

RESEARCH ARTICLE OPEN ACCESS

Family Breakup Dynamics in a Promiscuous Solitary Mammal

Rick W. Heeres¹  | Wisse Boot² | Emile Delen² | Miriam Tovar Heid² | Martin Leclerc³  | Shane Frank^{1,4}  | Alexander Kopatz⁵  | Fanie Pelletier⁶  | Henry Kuipers² | Martijn J. A. Weterings^{2,7}  | Andreas Zedrosser^{1,8} 

¹Department of Natural Sciences and Environmental Health, University of South-Eastern Norway, Bø, Norway | ²Wildlife Management, Department of Animal Management, Van Hall Larenstein University of Applied Sciences, Leeuwarden, the Netherlands | ³Département Des Sciences Fondamentales & Centre D'étude de la forêt, Université du Québec à Chicoutimi, Chicoutimi, Québec, Canada | ⁴Mammals Research Section, Colorado Parks and Wildlife, Fort Collins, Colorado, USA | ⁵Norwegian Institute for Nature Research, Trondheim, Norway | ⁶Département de Biologie, Université de Sherbrooke, Sherbrooke, Québec, Canada | ⁷Wildlife Ecology and Conservation Group, Wageningen University, Wageningen, the Netherlands | ⁸Institute of Wildlife Biology and Game Management, University of Natural Resources and Life Sciences, Vienna, Austria

Correspondence: Rick W. Heeres (rick.heeres@usn.no)**Received:** 6 June 2025 | **Revised:** 8 August 2025 | **Accepted:** 18 August 2025**Funding:** This work was supported by Svenska Jägarförbundet; Austrian Science Fund; Miljødirektoratet; Canada Research Chairs, CRC-2022-00486; E.W.R. Steacie Memorial Fund, 549146-2020; Mitacs, IT36631; Naturvårdsverket; Natural Sciences and Engineering Research Council of Canada, 2018-05405, 2025-06965.**Keywords:** maternal investment | movement behavior | parental care | solitary mammal | Sweden | *Ursus arctos*

ABSTRACT

Family breakup dynamics in mammals can be complex due to competing interests between parents and offspring. Parents need to balance their own as well as their offspring's fitness through either terminating care early or extending care. Yet, males can disrupt this trade-off as they may force females to focus on future litters by separating or killing offspring, especially in species where sexually selected infanticide occurs. Here, we investigated the family breakup dynamics in brown bears (*Ursus arctos*) by using GPS relocation data from 144 individuals (114 unique individuals: 23 mothers, 49 offspring, and 42 adult males) in south-central Sweden. We explored the movement of mothers, their offspring, and adjacent adult males to gain insights into the factors influencing family breakup. Our findings indicate that females with 2-year-olds tend to separate before the mating season, whereas females with yearlings typically experience breakups during the mating season. Our results show that females accompanied by yearlings increased their movement speeds 2 weeks before the family breakup. The movement speed of the families that separated was two to three times higher compared to families that remained together. Furthermore, males associated with family groups before and during the mating season. Several associations during the mating season between adult males and family groups occurred on the same day that the family broke up. The increased space use makes the family group more conspicuous on the landscape; this likely increases the detection probability by a male and increases the chance of family breakup. Maternal care tactics can influence both female and offspring fitness, and here we provided additional evidence of the interplay between female and adult male behavior in terminating care in a solitary carnivore.

1 | Introduction

Parental care is crucial for the survival and development of offspring in mammals (Clutton-Brock 1991; Clutton-Brock

et al. 1982). Parents provide a social and safe environment where offspring learn essential knowledge and skills related to shelter, foraging, predation, and conspecifics (Engebretsen et al. 2024; Mateo 2009). For example, hunting techniques in canids and

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2025 The Author(s). *Ecology and Evolution* published by British Ecological Society and John Wiley & Sons Ltd.

felids are passed on to offspring during foraging excursions with one or both parents (Bekoff et al. 1984). The quality and duration of parental care can influence the way offspring develop, adjust to their environment, and reproduce successfully later in life (Alberts 2019; Nowak 2000). However, parents need to balance their own as well as their offspring's fitness and commonly trade off between current and potential future reproduction. This trade-off can lead to conflicts between parents and offspring regarding the length of the parental care (Trivers 1972).

In most mammals, males provide little to no parental care. Thus, parental care usually is exclusively provided by females (Alonzo and Klug 2012; Bateson 1994; Shuster and Wade 2003). In some mammals, females cannot remate until their current offspring are weaned, abandoned, or dead (Lee 1996; Wolff and MacDonald 2004). The separation of offspring stops mammary stimulation and lactation, which would otherwise suppress hormone production (e.g., prolactin) inhibiting a female from getting into estrus (Asa 2012). Early separation can increase the number of offspring a female can produce in her lifetime, but early weaning of offspring may lower their survival due to limited experience in foraging or social skills (Klug and Bonsall 2014; Lee et al. 1991; Trivers 1972; Webb et al. 1999). However, early separation may also expose these individuals to other challenges including a high predation risk, high energetic demands, and competition with conspecifics (Clutton-Brock et al. 1985). Environmental factors such as resource availability, but also life history factors such as litter size as well as offspring sex and size can affect the duration of maternal care (Andersen et al. 2000; Balme et al. 2017; Johansson et al. 2021; Van de Walle et al. 2021). In general, higher resource abundance (i.e., the resource limitation hypothesis; Lee et al. 1991; Wilsterman et al. 2024) and smaller litter sizes are expected to shorten the duration of maternal care, while offspring sex (i.e., the sex-allocation hypothesis; Hewison et al. 2005; Moore et al. 2015), larger litter size, and smaller offspring are expected to increase maternal care duration (Van de Walle et al. 2021). Before family separation (i.e., the moment that mothers and offspring go their separate ways), females may exhibit behaviors such as aggression or increased avoidance towards their offspring to initiate the breakup (Trivers 1974). In cases of avoidance, the movement behavior (e.g., daily travel distance) of females before separation could shed light on female-induced breakup dynamics. However, the process of family separation might not be a process that involves only the female and her offspring, as adult males vying for mating opportunities may play an important role in causing or initiating separation (Dahle and Swenson 2003b; Packer and Pusey 1983; Pusey and Packer 1994; Swenson, Sandegren, et al. 2001). Males may play a particularly important role in species with sexually selected infanticide (SSI; Agrell et al. 1998; Hrdy 1979) in which females enter estrus shortly after offspring loss or separation, and males therefore benefit from breaking up family groups (Dahle and Swenson 2003b; Steyaert et al. 2014). Consequently, investigating male presence and movement behavior during family breakup can inform us on how social associations may shape a parent-offspring conflict.

The brown bear (*Ursus arctos*) is a solitary large carnivore with a promiscuous mating system (Steyaert et al. 2012). The mating season lasts from early May to mid-July (Heeres et al. 2024; Spady et al. 2007; Steyaert et al. 2012). Family breakups

generally occur just before or during the first weeks of the mating season (Dahle and Swenson 2003b). For female brown bears in Scandinavia, the duration of maternal care is either 1.5 or 2.5 years (Dahle and Swenson 2003a; Van de Walle et al. 2021). Litter size and yearling body mass are important determinants of the short (1.5 years) and long (2.5 years) maternal care tactics in this population (Van de Walle et al. 2021). To initiate separation from offspring, females are presumed to alter their movement behavior to find mates (Dahle and Swenson 2003a, 2003b), and males have previously been hypothesized to play an important role in initiating family breakups (Dahle and Swenson 2003b). Until now, only the change in movement behavior after the loss of cubs-of-the-year (Steyaert et al. 2014) and the habitat selection of females with dependent offspring before and after breakups (Van de Walle et al. 2019) have been investigated. However, by understanding female reproductive tactics and movement behavior, as well as the influence of males on these tactics, we can determine if changes in female space use correlate with maternal care termination or continuation. The study of reproductive tactics in the wild is challenging; however, in this study, we have all data components (i.e., mother, offspring, adult males) affecting family breakups of brown bears, which allows us to gain new insights into this crucial but rarely documented process.

