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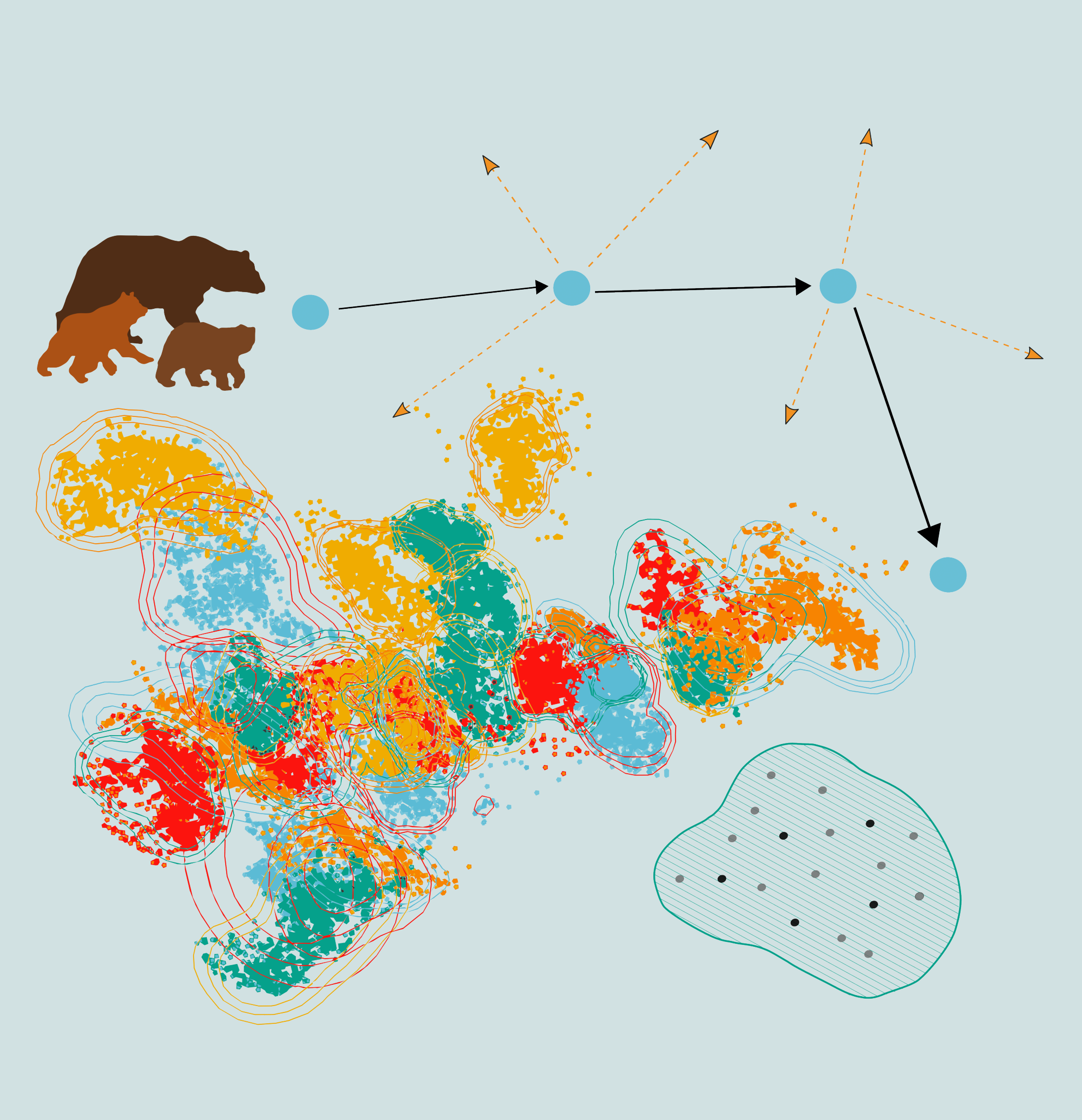
Jennifer Eve Hansen

The effects of social, familial, and anthropogenic factors on dispersal-related space use and movement behavior in Scandinavian brown bear (*Ursus arctos*)



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Dedication

For Emilio, Gabriel, and Dominic who will always be my greatest achievement.

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acquire resources over the years. You are heroes! When all else failed, I was thankful for the tool built by Miss Alexandra Elbakyan to put knowledge in the hands of all that seek it.

Although many students experience at least one mental health crisis in the pursuit of their PhD, the stigma associated with mental illness means that most suffer in silence. I am grateful that when I experienced my own mental health crisis, I had a wealth of support to get myself back on my feet. I am grateful to my committee, for their patience and understanding when I hit rock bottom. I am thankful for the assistance and guidance I received from the university. Thanks to Live for being so accommodating of my situation. Lastly, a big thanks to my care team: Dr. Gunhild Nytrøen, Nils Martin Sønderland, and Dr. Monica Mølnvik. Without the support of all the aforementioned individuals, I don’t know that I could have finished my PhD program.

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Abstract

Among mammals, dispersal is one of the most critical life phases whose outcomes have enormous consequences for survival and reproduction. However, there are several unknowns regarding dispersal and settlement decisions, particularly in elusive, solitary mammals. While the influence of the social environment on dispersal has been relatively well-studied for social species, whether it plays a role for solitary mammals is unclear. Similarly, studies on parent-offspring conflict (POC) and sibling competition (SC) in dispersal typically focus on social or territorial species. There is a need to examine whether the social context of the landscape and familial conflict influence settlement decisions in solitary, non-territorial mammals. In the first two studies in this thesis, we use female brown bears (*Ursus arctos*) as a model for investigating social and familial factors on settlement decisions in a solitary mammal. In the second study, we take an additional step of determining if where females settle influences their fitness, i.e. in lifetime survival and reproduction. For the third study, we shift focus to habitat selection and movement of male bears in response to anthropogenic features on the landscape. Studies measuring movement and selection for the purposes of generating connectivity maps often use only geolocation data of resident individuals in their analysis. Given that dispersers likely select resources and move in a way different from residents, it is important to include them in selection/movement analyses. Scale of selection has shown to be influential in past selection studies, so we consider also how males in these two life stages select resources in two scales, landscape and local.

