and males were collected between den emergence and family break-up (red shaded area) in south-central Sweden. Females from the two groups were all accompanied by yearlings during this period

Fig. 2 Contrasted habitat selection coefficients (and 95% confidence intervals) between adult males, females separating from their yearlings ("short-care females") and females keeping their yearlings for an additional year ("long-care females") for brown bears during the mating season in south-central Sweden, 2004-2016 (**a**). Positive coefficients ($\beta > 0$) indicate that resources are used in a larger proportion compared to their availability (defined as selection), negative coefficients ($\beta < 0$) indicate that resources are used in a lesser proportion compared to their availability (defined as avoidance), and null coefficients (95% confidence interval of β includes 0) mean that resources are used in proportion to their availability. The signs of "distance to" variables were reversed for ease of interpretation. For each variable tested in the global model, change in AIC after the removal of its interaction with the variable "group" (3 levels variable: "male", "short-care female" and "long-care female") for each variable in the best performing model explaining resource selection (**b**). Large ΔAIC values suggest large between-group differences in resource selection for the variables tested. Definitions: "Road" = distance to the nearest road, "Habitation" = distance to the nearest human habitation, "M.A.Forest" = mid-aged forest, "O.Forest" = old forest, "Bog" = bogs and tree-rich bogs, "Clearcut" = recently cut forest stand

Fig.1


Den emergence
Family break-up
Short-care females
Long-care females
Males
Winter
Spring
Summer
Fall
Winter
Spring
Period of GPS data collection and comparison

686 Fig. 2


a
Selection coefficient
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
-1.2
Males
Short-care females
Long-care females
Road
Habitation
M.A. Forest
O. Forest
Bog
Clearcut
Variable
b
ΔAIC
700
600
500
400
300
200
100
0
Road
Habitation
M.A. Forest
O. Forest
Bog
Clearcut
Variable

687

Title: Proximity to humans is associated with longer maternal care in brown bears

Journal: Behavioral Ecology and Sociobiology

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Electronic Supplementary Material 1: Supporting tables and figures

Table S1 Summary characteristics for brown bears within each group considered in the analyses. Start and end dates refer to the period during which GPS data were collected for each bear-year. Start date corresponds to den emergence, i.e. the first date when available GPS data showed movements away from the denning site. For short-care females, end date corresponds to actual family break-up date. For males and long-care females, it corresponds to a fictive date of family break-up randomly drawn from the density distribution of family break-ups obtained for short-care females. No. relocations corresponds to the total number of geographic localisations used in the analyses (half corresponds to actual GPS relocations, i.e. resource use, and the other half to randomly drawn locations within the bear annual home range, i.e. resource availability)

ID	Start date	End date	Group	Age	No. relocations
B_3	2007-04-16	2007-06-29	Male	16	3040
B_3	2008-04-28	2008-07-11	Male	17	3272
B_7	2008-04-20	2008-05-27	Male	10	1694
B_8	2003-04-17	2003-06-08	Male	5	2206
B_14	2008-04-13	2008-05-17	Male	5	1614
B_14	2009-04-12	2009-06-13	Male	6	1536
B_14	2010-04-15	2010-07-05	Male	7	3782
B_14	2011-04-18	2011-05-27	Male	8	1892
B_14	2012-04-01	2012-05-21	Male	9	1584
B_14	2014-04-26	2014-05-14	Male	11	796
B_16	2008-04-19	2008-06-02	Male	8	2100
B_16	2010-04-11	2010-05-19	Male	10	1722
B_16	2011-04-10	2011-05-05	Male	11	1082
B_17	2008-04-20	2008-05-15	Male	6	924
B_17	2010-04-15	2010-06-22	Male	8	2382
B_17	2012-04-01	2012-05-22	Male	10	1292
B_17	2013-04-21	2013-06-12	Male	11	2306
B_17	2014-04-18	2014-05-09	Male	12	1030
B_19	2008-04-16	2008-07-15	Male	5	2674
B_19	2010-04-17	2010-05-19	Male	7	1544
B_19	2011-04-11	2011-06-19	Male	8	3144
B_20	2008-04-18	2008-05-30	Male	16	1896
B_21	2008-04-19	2008-07-05	Male	6	2940
B_21	2010-04-29	2010-05-23	Male	8	1116
B_21	2011-04-01	2011-07-07	Male	9	4474
B_21	2012-04-01	2012-06-30	Male	10	2948
B_21	2013-06-02	2013-07-09	Male	11	1786
B_22	2012-04-09	2012-06-13	Male	5	2468
B_22	2013-04-13	2013-05-22	Male	6	1752
B_23	2012-04-01	2012-05-12	Male	5	1798
B_23	2013-04-19	2013-05-22	Male	6	1604