The objective of this study was to examine the movement behavior of family groups, including mother and offspring, and adult males during the mating season in relation to family breakup dynamics in a solitary-living mammal. We used GPS relocation data from 23 unique mothers (29 bear-years; because some females were followed during several years and they had offspring), 42 unique males (75 bear-years), and 49 unique offspring (1.5 and 2.5 years old) brown bears during the mating season in southcentral Sweden. We determined family breakup dates based on family movement behavior. We contrasted the daily travel distance of mothers before breakups with mothers that remained with their offspring. In addition, we determined male spatial and temporal proximity to family groups to investigate their potential role in family breakups. In American black bears (*Ursus americanus*) females with 2-year-olds instigate family breakup before the mating season (Clevenger and Pelton 1990). Thus, we predicted that (1) females accompanied by 2-year-olds should breakup earlier than females accompanied by yearlings. Parental care might be biased to either male or female offspring (Trivers and Willard 1973). We therefore expected that the breakup dates might differ between the sexes of the offspring, as males tend to disperse earlier than females (Zedrosser et al. 2007). Thus, we predicted that (2) male offspring separated from their mothers earlier than female offspring in both the yearling and 2-year-old age groups. Females accompanied by yearlings focusing on future reproduction should show different movement behaviors during the mating season compared to females that remained with their yearlings. Also, females that stay with their yearlings for an additional year are expected to avoid potentially infanticidal males, that is, males other than the ones they mated with the previous mating season (Dahle and Swenson 2003b; Heeres et al. 2025; Swenson, Dahle, and Sandegren 2001), and adjust their movement behavior accordingly. The change in behavior may mainly be displayed by reduced movement speed and changing habitat selection (Heeres et al. 2025; Steyaert et al. 2016; Van de Walle et al. 2019). Therefore, we predicted that (3) females experiencing a family

breakup have higher daily travel distances before the breakup compared to females that remained with their offspring. Families including either yearlings (1.5 years old) or 2-year-olds (2.5 years old) can breakup before or at the beginning of the mating season (Dahle and Swenson 2003b). Lastly, in several bear species, male-initiated family breakups have been documented (Dahle and Swenson 2003b; Ternent and Garshelis 1998). Yet, the movement dynamics before and following male interference on both the family and male have not been described in detail before. We therefore provide anecdotal observations from males interacting with family groups containing yearlings and 2-year-olds.

2 | Material and Methods

2.1 | Study Area

The study area is approximately 13,000 km² and located in south-central Sweden (61°N, 15°E). The area features relief ranging from 100 to 800 m above sea level, and is largely composed of bogs, lakes, and intensively managed coniferous forests. The mean temperatures in January and July are −7°C and 15°C, respectively (Bischof et al. 2018) and snow cover usually lasts from late October until early May. Human settlements are primarily found in the northern and southern parts of the study area. There are some high-traffic roads (0.14 km/km²), but cabins and low-traffic paved roads are scattered throughout the area (0.3/km² and 0.7 km/km², respectively; Martin et al. 2010). Human activity is higher during summer and fall due to hunting or berry and mushroom picking seasons (Ordiz et al. 2011). Brown bear population density in the study area is estimated at approximately 23 bears per 1000 km² (Bischof et al. 2019). Brown bears in Sweden are legally hunted from 21 August to 15 October or until quotas are filled, and around 10% are harvested from the total population annually (Bischof et al. 2019).

2.2 | Bear Individual Characteristics and Monitoring

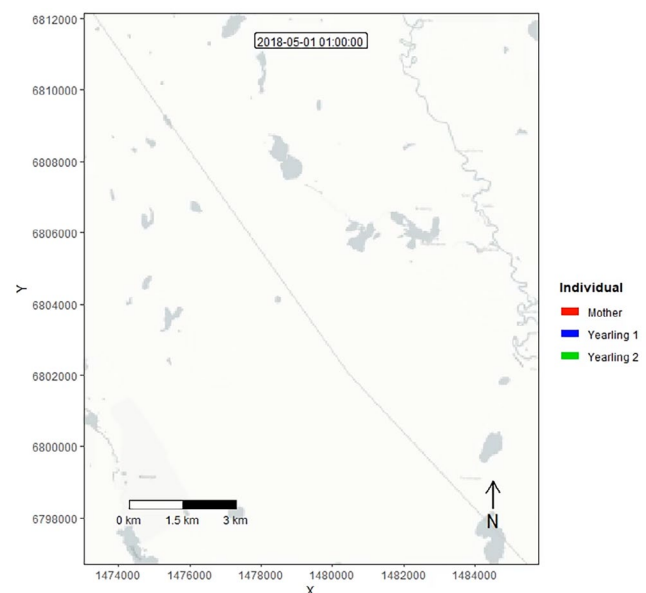
The Scandinavian Brown Bear Research Project (SBBRP) follows a strict capture protocol (Graesli et al. 2025). Bears were darted from a helicopter using a remote drug delivery system (Dan-Inject, Børkop, Denmark) and GPS-collared (GPS Plus; Vectronic Aerospace GmbH, Berlin, Germany) on an annual basis. The collars were programmed to relocate all individuals every hour. See Graesli et al. (2025) for more details on captures and handling. All aspects of animal capture and handling were approved under an ethical permit by the 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).

We had access to location data of 29 families, including 29 adult females (i.e., mothers; 23 unique females) and 49 offspring (yearlings: $n = 21$, 2-year-olds: $n = 28$) during their active period (i.e., excluding hibernation) between 2007 and 2021. Location data of 42 unique adult males (> 3 years old; 75 bear-years) were

available as well. The age (e.g., year of birth) of most bears was known because they were captured as part of a family group. For bears not followed from birth, a premolar tooth was extracted for age determination (Matson et al. 1993). Female reproductive status was determined at capture or via visual observations from a helicopter several times per year (Van de Walle et al. 2021). These visual observations also made it possible to detect if family groups had broken up during the year. Based on the age of the offspring and the occurrence of a family breakup, we defined three states: (1) *yearling breakup*; females with yearlings where a breakup occurred, (2) *yearling family*; females with yearlings that stayed together until the next hibernation event, and (3) *2-year-old breakup*; females with 2-year-olds where a breakup occurred.

2.3 | Breakup Date

Initially, a family breakup date was determined when a mother and her offspring were separated by more than 500 m (Lee and Vaughan 2004) for at least 24 h. However, this threshold proved inaccurate, as there were numerous instances where offspring and mothers were found further than 500 m for a day but reunited again for an extended period (e.g., several weeks). Therefore, to achieve a more accurate determination of the breakup date, we visually inspected the movement trajectories (Video 1, Figure 1) of family groups before and during the mating season using the *moveVis* package (Schwalb-Willmann et al. 2020) in R 4.4.2 (R Development Core Team 2024). These movement trajectories allowed us to confirm that no reassociations (i.e., within 500 m for at least a week) of the offspring and the mother occurred during the mating season. We identified the breakup date per offspring, making it possible to check for sex-related differences in breakup timing.