Our first study showed evidence of females using cues from the social landscape when making settlement decisions, including settling preferentially where they can overlap their mother and familiar females. They also select settlement ranges with higher density than their natal range, perhaps a form of conspecific attraction. The results indicate solitary mammals may be more socially aware than previously understood. Our second study indicated weak evidence for POC and stronger evidence of SC in female settlement. Female offspring settle closer to the natal range if their mother died prior to settlement and in pairs of female siblings, one settles significantly closer to the natal range. Thus, familial conflict between siblings may be greater than between mother and daughter. We found contradictory results regarding where a female settled and her fitness outcomes. This may be due to high population turnover from the annual harvest. Our third study revealed unique patterns of male resource selection and movement in two life stages. In general, resident males showed clearer patterns of selection and avoidance while dispersers were largely indifferent. However, both life stages showed some avoidance of anthropogenic features on the landscape. Resident males showed some unique patterns in selection in different scales, while dispersers did not. These patterns likely reflect resident males greater experience with the broader landscape and the relative naivety of dispersers. Connectivity studies would therefor benefit from including dispersing individuals when generating least-cost pathways and resistance surfaces.

Keywords: dispersal, social landscape, familial conflict, fitness, space use, movement, connectivity, brown bear

List of papers

Article 1

Hansen, J.E., Hertel, A.G., Frank, S.C., Kindberg, J., Zedrosser, A. 2022. Social environment shapes female settlement decisions in a solitary carnivore. Behavioral Ecology 33: 137-146. https://doi.org/10.1093/beheco/arab118

Article 2

Hansen, J.E., Hertel, A.G., Frank, S.C., Kindberg, J., Zedrosser, A. 2022. How familial conflict affects home range settlement and fitness in a solitary mammal residing in a human dominated landscape. Manuscript in revision at Animal Behaviour (first submitted 27 May 2022).

Article 3

Thorsen, N.H., Hansen, J.E., Støen, O.-G., Kindberg, J., Zedrosser, A., Frank, S.C. 2022. Human infrastructure influences life stage-dependent movement and habitat selection in a large carnivore. Manuscript, revised and resubmitted to Movement Ecology (initial submission 16 February 2022, resubmitted 07 September 2022).

Abbreviations

HR Home range

NHR Natal home range

SHR Settlement home range

POC Parent-offspring conflict

SC Sibling competition

GLMM Generalized linear mixed models

RSF Resource selection function

iSSA Integrated step selection analysis

SSI Sexually selected infanticide

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1 Introduction

"No wild animal roams at random over the country: each has a home region, even if it has not an actual home." – Ernest Thompson Seton (1909)

1.1 Space use and dispersal in mammals

There are few factors more influential to the survival and reproduction of an individual than the place they inhabit. The space they occupy provides access to resources necessary for survival and reproduction, such as food (Kelt and Van Vuren 2001), shelter (Marks and Bloomfield 2006), and mates (Sandell 1989). The home range concept was popularized nearly 80 years ago by Burt (1943), who described a home range as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young," i.e. an area reflective of restricted space use containing the elements necessary for survival and reproduction (Powell 2000). More recently, home ranges are understood as an emergent property of movement and resource use in an area over time (Horne et al. 2020). Factors associated with how and where an individual selects the spaces they occupy, are generally representative of the movement associated with acquisition of limiting resources (selection) and circumventing risks (avoidance) (van Moorter et al. 2016). In many mammalian species, dependent offspring rely on resources found in their natal ranges. When they become independent, they must begin a new life stage of dispersing away from the natal range, a process fraught with uncertainty and risk (Cote and Clobert 2010). Much can influence an individual as they disperse from the natal home range, including human disturbance (Bonte et al. 2012) or competition from conspecifics (Costello 2010). Even in non-territorial and solitary species, competition for resources can occur, especially for those whose home ranges overlap (McLoughlin et al. 2000). Due to the difficulty of studying elusive and solitary species (Kindberg et al. 2009), there are still many unknowns regarding the mechanisms influencing movement and space use in the dispersal and settlement processes. Increasing our knowledge on the factors that influence how non-territorial, solitary individuals move through space and select home ranges after independence, i.e. the dispersal process, may aid in improved management and conservation of populations.

1.2 Social/familial dynamics and anthropogenic influences on dispersal

Dispersal and settlement processes do not occur in a vacuum and individuals are exposed to other species or conspecifics on the landscape as they move and acquire resources. The efficiency of which an individual uses the space and resources around them is partially due to the amount of information they have access to (Little et al. 2022). The information an individual receives from its neighbors may influence how it moves and uses space (Dall et al. 2005), including in dispersal and settlement behavior (Schmidt et al. 2010). Information on the social context surrounding an individual may come from related individuals, that may overlap more in space than unrelated animals (Støen 2006). Familiarity may also be a factor for settlement decisions, e.g. as in the “dear enemy” hypothesis in which individuals tolerate their familiar neighbors more than unfamiliar individuals (Rosell and Bjørkøyli 2002). Population density is a third social consideration that is often considered as a contributor to dispersal decisions (Matthiopoulos et al. 2015), although it can be difficult to detect/quantify (Matthysen 2005). Social factors have often been ignored in solitary species, but recent research indicates that solitary species may possess greater social awareness than previously thought (Elbroch et al. 2017, Frank 2017). As such, there is a need to better understand how social factors, e.g. relatedness, familiarity, and density, influence settlement decisions in solitary mammals.