B_25	2009-04-15	2009-07-05	Male	5	3668
B_25	2010-04-15	2010-06-28	Male	6	3338
B_26	2009-05-17	2009-07-01	Male	7	2062
B_27	2009-05-17	2009-06-15	Male	6	1384
B_28	2010-04-16	2010-06-27	Male	10	3354
B_28	2011-04-12	2011-05-24	Male	11	1834
B_29	2011-04-03	2011-05-10	Male	7	1408
B_29	2012-04-01	2012-05-11	Male	8	1050
B_30	2010-05-31	2010-06-12	Male	6	272
B_30	2011-04-10	2011-05-12	Male	7	1216
B_31	2013-04-20	2013-06-09	Male	5	262
B_32	2013-04-23	2013-05-03	Male	13	492
B_32	2014-04-01	2014-07-11	Male	14	4140
B_32	2015-04-01	2015-06-24	Male	15	3854
B_32	2016-04-05	2016-07-09	Male	16	3126
B_33	2014-04-19	2014-06-01	Male	6	2072
B_34	2015-04-06	2015-06-15	Male	6	3056
B_35	2013-06-02	2013-06-28	Male	6	1236
B_37	2008-04-11	2008-06-03	Male	19	2472
B_37	2009-04-09	2009-05-31	Male	20	1468
B_37	2010-04-23	2010-06-24	Male	21	2898
B_1	2008-05-01	2008-05-29	Long-care female	14	1378
B_4	2009-04-22	2009-07-09	Long-care female	9	1920
B_4	2012-05-05	2012-05-23	Long-care female	12	578
B_4	2015-04-27	2015-05-17	Long-care female	15	668
B_6	2013-05-18	2013-05-29	Long-care female	12	570
B_12	2013-04-26	2013-05-27	Long-care female	8	1318
B_13	2014-04-17	2014-06-30	Long-care female	9	3426
B_18	2010-04-27	2010-05-13	Long-care female	10	814
B_18	2014-05-01	2014-06-05	Long-care female	14	1724
B_24	2010-05-06	2010-05-22	Long-care female	13	804
B_38	2006-05-06	2006-06-21	Long-care female	13	1890
B_38	2009-04-29	2009-05-21	Long-care female	16	1092
B_1	2004-04-19	2004-07-15	Short-care female	10	3258
B_2	2008-05-03	2008-05-08	Short-care female	9	284
B_5	2007-04-19	2007-06-18	Short-care female	6	2850
B_6	2011-04-28	2011-07-13	Short-care female	10	3590
B_9	2011-04-29	2011-07-13	Short-care female	18	3550
B_10	2006-05-01	2006-05-06	Short-care female	6	272
B_10	2011-05-04	2011-05-19	Short-care female	11	758
B_10	2013-05-25	2013-06-04	Short-care female	13	518
B_11	2011-05-08	2011-05-26	Short-care female	10	624
B_13	2012-04-27	2012-05-03	Short-care female	7	282
B_15	2012-05-05	2012-05-21	Short-care female	11	798
B_15	2014-04-30	2014-05-19	Short-care female	13	944
B_36	2008-05-03	2008-05-08	Short-care female	18	280
B_39	2007-04-22	2007-06-20	Short-care female	11	2790

Table S2 Model-based predictions of selection coefficients for Scandinavian brown bear adult males, short-care females and long-care females in south-central Sweden, 2004-2016

	Males			Short-care females			Long-care females		
		95% CI			95% CI			95% CI	
Variable	Selection coefficient	Lower	Upper	Selection coefficient	Lower	Upper	Selection coefficient	Lower	Upper
Road	0.05	0.04	0.07	-0.07	-0.10	-0.04	0.09	0.05	0.13
Habitation	-0.09	-0.11	-0.08	0.07	0.04	0.10	0.43	0.39	0.47
Old_Forest	-0.23	-0.26	-0.20	-0.17	-0.26	-0.09	-0.14	-0.23	-0.04
Mid_Aged_Forest	-0.18	-0.21	-0.15	-0.10	-0.18	-0.02	-0.37	-0.46	-0.29
Bog	-0.56	-0.60	-0.51	-0.56	-0.67	-0.46	-1.00	-1.14	-0.86
Clearcut	-0.33	-0.39	-0.27	0.24	0.08	0.40	0.01	-0.16	0.17