VIDEO 1 | Video content can be viewed at <https://onlinelibrary.wiley.com/doi/10.1002/ece3.72070>.

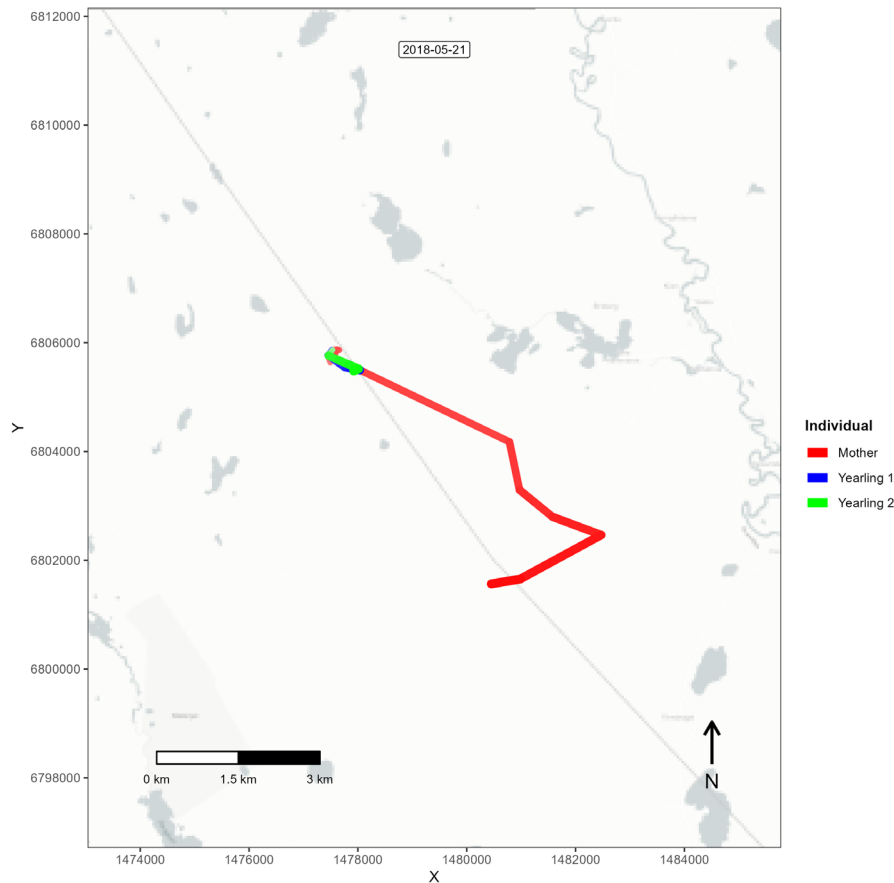


FIGURE 1 | Animation, created by using *moveVis* package in R, showing the movement of a family including a mother (red line) and her two yearlings (green and blue lines) based on GPS location data in southcentral Sweden. The moment that the red dot and the green/blue dots separate shows the family breakup event.

2.4 | Female Movement Before Breakups

The *amt* package (Signer et al. 2019) was used to calculate the hourly travel distance and the total number of relocations per day (i.e., successful GPS fixes) for the females that either remained or separated from their yearlings. Once the breakup dates were set based on the visualization of the movement path of the family, we selected the movement data 14 days before the breakup. For the females that did not experience a breakup, we selected the data 14 days before the median breakup date (May 26: day of the year 146). Additionally, we determined the daily travel distance for all days that had at least 20 relocations to avoid underestimation of daily travel distances. Overall success rate of relocations in our study area is above 94% (Leclerc et al. 2016).

2.5 | Adult Male Presence at Breakups

To investigate the interference of males in relation to family breakups, we first identified if the family group encountered a GPS-collared male before or during the mating season. We calculated all pairwise distances between mothers and adult males utilizing hourly GPS relocations using the *spatsoc* package (Robitaille et al. 2019). We then used a distance threshold of 200m (including a 3-min temporal tolerance) to determine

social associations (i.e., two or more individuals within 200m at the same time; Heeres et al. 2024). The dates of a family breakup and all the associations a family had with an adult male were compared to determine if an adult male interfered in the family breakup. If an adult male was spatiotemporally associated with the family group during the day of the breakup, we investigated his and the family's movement patterns visually and determined how many times the male approached the family before the mating season and if the male was close to the family just before the family breakup.

2.6 | Statistical Analysis—Breakup Date

We investigated if the breakup dates of family groups were different between the offspring age groups and sexes with the help of Generalized Linear Mixed Models (GLMM), fitted with the *glmmTMB* package (Brooks et al. 2017), with a Poisson distribution (i.e., slightly skewed). We included the family group ID nested in mother ID as a random intercept to control for pseudoreplication (Millar and Anderson 2004). The *DHARMa* package (Hartig 2022) was used to evaluate model fit. We evaluated different candidate models (Appendix S1, Table S1) and determined the most parsimonious one with the corrected Akaike Information Criteria (AICc; *AICcmodavg* package: Mazerolle 2023).

2.7 | Statistical Analysis—Mother Movement Before Breakups

We investigated the movement patterns of mothers with yearlings before (14 days) family breakup using the *mgcv* package (Wood 2017) and fitted a hierarchical generalized additive mixed model (HGAM; Pedersen et al. 2019) with a Gamma (log link) distribution. The model included the group classification (yearling family = 0, yearling family breakup = 1) to identify if there was a significant difference in daily travel distances between the two groups. Additionally, we included the number of successful fixes (relocations ≥ 20) as an offset variable to control for its potential influence on the daily total travel distance. We used a GAMM as we expected a non-linear pattern (Wood 2017) and we used the number of days before the breakup date as a covariate in the smoothers (Pedersen et al. 2019). We included an AR1 temporal autocorrelation structure by using the day of the year combined with the individual ID (Mitchell et al. 2019; Zuur et al. 2009). We also added the unique ID of the mother as a random variable to consider individual differences of adult females. The model fit was validated using both the *mgcv* and *mgcViz* packages (Fasiolo et al. 2020).

3 | Results

3.1 | Breakup Dates

We found a significant difference (Figure 2) in the breakup dates between family groups with yearlings ($n=21$) and 2-year-olds ($n=28$) using a GLMM model. The most parsimonious model only included the age of the offspring (Appendix S1: Table S1). Families with 2-year-olds broke up earlier in the season in comparison to families with yearlings ($\beta = -0.82$ (log-scale), $p < 0.001$; Table 1 and Appendix S1: Table S1 & Figure S1). Therefore, the sex of the offspring did not influence the timing of family breakups for yearlings and 2-year-olds.