Familial conflict, i.e. parent-offspring conflict (POC) and sibling competition (SC), may also influence the dispersal behavior of individuals (Matthysen 2012). For species that produce multiple litters/broods over their lifespan, POC can arise over the allocation of limiting resources (Trivers 1974). A parent will try to allocate these resources evenly within and across their litters/broods in order to maximize their fitness, but individual offspring are expected to act selfishly in order to maximize their personal fitness (Kilner and Hinde 2008). For example, within a litter, one offspring may attempt to extract more of a resource from their mother, often at the expense of their siblings (SC) (Trillmich and Wolf 2008). This selfish behavior may extend across litters in that offspring can trigger both POC and SC in their attempt to increase the amount of the resources they acquire and thereby deprive their current and future siblings of an equitable amount of said resource (Smiseth et al. 2007). How POC and SC influence settlement behavior is unclear and their remains a knowledge gap in how competition over space use may reflect familial conflict in the settlement process.

In addition to social and familial dynamics on the landscape, individuals' space use and movement are likely influenced by anthropogenic features on the landscape (Ripple et al. 2014, Seidler et al. 2015). Human disturbance has been documented to alter space use and movement patterns of mammals across the globe (Tucker et al. 2018). While mammals generally avoid built up environments and areas with human activity (Rogala et al. 2011, Ripple et al. 2014), others may be drawn to them for anthropogenic food sources or as "human shields" (Lamb et al. 2017b, Moll et al. 2018). For long-distance dispersing mammals, it may be impossible to avoid areas of human disturbance (Bartoń et al. 2019), especially given their lack of information of the greater area into which they are dispersing (Stamps 2001). Resident individuals, however, may possess knowledge of anthropogenic features on the landscape and their movement may differ from naïve dispersers (Elliot et al. 2014, Rio-Maior et al. 2019). While it is likely that anthropogenic factors are influencing the general space use and movement of solitary mammals, whether those influences differ based on life stage, e.g. resident or disperser, is less clear (but see (Elliot et al. 2014, Barry et al. 2020)). Additionally, whether dispersing and resident individuals' space use and movement respond to anthropogenic features at a broader scale is similarly unclear.

1.3 The scales of selection in movement and dispersal

In a seminal paper, Johnson (1980) introduced a hierarchical framework of resource selection, containing four orders of scale, each dependent on the preceding level. These scales are 1) first-order, representing the entire habitable range for a species, 2) second-order selection, that of an individual's home range, 3) third-order selection, an individual's use of components within their home range, and 4) fourth order, representing restricted space use, such as foraging within a given patch or selecting a den in a particular area (Johnson 1980). These scales of selection often reflect different life stages or seasonal behavior of an individual (O'Neill et al. 2020). Dispersal decisions, e.g. in movement and settlement range selection, can thus be analyzed at varying scales dependent on the life stage and behavioral state of an individual.

The scale of selection can vary seasonally or with life stages, as in mate finding (Cudworth and Koprowski 2010) and dispersal (Morrison et al. 2015). For example, individuals dispersing from their natal range to settle their own home range are reflecting space use at a much higher scale (second-order) than those foraging in a patch within their established home range (fourth-order). Movement and resource selection are also reflective of differences in scale (Cosgrove et al. 2018) and life stage of an individual (Desbiez et al. 2020). For example, immature animals are often limited by the movement of their parents and lack information on the greater context of the landscape beyond their natal ranges (Dall et al. 2005). Once independent, their movement patterns may change as they disperse away from their parents and settle their own home range prior to breeding (Delgado et al. 2009). Given that space use and movement are life stage or behavioral state dependent (Morrison et al. 2015, Desbiez et al. 2020), it is important to incorporate the appropriate scale of selection when examining dispersal decisions.

1.4 The model species

The brown bear (*Ursus arctos*) is a large, non-territorial, solitary carnivore that resides in home ranges of various sizes. Male home ranges are much larger and typically overlap several female home ranges (Dahle et al. 2006). Female home ranges greatly overlap each other and fluctuate in size and location based on whether a female is traveling with offspring or is alone (Dahle and Swenson 2003c, Steyaert et al. 2013). Because they are a non-territorial species, there is no defense of their home ranges. Offspring spend between a year and a half and two and a half years in their natal range (their mother's home range) before dispersal and settling their own breeding ranges (Dahle and Swenson 2003a). Following family breakup, independent offspring must settle a home range of their own (Dahle and Swenson 2003b). Male offspring almost always disperse away from the natal range, most likely to avoid inbreeding with relatives (Zedrosser et al. 2007). Females are mainly philopatric (overlapping their natal range), but up to 40% of females in the Scandinavian population disperse away from the natal range (Støen et al. 2006a).

Although brown bears are considered a non-social species, there are times in which social dynamics come into play. For example, males compete for access to females during the mating season and males and females may encounter and mate with several individuals during this period (Steyaert et al. 2013). Females are in competition with each other for resources on the landscape (Zedrosser et al. 2006), e.g. foraging patches and denning locations, and due to their overlapping home ranges may encounter one another on the landscape. The effect of this competition is clearly visible when females shift their home ranges to “take over” parts of a home range from a harvested neighboring female (Frank 2017). The most well-established social period for brown bears is when dependent offspring reside with their mothers. It is during this period that dependent offspring learn various survival skills from their mothers, such as learning about foraging resources (Jimbo et al. 2022) or avoidance of dangerous males (Steyaert et al. 2013). Additionally, males and females show differing space-use patterns in their respective resource selection. Males are more likely to avoid anthropogenic features such as human settlements while females with dependent offspring are more likely to select those features (Steyaert et al. 2013).