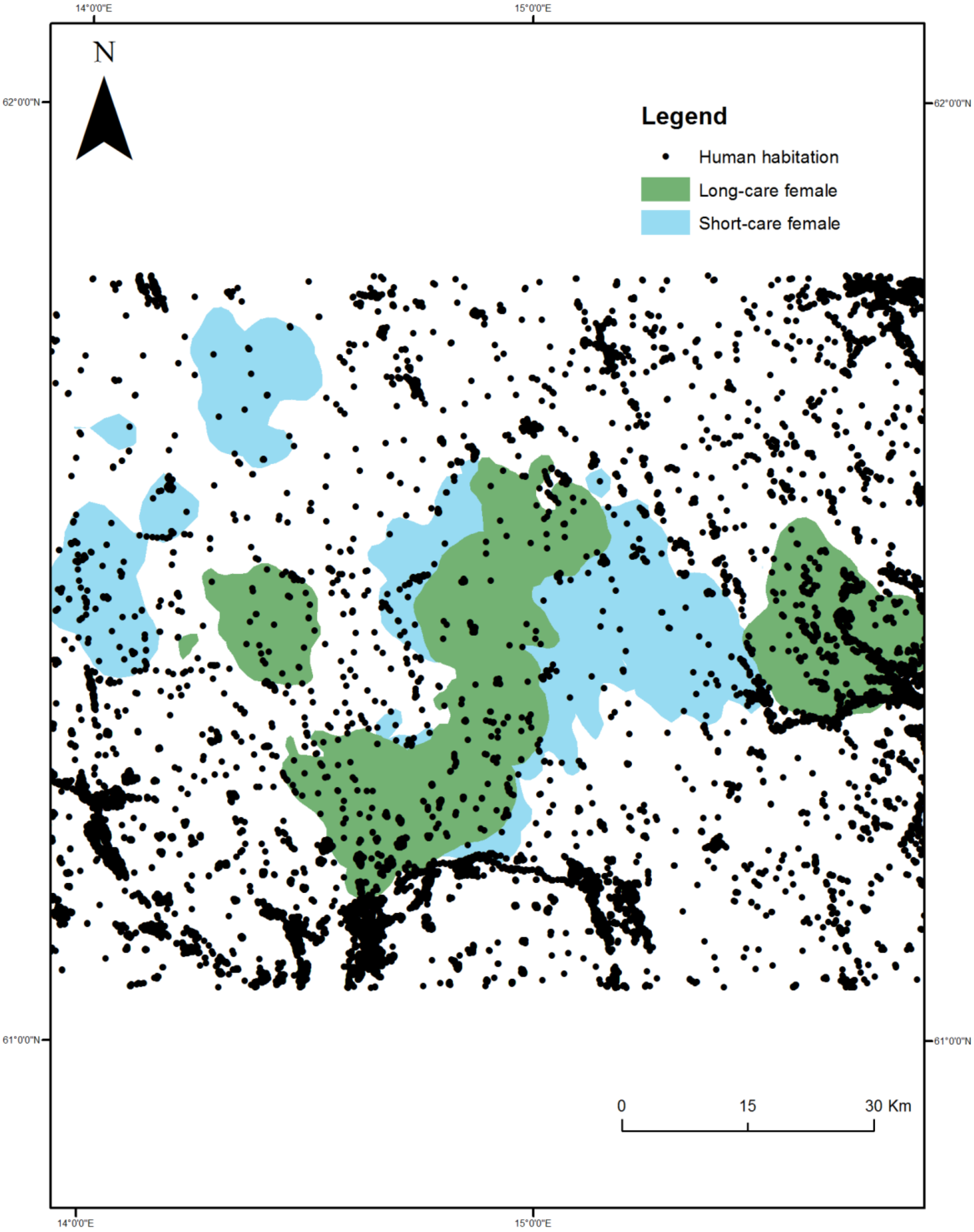

Fig S1 Distribution of human habitations in the study area (black dots) along with the home range of short- (blue areas) and long- (green areas) care female brown bears in southcentral Sweden.