3.2 | Movement Behavior of Mothers Before Break Ups

We found that females who separated from their yearlings ($n=15$) had significantly higher daily travel distances before the breakup in comparison to females that did not breakup ($n=10$) during the same period ($\beta = 0.545$, $p < 0.001$; Figure 3). There

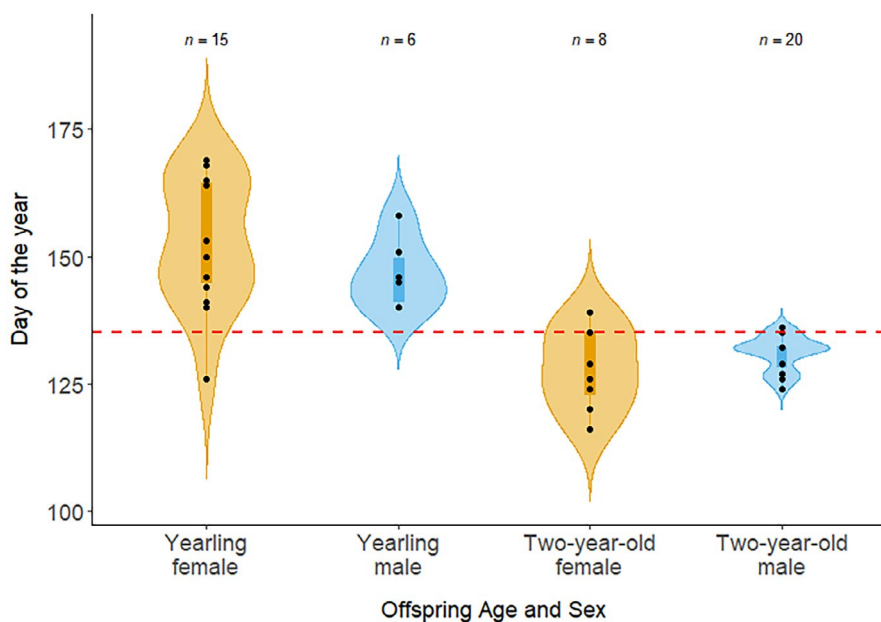


FIGURE 2 | Breakup dates for brown bear family groups ($n=29$) southcentral Sweden (2007–2021), including one or more yearlings ($n=15$, individuals = 21) or 2-year-olds ($n=14$, individuals = 28). Breakup dates were conjointly determined by spatiotemporal thresholds and animations. The mating season starts around the day of the year 135 (May 15), indicated by the horizontal red dotted line.

TABLE 1 | The median and range of the breakup date (day of the year; doy) per age and sex class of offspring of brown bears (family groups: $N=29$) in southcentral Sweden (2007–2021). Breakup dates were conjointly determined by spatiotemporal thresholds and spatial animations.

Age	<i>n</i>	Sex	Samples	Median date (doy)	Range (min-max)
Yearling	21	Female	15	150	126–169
		Male	6	146	140–158
2-year-olds	28	Female	8	128	116–139
		Male	20	132	124–136

was a steady increase in the daily travel distance over the 14 days before the family breakup.

3.3 | Male Presence During Breakups

Our data showed that 11 of 29 families (37.9%) did not associate with a GPS-collared male before or during the mating season. We observed 14 of 29 families (48.3%) that associated with GPS-collared males before and/or during the mating season, but not on the day of a family breakup, and 4 of 29 females (13.8%) associated with a GPS-collared male during the day of the family breakup ($n=1$ family with yearlings; $n=3$ family with 2-year-olds). After the initial association between the female with yearlings and an adult male, followed by family breakup, we observed that males did not always stay close to the female but occasionally moved away and came back in proximity to the female over a few weeks, followed by a longer association close to or during the mating season (Figure 4 and Appendix S2: Male Family Breakup 1). We also observed one occasion where a male visited a family three times before the mating season; however, the family reunited shortly after the first two visits. The male was in proximity during the family breakup a week later and remained with the female for several days after (Figure 4 and Appendix S2: Male Family Breakup 2).

4 | Discussion

The objective of this study was to examine the movement behavior of mothers, offspring, and adult males before and during family breakups in brown bears. We found, as predicted, that females with yearlings' primarily break up during the mating season, whereas females with 2-year-olds break up before the mating season. We also showed that the breakup date was not correlated to the sex of the offspring, neither for yearlings nor

2-year-olds. As predicted, females that broke up from their yearlings traveled significantly longer daily distances before breakup, in contrast to females that remained with their yearlings. Lastly, we observed few occasions (4 out of 29) during which a GPS-collared male was present on the day of the family breakup. However, GPS-collared males visited family groups and lone females (if family breakup already occurred) before the mating season regularly.

The timing of separation from offspring can lead to parent-offspring conflicts (Sunde 2008), especially in species where females can only reproduce once their current offspring have weaned or dispersed (Trivers 1974). In American black bears, it has been suggested that it is the mother who initiates a family breakup (Clevenger and Pelton 1990; Rogers 1987). Physiological factors, such as ending lactation or entering estrus, might urge the female to break up with the offspring (Asa 2012). In brown bears, it seems that the majority of breakups occur at the beginning of the mating season (Dahle and Swenson 2003b). However, our results showed a further differentiation of this timeline, with females with 2-year-olds generally breaking up before the mating season, while most females with yearlings' break up during the mating season. Breakups with yearlings might result in more pronounced parent-offspring conflict, as some females show increasing movement distances, which are likely to result in separation from their offspring. This increase in travel distances likely tires out the offspring (i.e., increase energy expenditure) but might also lead to a higher probability of detection by roaming males, likely indirectly promoting male participation in family separation. Additionally, the sex-allocation hypothesis (Trivers and Willard 1973) is based on the idea that parental care might be biased to either male or female offspring (Hewison et al. 2005; Koskela et al. 2009; Moore et al. 2015) and this could potentially lead to different breakup dates for offspring of the same litter based on their sex. However, we did not find a difference in the breakup date between the sexes for either yearlings or 2-year-olds. This is likely because families that are broken up by adult males cause all offspring to separate at the same time, making it difficult to identify clear sex-specific breakup dates for many species in which sexually selected infanticide is common.

After emerging from their den, males utilize a "roam-to-mate" behavior to detect and approach females (Dahle and Swenson 2003c). We found anecdotal evidence of males approaching family groups before the mating season potentially to explore the reproductive status of the female. This is also common among other species, such as rodents and ungulates (Eisenberg and Kleiman 1972; Grau 1976; Johansson and Jones 2007; Weir and Rowlands 1973). This suggests that males seem to prepare for the mating season and investigate which females are "available" in their home range. This also helps to identify family groups and additional opportunities to reproduce by separating the mother from their offspring. The advantage for adult males of breaking up family groups is that they "initiate" mating opportunities that otherwise might not have been available (Lukas and Huchard 2014). Sexually selected infanticide is a common male mating tactic in brown bears (Bellemain et al. 2006; Steyaert et al. 2012) and is only successful when the offspring are killed during the mating season, which leads to the female entering estrus within several days (Steyaert et al. 2014). Therefore, males could have an incentive to break up family

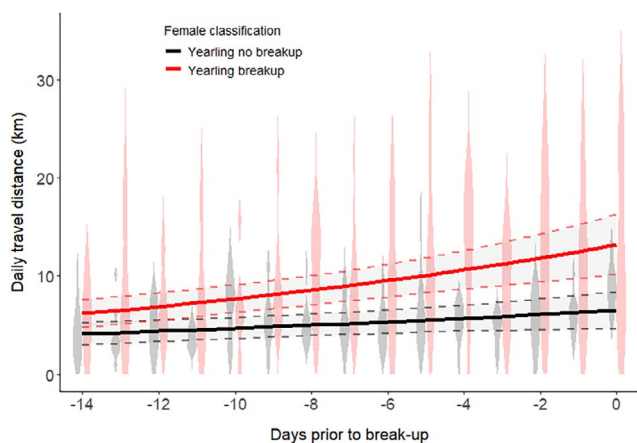


FIGURE 3 | The change in daily travel distance (km) by female brown bears accompanied by dependent offspring in southcentral Sweden (2007–2021) across 14 days prior to a family breakup. The lines represent the mean daily travel distance of females with yearlings experiencing a breakup ($n=15$; red line) and females with yearlings without a breakup ($n=10$; black line). For families without breakup, we selected the 14 days prior to the median breakup date (doy 146; May 26). The shaded areas and dotted lines represent the 95% confidence bands. The violin plots in the background show the raw daily travel distance data per female classification.