2 Objectives

Main objectives

The main objectives in this thesis are 1) to examine patterns of space use in female settlement patterns in relation to social dynamics, 2) to see if familial conflict is reflected in female settlement patterns and how those patterns affect fitness, and 3) to investigate how the environment, especially anthropogenic features, influences males' resource selection and movement patterns during dispersal and residency stages. I use the brown bear as a model species to address these objectives.

Objective 1: *How does the social environment influence settlement space use for female brown bears?*

Although brown bears are a solitary species, they display sociality in distinct phases of their lives. During the mating period (May-July), males and females roam-to-mate and can mate with multiple individuals during the breeding season, i.e. they are promiscuous (Steyaert et al. 2012). The primary social period, however, is when dependent offspring are with their mothers in the natal period (Gilbert 1999). Cubs are altricial when born in the den in either January or February and are completely dependent on their mother for survival. After emerging from the den, offspring travel with their mother for at least one year and sometimes two before family breakup (Dahle and Swenson 2003a). During the natal period through family breakup, cubs remain in close physical proximity to their mothers and siblings (Dahle and Swenson 2003b).

Females may settle where they can overlap or are adjacent to the natal range (philopatry) or can disperse away from the natal range (McLellan and Hovey 2001). In Scandinavian brown bears, females typically exhibit philopatry, but dispersal is not uncommon (Støen et al. 2006a). Because female bears exhibit a high level of philopatry, an overlapping spatial pattern of related females may emerge, sometimes called 'matrilineal assemblages' or 'kin clusters.' These clusters are made up of mothers, daughters, grandmothers, sisters, aunts, and female cousins and relatedness generally decreases with increasing distance from a given female's home range (Støen et al. 2005).

Outside of mating and the rearing of offspring, little information is available whether brown bears have any social contact with one another. Scent communication suggests that they are at least aware of one another on the landscape (Clapham et al. 2012, Clapham et al. 2014). Both males and females extensively use rub objects for scent communication (Morehouse et al. 2021). It is thought that scent communication is primarily for mating purposes, e.g. finding available females or assessing male rivals (Lamb et al. 2017a, Sergiel et al. 2017). However, it may serve more extensive purposes, such as establishing familiarity with overlapping individuals (neighbors). For our first objective, we seek to determine whether females select their settlement home ranges based on characteristics (e.g. relatedness, familiarity) of the surrounding social landscape.

Objective 2: *How does familial conflict influence female settlement space use and fitness?*

Familial conflict arises when related individuals attempt to secure a limiting resource at the expense of a related individual (Hamilton 1964). One form of this is parent-offspring conflict (POC), in which offspring try to obtain a given resource at the cost of their mother's fitness (Trivers 1974). A mother's individual offspring have more to gain by depriving their current and future siblings of these resources, as they are most related to themselves (Godfray 1995), a form of familial conflict is known as sibling competition (SC). Familial conflict is often studied in the period of maternal care (Maestripieri 2002, Jones et al. 2020) and there is little knowledge of how it might occur after offspring gain their independence. Following independence, young female brown bears must settle a home range of their own to begin breeding (Dahle et al. 2006). Given the extensive overlap of females on the landscape, it is assumed that space use is a limited resource that females must compete for during the settlement period (Støen et al. 2006a). Competition for breeding ranges may occur between a mother and her independent daughters, among female siblings, with other related females, and other neighboring females on the landscape (Ordiz et al. 2008).

Female brown bears vary greatly in their longevity and reproductive success (Zedrosser et al. 2013). It is unknown whether where a female settles is related to her personal fitness (Støen et al. 2005). It is possible that females are selecting their settlement home ranges preferentially for beneficial resources, such as familiarity with forage and refugia (Ranc et al. 2020) or where they find familiar neighbors (Siracusa et al. 2021). Females that manage to settle a home range in a more favorable area may be conferred a fitness benefit (McLoughlin et al. 2007), either through greater survival or increased reproduction. Our objective in this study is to determine whether there is evidence for parent-offspring conflict and sibling conflict in the independent period when females are selecting their settlement home ranges. We also seek to determine whether where they settle confers to them a fitness benefit in survival or reproduction.

Objective 3: *How do anthropogenic factors influence male movement and space use in two life stages?*

As landscapes become increasingly human-dominated, animals are increasingly forced to alter their habitat selection and movement to accommodate human presence (Tucker et al. 2018). This is especially relevant as roads not only bifurcate landscapes and increase habitat fragmentation (Moreau et al. 2012) but also pose a mortality risk to the animals that use them for travel or must cross them to access areas beyond the road (Jaeger et al. 2005). Human settlements can also pose risks to animals that may be drawn to them for anthropogenic food sources (Lamb et al. 2017b, Penteriani et al. 2018). Human-wildlife conflicts often occur due to the presence of human settlements in an individual’s home range or territory (Nayeri et al. 2022).

As young male bears become independent from their mothers, they must disperse away from their natal range before they begin breeding (Zedrosser et al. 2007). Unlike female bears, males almost always settle far away from their natal range (Støen et al. 2006a) and are exposed to landscapes never before traversed. It is assumed that these naïve individuals experience greater risk while moving through areas they are unfamiliar with (Dobson 2013).

Resident males, however, have familiarity with their environment and are more likely to make informed decisions in resource selection and movement (Elliot et al. 2014).