Title: Proximity to humans is associated with longer maternal care in brown bears

Journal: Behavioral Ecology and Sociobiology

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Electronic Supplementary Material 2: Intra-individual comparison of habitat selection patterns

We compared habitat selection during the mating season of individual females (n=4) from the year they were with yearlings (time *t*; the year when the female kept the yearlings) to the year they were with 2-year-olds (time *t*+1; the year of mother-offspring separation). We had sufficient GPS data from den emergence until a randomly assigned date of family break-up (time *t*) and the date of actual family break-up (time *t+1*) for only four females. We used RSFs with the same fixed and random effect structure as described in the methods section, but this time "group" was set as a 2-levels factor ("keeping female" and "female with 2-year-olds") in interaction with all land cover types and human distances variables.

Table S3 Parameter estimates (β) from logistic regression to evaluate resource selection of brown bear females (n=4) between the year they were accompanied by dependent yearlings (keeping females) and the following year, when they have separated from their 2-year-old cubs in south-central Sweden, 2004-2016. Continuous variables were scaled. The signs of β coefficients for “distance to” variables were reversed for ease of interpretation. Positive coefficients (β > 0) indicate selection, negative coefficients (β < 0) indicate avoidance, and null coefficients (95% confidence interval of β includes 0) mean that resources are used in proportion to availability

		95% CI	
Model term	**β**	**Lower**	**Upper**
Intercept	-0.18	-0.40	0.05
Keeping female	0.13	-0.15	0.42
Distance to the nearest road	0.26	0.17	0.36
Distance to the nearest habitation	-0.09	-0.20	0.01
Mid-aged forest (1 vs 0)	-0.40	-0.67	-0.14
Old forest (1 vs 0)	0.76	0.51	1.01
Bog (1 vs 0)	-0.38	-0.73	-0.03
Clearcut (1 vs 0)	0.66	0.21	1.11
Keeping female * Distance to the nearest	0.20	0.07	0.32
Keeping female * Distance to the nearest	0.27	0.14	0.40
Keeping female * Mid-aged forest (1 vs 0)	0.06	-0.27	0.39
Keeping female * Old forest (1 vs 0)	-0.28	-0.59	0.03
Keeping female * Bog (1 vs 0)	-0.14	-0.58	0.29
Keeping female * Clearcut (1 vs 0)	-0.61	-1.20	-0.03

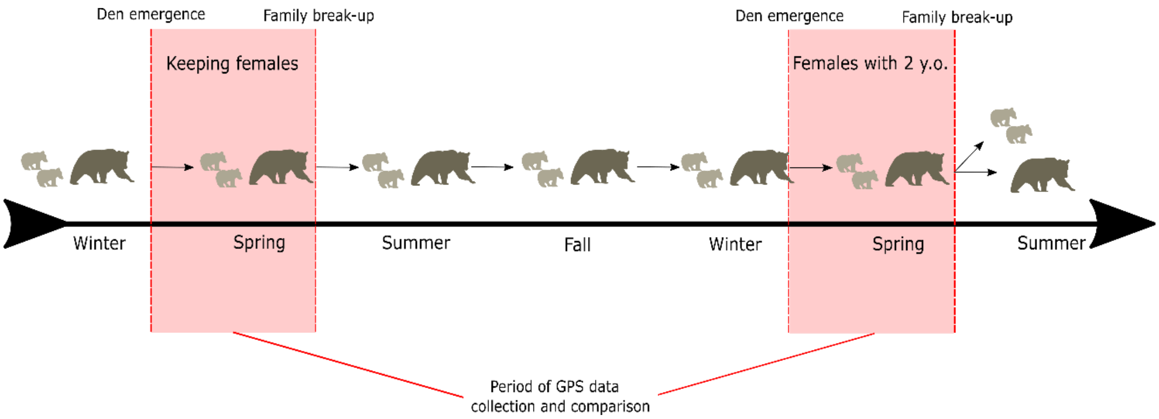

Fig S2 Timeline showing that GPS data used to make intra-individual comparisons of habitat selection patterns were collected between den emergence and the period of family break-up when females were accompanied by dependent yearlings and dependent 2 year-olds