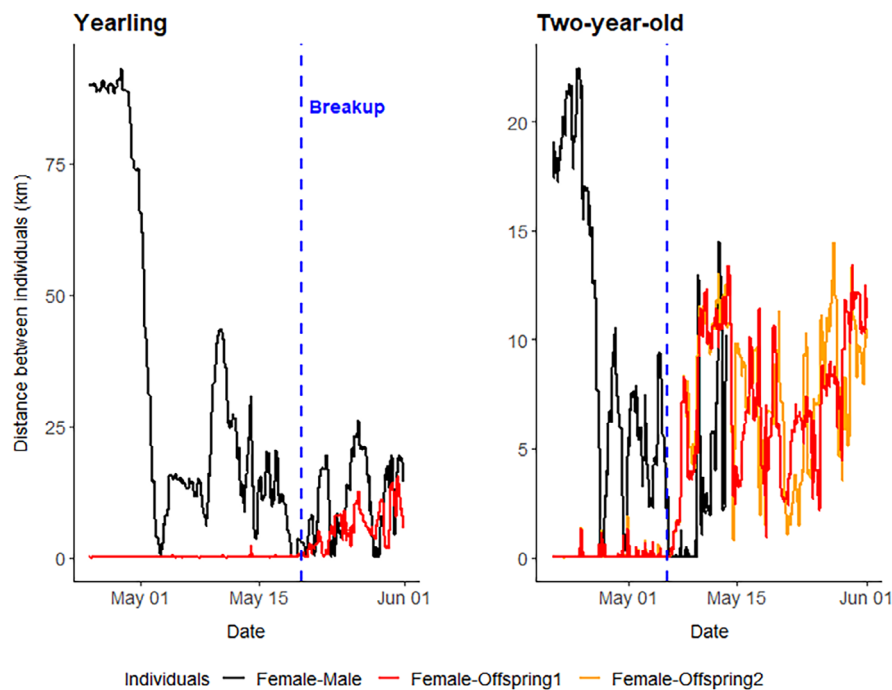


FIGURE 4 | The distance between mothers and offspring (red line) and mothers and adult male (black line) prior to and during the first weeks of the mating season for two families. The start of the mating season is around May 15. The blue dotted line is the breakup date of the family conjointly determined by using spatiotemporal thresholds and animations. All data were collected in southcentral Sweden (2007–2021).

groups, irrespective of the offspring's age, and thereby gain additional mating opportunities.

We did not have data regarding the physiological state (e.g., hormone levels) of females before the family breakups. Therefore, we are restricted to identifying changes in behavior, and here we use movement as a proxy for a female's motivation to break up with her offspring. In addition, we only observed 4 occasions where males were present near the family group at the time of the family breakup. However, this may be related to the small sample size of GPS-collared adult males per year. In addition, family groups may have interacted with uncollared males during the time of the breakup. Thus, we likely underestimate the impact of males on family breakup dynamics. Future studies should try to disentangle social dynamics before associations for not only family groups with adult males but also other groups (e.g., lone females). This could show that social information is gained not only with spatiotemporal associations but also other factors such as the “scentscape” (Clapham et al. 2012; Finnerty et al. 2022; Marin et al. 2021; Sergiel et al. 2017).

Maternal care is directly linked to the early survival of offspring and influences future reproduction by the mother (Mateo 2009). Therefore, it is crucial to understand which aspects influence the duration of maternal investment (Balme et al. 2017; Johansson et al. 2021; Van de Walle et al. 2021), but also the fitness benefits of either terminating or extending care for both the mother and offspring (Van de Walle et al. 2018). We do know that female brown bears benefit from providing longer maternal care, which may be related to artificial selection caused by the harvest regime (Van de Walle et al. 2018). However, it would be interesting to see if the duration of maternal care, short versus long maternal care (Zedrosser et al. 2013), also benefits the offspring (e.g., increased fitness, early primiparity). This would make it possible to evaluate the costs and

benefits of varying maternal care tactics and investigate their influence on population dynamics and demography.

Author Contributions

Rick W. Heeres: conceptualization (equal), data curation (lead), formal analysis (lead), methodology (equal), writing – original draft (lead), writing – review and editing (lead). **Wisse Boot:** conceptualization (supporting), formal analysis (supporting), methodology (equal), writing – review and editing (supporting). **Emile Delen:** conceptualization (supporting), formal analysis (supporting), methodology (equal), writing – review and editing (supporting). **Miriam Tovar Heid:** conceptualization (supporting), formal analysis (supporting), methodology (equal), writing – review and editing (supporting). **Martin Leclerc:** formal analysis (supporting), writing – review and editing (equal). **Shane Frank:** formal analysis (supporting), writing – review and editing (equal). **Alexander Kopatz:** project administration (equal), writing – review and editing (equal). **Fanie Pelletier:** funding acquisition (equal), supervision (equal), writing – review and editing (equal). **Henry Kuipers:** conceptualization (equal), formal analysis (supporting), methodology (equal), writing – review and editing (equal). **Martijn J. A. Weterings:** conceptualization (equal), formal analysis (supporting), methodology (equal), writing – review and editing (equal). **Andreas Zedrosser:** funding acquisition (equal), supervision (equal), writing – review and editing (equal).

Acknowledgments

We acknowledge the hard work of the numerous field workers and volunteers that have collected the data used for this study. The long-term funding of the Scandinavian Brown Bear Research Project (SBBRP) has been provided by the Swedish Environmental Protection Agency, the Norwegian Environment Agency, the Austrian Science Fund, and the Swedish Association for Hunting and Wildlife Management. R.W.H. was supported by the Mitacs Globalink Research Award (IT36631). M.L. was supported by the NSERC Discovery Grant (2025-06965). F.P.

was supported by the NSERC Discovery Grant (2018-05405), an E.W.R. Steacie Memorial Fellowship (549146-2020) and the Canada Research Chair program (CRC-2022-00486).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

R code and data that supports the findings of this study are available on our universities' USN Research Data Archive, here: <https://doi.org/10.23642/usn.29225816>. Additionally, the RAW GPS data that was used to create the data files for this study can be found here: <https://doi.org/10.23642/usn.24949185.v2>.