The scale at which male bears select habitat and move in these two life stages (dispersing and resident) may also be relevant for determining how they are influenced by anthropogenic factors (Bastille-Rousseau et al. 2018). For example, dispersing males may not show differences in scale of resource selection and movement due to their naivety of both the greater landscape and localized features (Blazquez-Cabrera et al. 2016). However, resident males are more familiar with the landscape and may select habitats and move through them based on the broader context as well as more localized resources and features (Gastón et al. 2016). For our third objective, we look at how anthropogenic factors influence male bear movement and habitat selection in two life stages, dispersing and resident at two different scales, landscape and local.

3 Methods

3.1 Study Area

The study area is located in central Sweden, primarily within the counties of Dalarna and Gävleborg, centered approximately around 61°N, 15 °E. Land cover in the area is predominantly Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) forest, of which approximately 80% is managed as harvestable timber. Land use varies in the area but is dominated by forestry, with a lesser prevalence of agriculture and built environments (mean building density is approximately 10.7/km^2). Human population density in the study area is approximately 8.78/km^2 (Statistics Sweden 2022). Private roads, smaller gravel roads used primarily for forestry, are more common in the study area than public roads, which are larger and typically paved.

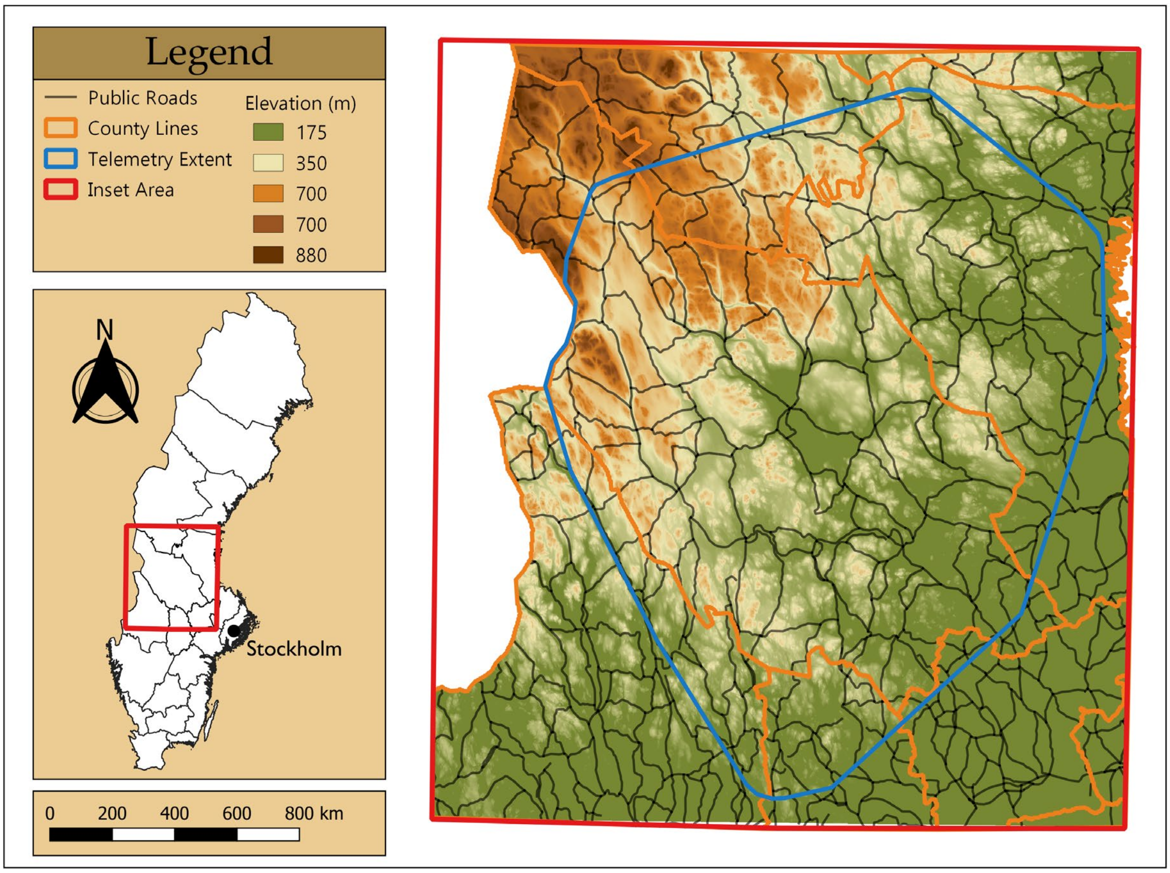

Figure 1. Map of the study area within Sweden showing extent of VHF and GPS telemetry data in blue and public roads in black.

3.2 Study population

The study population of brown bears in Scandinavia suffered extensive persecution historically and by the mid-19th century, only an estimated 130 individuals remained in Scandinavia (Swenson et al. 1995). The population has since successfully rebounded, with a steady population increase, peaking in 2008 at around 3300 bears (Kindberg et al. 2011) before stabilizing around 2800-3000 individuals (Bischof et al. 2020). The population in Sweden is subjected to an annual harvest, which has generally increased with the population of bears and is currently at approximately 10% of the population (Støen et al. 2018).

3.3 Data collection

Each spring after the denning period, brown bears in the study area are located and remotely immobilized from helicopters using darts containing a mixture of medetomidine and tiletamine-zolazepam (Dan-Inject) (Arnemo and Evans 2017). While bears are immobilized, various data are gathered including sex, age, body mass, reproductive status, and number of cubs (Dahle and Swenson 2003c, Zedrosser et al. 2006). Individuals are also marked at this time and may have one premolar removed to assess age, if unknown (Bischof et al. 2009). At the time of capture, bears of at least one year of age are fitted with a radio collar and recaptured bears may be refitted with a new collar, if necessary (Swenson et al. 2001b). Very high frequency (VHF) collars were fitted up to 2003 and thereafter to the present, bears were fitted with global positioning system (GPS) collars. All bear handling is done by permission of the Swedish Ethical Committee on Animal Research (C40/3, C212/9, C47/9, C210/10, C7/12, C268/12, C18/15) and by the Swedish Environmental Protection Agency (Dnr 35-846/03, Dnr 412-7093-08 NV, Dnr 412-7327-09 Nv, Dnr 31-11102/12, NV-01758-14).