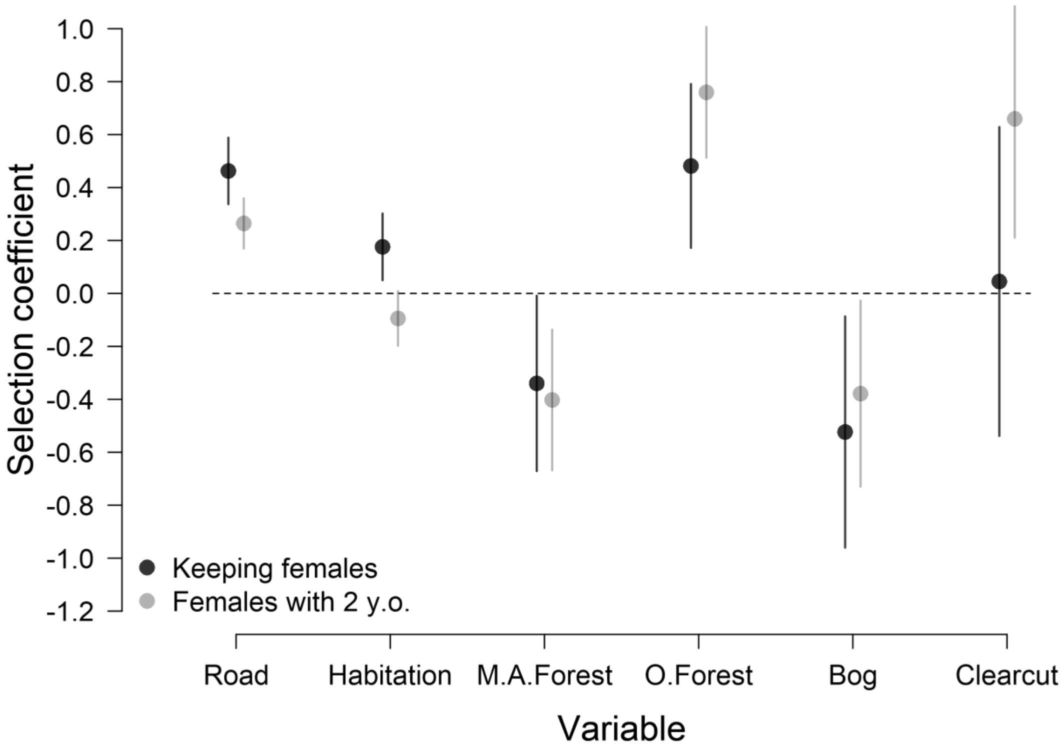

Fig S3 Changes in habitat selection coefficients (and 95% confidence intervals) of brown bear females (n=4) between the year they were accompanied by dependent yearlings (keeping females) and the following year, when they have separated from their 2-year-old cubs in south-central Sweden, 2004-2016. Positive coefficients ($\beta > 0$) indicate selection, negative coefficients ($\beta < 0$) indicate avoidance, and null coefficients (95% confidence interval of β includes 0) mean that resources are used in proportion to what is available. Definitions: “Road” = distance to the nearest road, “Habitation” = distance to the nearest human habitation, “M.A.Forest” = mid-aged forest, “O.Forest” = old forest, “Bog” = bogs and tree-rich bogs, “Clearcut” = recently cut forest stand. The signs of “distance to” variables were reversed for ease of interpretation