References

- Agregg, J., J. O. Wolff, and H. Ylönen. 1998. "Counter-Strategies to Infanticide in Mammals: Costs and Consequences." *Oikos* 83, no. 3: 507. <https://doi.org/10.2307/3546678>.
- Alberts, S. C. 2019. "Social Influences on Survival and Reproduction: Insights From a Long-Term Study of Wild Baboons." *Journal of Animal Ecology* 88, no. 1: 47–66. <https://doi.org/10.1111/1365-2656.12887>.
- Alonzo, S. H., and H. Klug. 2012. "Paternity, Maternity, and Parental Care." In *The Evolution of Parental Care*, edited by N. J. Royle, P. T. Smiseth, and M. Kölliker, 189–205. Oxford University Press.
- Andersen, R., J. Gaillard, J. D. C. Linnell, and P. Duncan. 2000. "Factors Affecting Maternal Care in an Income Breeder, the European Roe Deer." *Journal of Animal Ecology* 69, no. 4: 672–682. <https://doi.org/10.1046/j.1365-2656.2000.00425.x>.
- Asa, C. S. 2012. "Reproductive Biology and Endocrine Studies." In *Carnivore Ecology and Conservation*, edited by L. Boitani and R. A. Powell, 273–293. Oxford University Press.
- Balme, G. A., H. S. Robinson, R. T. Pitman, and L. T. B. Hunter. 2017. "Flexibility in the Duration of Parental Care: Female Leopards Prioritise Cub Survival Over Reproductive Output." *Journal of Animal Ecology* 86, no. 5: 1224–1234. <https://doi.org/10.1111/1365-2656.12713>.
- Bateson, P. 1994. "The Dynamics of Parent-Offspring Relationships in Mammals." *Trends in Ecology & Evolution* 9, no. 10: 399–403. [https://doi.org/10.1016/0169-5347\(94\)90066-3](https://doi.org/10.1016/0169-5347(94)90066-3).
- Bekoff, M., T. J. Daniels, and J. L. Gittleman. 1984. "Life History Patterns and the Comparative Social Ecology of Carnivores." *Annual Review of Ecology and Systematics* 15: 191–232.
- Bellemain, E., J. E. Swenson, and P. Taberlet. 2006. "Mating Strategies in Relation to Sexually Selected Infanticide in a Non-Social Carnivore: The Brown Bear." *Ethology* 112, no. 3: 238–246. <https://doi.org/10.1111/j.1439-0310.2006.01152.x>.
- Bischof, R., C. Bonenfant, I. Maren Rivrud, et al. 2018. "Regulated Hunting Re-Shapes the Life History of Brown Bears." *Nature Ecology and Evolution* 2: 116–123. <https://doi.org/10.1038/s41559-017-0400-7>.
- Bischof, R., C. Milleret, P. Dupont, J. Chipperfield, H. Brøseth, and J. Kindberg. 2019. "RovQuant: Estimating Density, Abundance and Population Dynamics of Bears, Wolverines and Wolves in Scandinavia." In *MINA fagrapport* (Vol. 63). MINA fagrapport 63.
- Brooks, M. E., K. Kristensen, K. J. Van Benthem, et al. 2017. "glmmTMB Balances Speed and Flexibility Among Packages for Zero-Inflated Generalized Linear Mixed Modeling." *R Journal* 9, no. 2: 378–400. <https://doi.org/10.32614/RJ-2017-066>.
- Clapham, M., O. T. Nevin, A. D. Ramsey, and F. Rosell. 2012. "A Hypothetico-Deductive Approach to Assessing the Social Function of Chemical Signalling in a Non-Territorial Solitary Carnivore." *PLoS One* 7, no. 4: e35404. <https://doi.org/10.1371/journal.pone.0035404>.
- Clevenger, A. P., and M. R. Pelton. 1990. "Pre and Post Breakup Movements and Space Use of Black Bear Family Groups in Cherokee National Forest, Tennessee." *Bears: Their Biology and Management* 8: 289. <https://doi.org/10.2307/3872931>.
- Clutton-Brock, T. H. 1991. "Parental Care in Birds and Mammals." In *The Evolution of Parental Care*, edited by T. H. Clutton-Brock, 130–152. Princeton University Press.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1985. "Parental Investment and Sex Differences in Juvenile Mortality in Birds and Mammals." *Nature* 313, no. 5998: 131–133. <https://doi.org/10.1038/313131a0>.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. *Red Deer Behavior and Ecology of Two Sexes*. Wildlife Behavior and Ecology series. University of Chicago Press.
- Dahle, B., and J. E. Swenson. 2003a. "Factors Influencing Length of Maternal Care in Brown Bears (*Ursus arctos*) and Its Effect on Offspring." *Behavioral Ecology and Sociobiology* 54, no. 4: 352–358. <https://doi.org/10.1007/s00265-003-0638-8>.
- Dahle, B., and J. E. Swenson. 2003b. "Family Breakup in Brown Bears: Are Young Forced to Leave." *Journal of Mammalogy* 84, no. 2: 536–540. [https://doi.org/10.1644/1545-1542\(2003\)084<0536:FBIBBA>2.0.CO;2](https://doi.org/10.1644/1545-1542(2003)084<0536:FBIBBA>2.0.CO;2).
- Dahle, B., and J. E. Swenson. 2003c. "Seasonal Range Size in Relation to Reproductive Strategies in Brown Bears *Ursus arctos*." *Journal of Animal Ecology* 72, no. 4: 660–667. <https://doi.org/10.1046/j.1365-2656.2003.00737.x>.
- Eisenberg, J. F., and D. G. Kleiman. 1972. "Olfactory Communication in Mammals." *Source: Annual Review of Ecology and Systematics* 3: 1–32.
- Engelbrechtsen, K. N., C. Rushing, D. DeBloois, and J. K. Young. 2024. "Increased Maternal Care Improves Neonate Survival in a Solitary Carnivore." *Animal Behaviour* 210: 369–381. <https://doi.org/10.1016/j.anbehav.2024.01.012>.
- Fasiolo, M., R. Nedellec, Y. Goude, and S. N. Wood. 2020. "Scalable Visualization Methods for Modern Generalized Additive Models." *Journal of Computational and Graphical Statistics* 29, no. 1: 78–86. <https://doi.org/10.1080/10618600.2019.1629942>.
- Finnerty, P. B., C. McArthur, P. Banks, C. Price, and A. M. Shrader. 2022. "The Olfactory Landscape Concept: A Key Source of Past, Present, and Future Information Driving Animal Movement and Decision-Making." *Bioscience* 72, no. 8: 745–752. <https://doi.org/10.1093/biosci/biac039>.
- Graesli, A. R., J. M. Arnemo, and A. L. Evans. 2025. *Biomedical Protocol Brown Bears (*Ursus arctos*)*. University of Inland Norway. <https://doi.org/10.13140/RG.2.2.27567.44966>.
- Grau, G. A. 1976. "Olfaction and Reproduction in Ungulates." In *Mammalian Olfaction, Reproductive Processes, and Behavior*, 219–242. Elsevier. <https://doi.org/10.1016/B978-0-12-221250-5.50016-4>.
- Hartig, F. 2022. "DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models [Computer Software]." <https://CRAN.R-project.org/package=DHARMa>.
- Heeres, R. W., M. Leclerc, S. Frank, A. Kopatz, F. Pelletier, and A. Zedrosser. 2024. "Are Nonsocial Species More Social Than We Think? Seasonal Patterns in Sociality in a Solitary Terrestrial Carnivore." *Animal Behaviour* 216: 107–130. <https://doi.org/10.1016/j.anbehav.2024.07.022>.
- Heeres, R. W., M. Leclerc, S. Frank, A. Kopatz, F. Pelletier, and A. Zedrosser. 2025. "Flexibility in Female Spatiotemporal Behavioral Tactics to Counter Infanticide Risk During the Mating Season." *Movement Ecology* 13, no. 1: 35. <https://doi.org/10.1186/s40462-025-00561-6>.