We used VHF and GPS location data from individuals to estimate annual home ranges of individuals. VHF locations were obtained once a week on average and GPS locations were collected hourly. We used the R package ‘adehabitatHR’ (Calenge 2006) to estimate the 95%

kernel density estimated home range for females with adequate location data (VHF: >= 20, GPS: >= 1000). We used the ad-hoc reference bandwidth as a smoothing parameter and a fixed, bivariate normal kernel (Worton 1989). We then calculated the harmonic mean (centroid) for each female's annual home range. We used the home range of the mother in the natal year for focal females, as cubs of the year travel with their mother at that time and they are not yet equipped with radio collars (Swenson et al. 2001b). We took the settlement range of females at four years of age or prior to primiparity if females began breeding before 4 years. We selected four years of age because most females have dispersed by that age (Støen et al. 2006a) and the average age of primiparity in this population is 4.71 (± 0.65) (Zedrosser et al. 2009).

For male bears, we exclusively used hourly-sampled GPS data from 2007-2017. We identified dispersing individuals first by visual inspection of tracks and then by fitting hidden Markov models (HMM) to determine behavioral states (Michelot et al. 2016). Dispersal tracks were isolated from the greater set of location data based on the behavioral state assignment from the HMMs. For resident males, we looked only at individuals that had been independent from their mothers for at least three years. We filtered the data for individuals with at least 70% coverage of locations in the active period- den emergence to the onset of the hunting season (25 April to 20 August).

We obtained bear density for each year from a set of 10 x 10 km raster layers spanning 1998-2015. The density value in each cell was based on non-invasive scat sampling and genetic identification of individuals using six microsatellites. Because the number of scat samples varied across the population, they were weighted by the number of scats collected from each individual. More details on the density calculation can be found in Frank et al. (2017) and Kindberg et al. (2011)

We made use of extensive longitudinal data that contained demographic information on marked individuals including birth and death, parentage, and family break up. From this longitudinal dataset, we were able to assign mothers to female offspring, to get ages at family breakup and dispersal, as well as lifetime survival probabilities and reproductive success. We obtained hair and tissue samples collected from 1614 individuals in the population to genotype and determine relatedness; sixteen microsatellites were used to determine the identity of an individual (Frank et al. 2020). We used the Lynch-Ritland estimator (Lynch and Ritland 1999) for relatedness and used a cutoff value of 0.125 for relatives.

Habitat information, including landcover, human settlements, roads, and digital elevation models came from the Swedish Mapping, Cadastral and Land Registration Authority (Naturvårdsverket 2014, Swedish Land Survey 2018). Landcover included managed forests of varying ages, water, bogs, and agricultural lands. The roads data included both major and minor (mostly forestry) roads and human settlement data included buildings and structures (e.g. houses, cabins, outbuildings).

3.4 Variables

For our first objective, we created four variables that represented the social environment: 1) presence of the mother, 2) relatedness to neighboring females, 3) familiarity of neighboring females, and 4) the difference in density between the natal and settlement range. We took the centroid of all available females' home ranges and created a circular buffer with a radius of 7 km. This represented the average home range size for females without overrepresenting their space use. In the natal and settlement years of a focal female, we identified all the females whose home ranges overlapped their natal and settlement home ranges. For the settlement year, we noted if the range of a focal female's mother overlapped; if so the mother was considered present. We assigned all the overlapping females in the settlement range that *also* overlapped the natal range as familiar females, regardless of relatedness. Using the pedigree constructed via genotyping, we found the total number of overlapping related females, with relatedness determined at or above 0.125 on the Lynch-Ritland scale (Lynch and Ritland 1999). The number of familiar females and related females were both divided by the total number of all overlapping females to derive the familiarity index and relatedness ratio, respectively. We calculated density in the focal females' natal and settlement ranges as the total number of overlapping females. We then subtracted the density in the natal range from that of the settlement range to determine the relative change in density. We also measured the percent overlap between a focal female's settlement range and her mother's range in the settlement year. If the focal female's mother died prior to settlement, we used the percent overlap with her last known home range. See figure 2 for a visual representation of the methods for constructing and quantifying the social landscape.