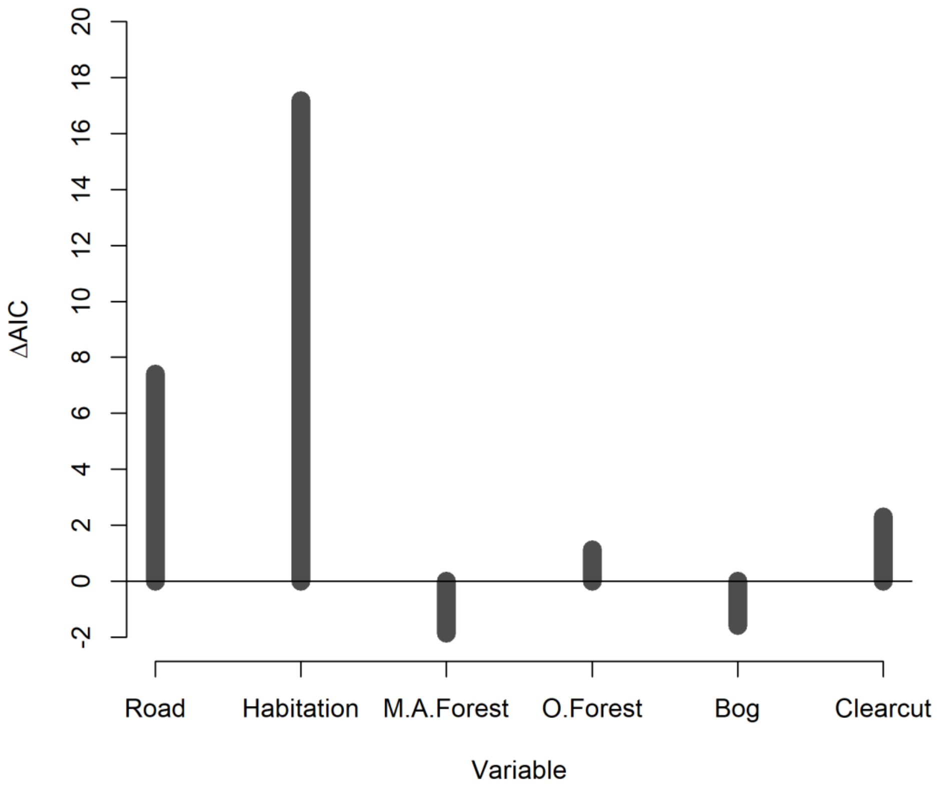

Fig S4 Change in AIC after the removal of an interaction term with “group” (2 levels factor: keeping females and females with 2-year-olds) for each variable in the global model explaining resource selection of female brown bears in south-central Sweden, 2004-2016. Only females that were monitored both when accompanied by dependent yearlings and the following year, when they have separated from their 2-year-old cubs were included in the model (n=4 females, corresponding to 8 bear-years). Large and positive ΔAIC values suggest large between-group differences in resource selection for the variables tested, whereas negative values suggest poorer model fit. Definitions: “Road” = distance to the nearest road, “Habitation” = distance to the nearest human habitation, “M.A.Forest” = mid-aged forest, “O.Forest” = old forest, “Bog” = bogs and tree-rich bogs, “Clearcut” = recently cut forest stand

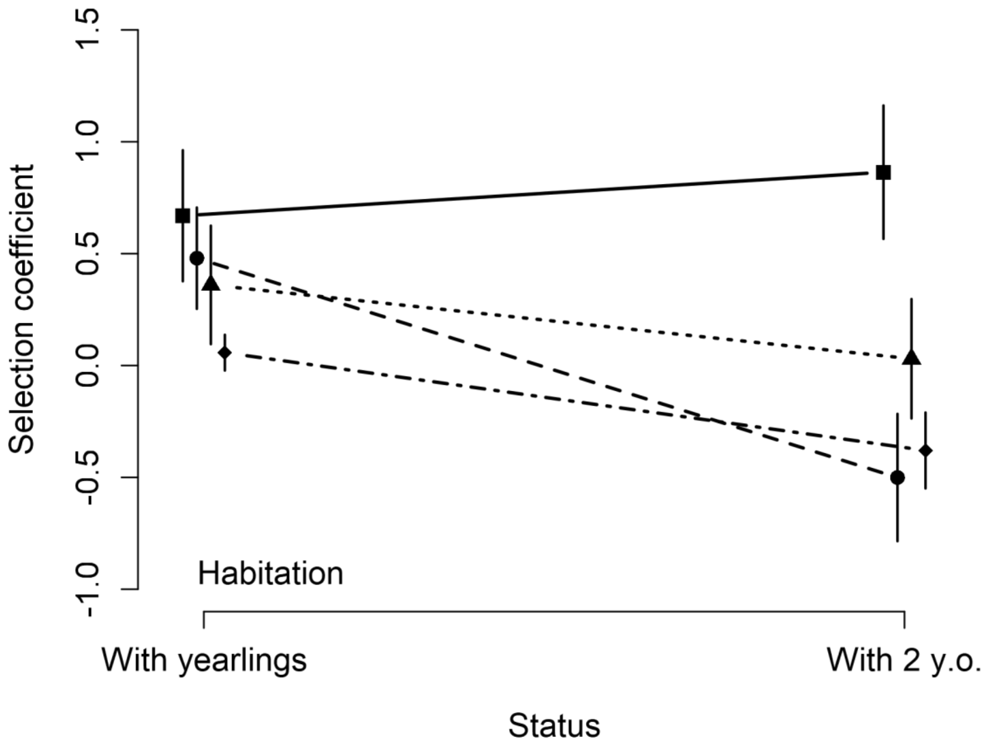

Fig S5 Change in selection (selection coefficient and 95% confidence intervals) for human habitation of brown bear females (n=4) between the year they were accompanied by dependent yearlings (“With yearlings”) and the following year, when they have separated from their 2-year-olds (“With 2 y.o.”) during the mating season in south-central Sweden, 2004-2016. Each line represents a different individual female. Positive coefficients ($\beta > 0$) indicate selection, negative coefficients ($\beta < 0$) indicate avoidance, and null coefficients (95% confidence interval of β includes 0) mean that resources are used in proportion to what is available