- Hewison, A. J. M., J. Gaillard, P. Kjellander, C. Toïgo, O. Liberg, and D. Delorme. 2005. "Big Mothers Invest More in Daughters—Reversed Sex Allocation in a Weakly Polygynous Mammal." *Ecology Letters* 8, no. 4: 430–437. <https://doi.org/10.1111/j.1461-0248.2005.00743.x>.
- Hrdy, S. B. 1979. "Infanticide Among Animals: A Review, Classification, and Examination of the Implications for the Reproductive Strategies of Females." *Ethology and Sociobiology* 1, no. 1: 13–40. [https://doi.org/10.1016/0162-3095\(79\)90004-9](https://doi.org/10.1016/0162-3095(79)90004-9).
- Johansson, B. G., and T. M. Jones. 2007. "The Role of Chemical Communication in Mate Choice." *Biological Reviews* 82, no. 2: 265–289. <https://doi.org/10.1111/j.1469-185X.2007.00009.x>.
- Johansson, Ö., G. Ausilio, M. Low, P. Lkhagvajav, B. Weckworth, and K. Sharma. 2021. "The Timing of Breeding and Independence for Snow Leopard Females and Their Cubs." *Mammalian Biology* 101, no. 2: 173–180. <https://doi.org/10.1007/s42991-020-00073-3>.
- Klug, H., and M. B. Bonsall. 2014. "What Are the Benefits of Parental Care? The Importance of Parental Effects on Developmental Rate." *Ecology and Evolution* 4, no. 12: 2330–2351. <https://doi.org/10.1002/ece3.1083>.
- Koskela, E., T. Mappes, T. Niskanen, and J. Rutkowska. 2009. "Maternal Investment in Relation to Sex Ratio and Offspring Number in a Small Mammal—A Case for Trivers and Willard Theory?" *Journal of Animal Ecology* 78, no. 5: 1007–1014. <https://doi.org/10.1111/j.1365-2656.2009.01574.x>.
- Leclerc, M., E. Vander Wal, A. Zedrosser, J. E. Swenson, J. Kindberg, and F. Pelletier. 2016. "Quantifying Consistent Individual Differences in Habitat Selection." *Oecologia* 180, no. 3: 697–705. <https://doi.org/10.1007/s00442-015-3500-6>.
- Lee, D. J., and M. R. Vaughan. 2004. "Black Bear Family Breakup in Western Virginia." *Northeastern Naturalist* 11, no. 2: 111–122. [https://doi.org/10.1656/1092-6194\(2004\)011\[0111:BBFBW\]2.0.CO;2](https://doi.org/10.1656/1092-6194(2004)011[0111:BBFBW]2.0.CO;2).
- Lee, P. C. 1996. "The Meanings of Weaning: Growth, Lactation, and Life History." *Evolutionary Anthropology* 5, no. 3: 87–98. [https://doi.org/10.1002/\(SICI\)1520-6505\(1996\)5:3<87::AID-EVAN4>3.0.CO;2-T](https://doi.org/10.1002/(SICI)1520-6505(1996)5:3<87::AID-EVAN4>3.0.CO;2-T).
- Lee, P. C., P. Majluf, and I. J. Gordon. 1991. "Growth, Weaning and Maternal Investment From a Comparative Perspective." *Journal of Zoology* 225, no. 1: 99–114. <https://doi.org/10.1111/j.1469-7998.1991.tb03804.x>.
- Lukas, D., and E. Huchard. 2014. "The Evolution of Infanticide by Males in Mammalian Societies." *Science* 346, no. 6211: 841–844. <https://doi.org/10.1126/science.1257226>.
- Marin, A. C., A. T. Schaefer, and T. Ackels. 2021. "Spatial Information From the Odour Environment in Mammalian Olfaction." *Cell and Tissue Research* 383, no. 1: 473–483. <https://doi.org/10.1007/s00441-020-03395-3>.
- Martin, J., M. Basille, B. van Moorter, J. Kindberg, D. Allainé, and J. E. Swenson. 2010. "Coping With Human Disturbance: Spatial and Temporal Tactics of the Brown Bear (*Ursus arctos*)." *Canadian Journal of Zoology* 88, no. 9: 875–883. <https://doi.org/10.1139/Z10-053>.
- Mateo, J. M. 2009. "Maternal Influences on Development, Social Relationships, and Survival Behaviors." In *Maternal Effects in Mammals*, edited by D. Maestripietri and J. M. Mateo, 133–158. University of Chicago Press. <https://doi.org/10.7208/chicago/9780226501222.003.0007>.
- Matson, G., L. Van Daele, E. Goodwin, L. Aumiller, H. Reynolds, and H. Hristienko. 1993. *A Laboratory Manual for Cementum Age Determination of Alaska Brown Bear First Premolar Teeth*. Alaska Department of Fish and Game Division of Wildlife Conservation.
- Mazerolle, M. J. 2023. "Model Selection and Multimodel Inference Using the AICcmodavg Package [Computer Software]." <https://cran.r-project.org/package=AICcmodavg>.
- Millar, R. B., and M. J. Anderson. 2004. "Remedies for Pseudoreplication." *Fisheries Research* 70, no. 2–3: 397–407. <https://doi.org/10.1016/j.fishres.2004.08.016>.
- Mitchell, D. J., A. M. Dujon, C. Beckmann, and P. A. Biro. 2019. "Temporal Autocorrelation: A Neglected Factor in the Study of Behavioral Repeatability and Plasticity." *Behavioral Ecology* 31, no. 1: 222–231. <https://doi.org/10.1093/beheco/arz180>.
- Moore, E. P. B., M. Hayward, and K. A. Robert. 2015. "High Density, Maternal Condition, and Stress Are Associated With Male-Biased Sex Allocation in a Marsupial." *Journal of Mammalogy* 96, no. 6: 1203–1213. <https://doi.org/10.1093/jmammal/gyv129>.
- Nowak, R. 2000. "Role of Mother-Young Interactions in the Survival of Offspring in Domestic Mammals." *Reviews of Reproduction* 5, no. 3: 153–163. <https://doi.org/10.1530/ror.0.0050153>.
- Ordiz, A., O.-G. Støen, M. Delibes, and J. E. Swenson. 2011. "Predators or Prey? Spatio-Temporal Discrimination of Human-Derived Risk by Brown Bears." *Oecologia* 166, no. 1: 59–67. <https://doi.org/10.1007/s00442-011-1920-5>.
- Packer, C., and A. E. Pusey. 1983. "Adaptations of Female Lions to Infanticide by Incoming Males." *American Naturalist* 121, no. 5: 716–728.
- Pedersen, E. J., D. L. Miller, G. L. Simpson, and N. Ross. 2019. "Hierarchical Generalized Additive Models in Ecology: An Introduction With Mgc." *PeerJ* 2019, no. 5: e6876. <https://doi.org/10.7717/peerj.6876>.
- Pusey, A. E., and C. Packer. 1994. "Infanticide in Lions: Consequences and Counterstrategies." In *Infanticide & Parental Care*, edited by S. Parmigiani, F. S. Vom Saal, S. Parmigiani, and F. S. Vom Saal. Harwood Academic Publishers.
- R Development Core Team. 2024. *R: A Language and Environment for Statistical Computing [Computer Software]*. R Foundation for Statistical Computing.
- Robitaille, A. L., Q. M. R. Webber, and E. Vander Wal. 2019. "Conducting Social Network Analysis With Animal Telemetry Data: Applications and Methods Using Spatsoc." *Methods in Ecology and Evolution* 10, no. 8: 1203–1211. <https://doi.org/10.1111/2041-210X.13215>.
- Rogers, L. L. 1987. "Effects of Food Supply and Kinship on Social Behavior Movements and Population Growth of Black Bears in Northeastern Minnesota USA." *Wildlife Monographs* 97: 1–72.
- Schwalb-Willmann, J., R. Remelgado, K. Safi, and M. Wegmann. 2020. "moveVis: Animating Movement Trajectories in Synchronicity With Static or Temporally Dynamic Environmental Data in R." *Methods in Ecology and Evolution* 11, no. 5: 664–669. <https://doi.org/10.1111/2041-210X.13374>.
- Sergiel, A., J. Naves, P. Kujawski, et al. 2017. "Histological, Chemical and Behavioural Evidence of Pedal Communication in Brown Bears." *Scientific Reports* 7: 1052. <https://doi.org/10.1038/s41598-017-01136-1>.
- Shuster, S. M., and M. J. Wade. 2003. "Mating Systems and Strategies." In *Mating Systems and Strategies*, edited by J. R. Krebs and T. Clutton-Brock. Princeton University Press. <https://doi.org/10.2307/j.ctvs32sqk>.
- Signer, J., J. Fieberg, and T. Avgar. 2019. "Animal Movement Tools (Amt): R Package for Managing Tracking Data and Conducting Habitat Selection Analyses." *Ecology and Evolution* 9, no. 2: 880–890. <https://doi.org/10.1002/ece3.4823>.
- Spady, T. J., D. G. Lindburg, and B. S. Durrant. 2007. "Evolution of Reproductive Seasonality in Bears." *Mammal Review* 37, no. 1: 21–53. <https://doi.org/10.1111/j.1365-2907.2007.00096.x>.
- Steyaert, S. M. J. G., A. Endrestøl, K. Hackländer, J. E. Swenson, and A. Zedrosser. 2012. "The Mating System of the Brown Bear *Ursus arctos*." *Mammal Review* 42, no. 1: 12–34. <https://doi.org/10.1111/j.1365-2907.2011.00184.x>.
- Steyaert, S. M. J. G., M. Leclerc, F. Pelletier, et al. 2016. "Human Shields Mediate Sexual Conflict in a Top Predator." *Proceedings of the Royal Society B: Biological Sciences* 283, no. 1833: 20160906. <https://doi.org/10.1098/rspb.2016.0906>.