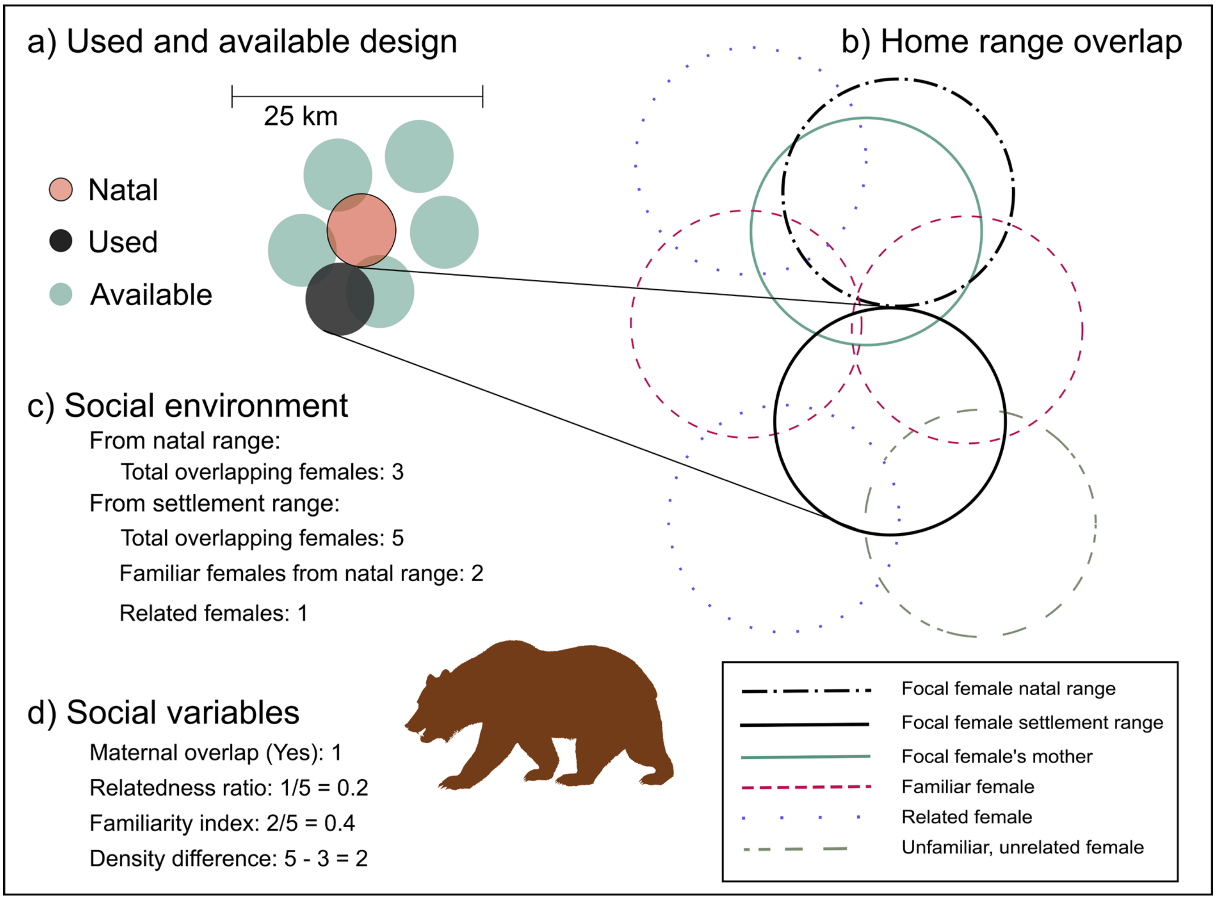

Figure 2. (From Paper 2) Schematic of how social variables were derived for the study on the influence of social environment on female brown bear settlement home range (SHR) selection. a) Used and available SHR design for the resource selection function. For each used SHR, 5 random available home ranges are created within 25 km of the natal home range. b) A focal female's natal home range (NHR) and each used and available settlement home range were overlaid with the home ranges of all other females on the landscape. c) Social environment variables were extracted based on the overlapping females, including the density (total overlapping females) in the NHR and SHR, the number of related and known females overlapping the SHR, and whether the focal female's SHR overlapped her mother's home

range. d) Four social variables (maternal overlap, relatedness ratio, familiarity index, and density difference) were derived based on social environment values extracted in b. Example calculations are given below each (c) and (d).

For our second objective, to examine whether parent-offspring conflict (POC) or sibling competition (SC) influenced space use following independence, we created several variables representing POC and SC. The first variable to represent POC was the age of the mother at birth, the second was the type of litter (containing a single female or multiple female offspring), and the third whether the mother had died prior to the settlement year. We represented SC with two variables, an assignment of the settlement distance from the natal range between pairs of female siblings, one ‘closer’ and one ‘farther.’ The second variable representing SC was the body size, measured as head circumference as a yearling. We measured distance settled from the natal range as the Euclidean distance between the centroids of the natal and settlement ranges (settlement range was represented by a focal female’s annual home range at four years of age). We calculated three variables to investigate the potential influence of settlement distance on fitness of females. The first was lifetime survival, which was measured as the lifespan of females with known birth and death events or was right-censored as the last known age of females that were still living or had unknown fates (Murray and Bastille-Rousseau 2020). The second variable was a binary variable of whether a female survived to reproduce and weans at least one offspring. The final variable was lifetime reproductive success, which was calculated as the total number of weaned offspring divided by the number of breeding attempts by each female.

For our third objective, we calculated variables representing anthropogenic features that could influence male movement and resource selection, including the distance to major and minor roads and to buildings. We also selected ‘core’ habitat components that have been shown to be relevant for brown bears such as terrain ruggedness, clearcuts, water, and bogs. We obtained a digital elevation model used to calculate terrain ruggedness, landcover data, and anthropogenic features from the Swedish Mapping, Cadastral and Land Registration Authority (Swedish Land Survey 2018). Each variable was rasterized to a 25 m resolution; we created additional 25 m resolution raster files to measure the distance of each geolocation to a given habitat or anthropogenic feature.

3.5 Statistical Analyses

We used a second-order resource selection approach (Johnson 1980) for our first objective of looking at the influence of the social environment on settlement decisions of female bears. We set the focal females' settlement range as 'used' and randomly selected five 'available' home ranges (Manly et al. 2002) that were within the dispersal kernel distance for female bears (see Figure 2). We fit a binomial generalized linear mixed model (GLMM) containing the predictor variables 'mother present,' 'familiarity index,' 'relatedness ratio,' and 'density difference.' The response variable was whether the settlement range was 'used' or 'available,' with 'focalID' as a random variable in the model (Duchesne et al. 2010). We fit all possible subsets of the full model and used Akaike's Information Criterion (AIC) to find the most parsimonious model(s) and look for informative variables (Arnold 2010). Models within 2 ΔAICc of the most-supported model were retained and used for model averaging (Grueber et al. 2011). Lastly, we used a Wilcoxon test to compare the percent of overlap between a focal female's settlement range and her mother's home range.