Steyaert, S. M. J. G., J. E. Swenson, and A. Zedrosser. 2014. "Litter Loss Triggers Estrus in a Nonsocial Seasonal Breeder." *Ecology and Evolution* 4, no. 3: 300–310. <https://doi.org/10.1002/ece3.935>.

Sunde, P. 2008. "Parent-Offspring Conflict Over Duration of Parental Care and Its Consequences in Tawny Owls *Strix aluco*." *Journal of Avian Biology* 39, no. 2: 242–246. <https://doi.org/10.1111/j.2008.0908-8857.04194.x>.

Swenson, J. E., B. Dahle, and F. Sandegren. 2001. "Intraspecific Predation in Scandinavian Brown Bears Older Than Cubs-of-The-Year." *Ursus* 12: 81–91.

Swenson, J. E., F. Sandegren, S. Brunberg, P. Segerström, and P. Segerström. 2001. "Factors Associated With Loss of Brown Bear Cubs in Sweden." *Ursus* 12: 69–80.

Ternent, M. A., and D. L. Garshelis. 1998. "Male-Instigated Break-Up of a Family of Black Bears." *Ursus* 10: 575–578.

Trivers, R. 1972. "Parental Investment and Sexual Selection." In *Sexual Selection and the Descent of Man*, edited by B. Campbell, 1871–1971. Aldine.

Trivers, R. 1974. "Parent-Offspring Conflict." *American Zoologist* 14, no. 1: 249–264. <https://doi.org/10.1093/icb/14.1.249>.

Trivers, R. L., and D. E. Willard. 1973. "Natural Selection of Parental Ability to Vary the Sex Ratio of Offspring." *Science* 179, no. 4068: 90–92. <https://doi.org/10.1126/science.179.4068.90>.

Van de Walle, J., M. Leclerc, S. M. J. G. Steyaert, A. Zedrosser, J. E. Swenson, and F. Pelletier. 2019. "Proximity to Humans Is Associated With Longer Maternal Care in Brown Bears." *Behavioral Ecology and Sociobiology* 73: 158. <https://doi.org/10.1007/s00265-019-2764-y>.

Van de Walle, J., G. Pigeon, A. Zedrosser, J. E. Swenson, and F. Pelletier. 2018. "Hunting Regulation Favors Slow Life Histories in a Large Carnivore." *Nature Communications* 9, no. 1100: 1–10. <https://doi.org/10.1038/s41467-018-03506-3>.

Van de Walle, J., A. Zedrosser, J. E. Swenson, and F. Pelletier. 2021. "Disentangling Direct and Indirect Determinants of the Duration of Maternal Care in Brown Bears: Environmental Context Matters." *Journal of Animal Ecology* 90, no. 2: 376–386. <https://doi.org/10.1111/1365-2656.13371>.

Webb, J. N., A. I. Houston, J. M. McNamara, and T. Székely. 1999. "Multiple Patterns of Parental Care." *Animal Behaviour* 58, no. 5: 983–993. <https://doi.org/10.1006/anbe.1999.1215>.

Weir, B. J., and I. W. Rowlands. 1973. "Reproductive Strategies of Mammals." *Annual Review of Ecology and Systematics* 4, no. 1: 139–163. <https://doi.org/10.1146/annurev.es.04.110173.001035>.

Wilsterman, K., A. I. Bautista, C. E. Butler, M. Y. Juergens, and A. M. Larson. 2024. "Evolution of Litter Size: Proximate and Ultimate Mechanisms." *Integrative and Comparative Biology* 64, no. 6: 1643–1660. <https://doi.org/10.1093/icb/icae052>.

Wolff, J. O., and D. W. MacDonald. 2004. "Promiscuous Females Protect Their Offspring." *Trends in Ecology & Evolution* 19, no. 3: 127–134. <https://doi.org/10.1016/j.tree.2003.12.009>.

Wood, S. N. 2017. *Generalized Additive Models*. Chapman and Hall/CRC. <https://doi.org/10.1201/9781315370279>.

Zedrosser, A., F. Pelletier, R. Bischof, M. Festa-Bianchet, and J. E. Swenson. 2013. "Determinants of Lifetime Reproduction in Female Brown Bears: Early Body Mass, Longevity, and Hunting Regulations." *Ecology* 94, no. 1: 231–240. <https://doi.org/10.1890/12-0229.1>.

Zedrosser, A., O. G. Støen, S. Sæbø, and J. E. Swenson. 2007. "Should I Stay or Should I Go? Natal Dispersal in the Brown Bear." *Animal Behaviour* 74, no. 3: 369–376. <https://doi.org/10.1016/j.anbehav.2006.09.015>.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology With R*. Springer. <https://doi.org/10.1007/978-0-387-87458-6>.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Model selection for the Poisson GLMM models using the family breakup dates ($n = 49$) in Sweden (2007–2021). "Model" identifies the included variable(s), the "AICc" is the AICc estimate per model, the delta AICc, the " k " indicates the number of parameters, and "LogLik" represents the log likelihood. The most parsimonious model is shown in **bold**. The models including two-way interactions are indicated by the (x) between variables in the model information. All models included a nested random intercept including mother- and family-ID. **Figure S1:** Predicted breakup date range in relation to the age of the offspring (1.5-year-old yearlings = orange and 2.5-year-old two-year-olds = blue) in southcentral Sweden (2007–2021). The prediction plot is based on the most parsimonious model (Table S1), only including the age of the offspring as a fixed variable and a nested random effect of mother- and family-ID. The black dots represent the raw data ($n = 49$).