For our second objective which examined the influence of POC and SC on settlement distance and fitness, we first fit two GLMMs to investigate settlement distance. We fit a Gamma-distributed GLMM to examine POC containing the predictor variables 'mother's age,' 'litter type' (single or multiple), and 'mother's status' (living or dead) with the response variable 'distance settled from the natal range.' We included the variable 'body size' to control for differences in size amongst individuals, but it was not considered as a predictor variable. We then fit models containing all possible variations of the predictors (excluding body size) and used AIC to find the most-supported models (within 2 ΔAICc of the top model). For sibling competition, we fit a Gamma-distributed GLMM with 'distance settled from the natal range' as the response variable and 'settlement class' (closer or farther) and 'body size' as predictors. We included a random variable 'motherID' in both POC and SC models. An additional random variable, 'litterID,' was included in the SC model. To assess individual fitness, we first fit a survival curve to study females using age at death or oldest known age for right-censored individuals. We then fit a survival regression (Carroll 2003) with ‘distance settled from the natal range’ as the sole predictor variable and survival age as the response. We also fit a binomial GLMM with ‘survived to reproduction’ (yes or no) as the response variable and ‘distance settled from the natal range’ as a predictor, while controlling for body size. Our final fitness model was a zero-inflated Gamma GLMM that contained ‘lifetime reproductive success’ as a response and ‘distance settled from the natal range’ as a predictor while controlling for body size. All GLMMs for objectives one and two were fit using the R package ‘glmmTMB’ (Brooks et al. 2017) and assessed for fit using the ‘DHARMa’ package (Hartig 2022).

For our third objective, we used two modelling techniques to look at the different scales of selection, local and landscape. We used integrated step selection analysis (iSSA) (Avgar et al. 2016b) to examine how anthropogenic features and habitat components influenced local selection. This technique allowed us to simultaneously measure movement properties and habitat selection. We used the GPS tracks from the males’ dispersal tracks and resident ranges as the ‘used’ steps. For each used location, we randomly selected 20 ‘steps,’ in which lengths were sampled from a fitted gamma distribution and the angles were drawn from a uniform distribution. We used the R package ‘amt’ to prepare the step length data and fit the iSSA models (Signer et al. 2019). To examine selection at a landscape level, we used an exponential resource selection function (RSF) with availability defined as the 100% minimum convex polygon which encompassed all the male locations plus an ~18 km radius buffer. We then randomly sampled 20 locations from the availability area for each used location. For both the iSSA and RSF, we took the dispersal and resident (life stage) use and availability locations to fit models for individual bear years which we subsequently averaged to get population-level estimates. We used a conditional logistic regression for the iSSA, with a unique ‘stepID’ assigned for used versus available steps. For the RSF, we used a binomial generalized linear model (GLM) with ‘used’ or ‘available’ locations as the response variable. Our base models contained all the habitat covariates and terrain ruggedness index (TRI) as predictors. We then fit models containing the anthropogenic variables, building on the base models one predictor at a time. The full models contained all the habitat covariates, TRI, and all anthropogenic variables. To capture differences of movement characteristics between dispersers and residents in the iSSA, we included step lengths as well as the natural log for step lengths (Avgar et al. 2016a). We used AIC to compare each set of the iSSA and RSF models. For dispersers and residents, we summed the delta AIC of the candidate models and selected the models with the lowest mean AIC as the best model. All data handling and statistical analyses were done using the R programming language (R Core Team 2021).

4 Results and Discussion

4.1 Social environment and settlement

From our first study, we found evidence that the social environment influences settlement patterns for female bears. In our selection process, we identified three supported models (two models with ΔAICc ≤ 2 of the most-supported model), with at least one of the predictor variables occurring in the model set. The model averaging indicated that females selected settlement home ranges that overlapped their mother's range (β = 1.03, 95% CI: 0.3-1.67) and those of familiar females (β = 0.8, CI: 0.44-1.17). They also selected SHR in areas with a higher relative density (β = 0.67, CI: 0.32-1.03). Females exhibited indifference in their settlement patterns as it pertained to related females (β = -0.19, CI: -0.52-0.15). We also found a moderate degree of overlap between settling females and their mothers' ranges (overlap index 0.41 ± 0.23). Additionally, females with living mothers had less overlap (0.36 ± 0.2) than those whose mothers had died prior to settlement (0.49 ± 0.24).

The presence of the mother is clearly the most influential social factor when females are selecting settlement home ranges. Our results show that females select SHR that overlap their mothers' ranges, likely because the mother represents the highest degree of social tolerance on the landscape. A pattern of philopatry is seen in many mammal species (Arnaud et al. 2012, Clutton-Brock and Lukas 2012), which is probably due to a combination of familiarity with the resource distribution and social tolerance shown by their mother, aspects included in the resident fitness hypothesis (Wiggett and Boag 1992). Higher survival in female grey mouse lemurs (*Microcebus murinus*) was also associated with the presence of their mothers, where daughters who had mothers' present had a greater chance of surviving to the breeding season (Lutermann et al. 2006). High social tolerance from their mothers was also seen in female orangutans (*Pongo pygmaeus*) who have high spatial overlap with their mother's range from independence to the onset of breeding (Ashbury et al. 2020).

Besides the presence of their mother, females selected for SHR that overlapped familiar females. Although previous studies have demonstrated the value of living near kin (Clutton-

Brock 2009, Dobson et al. 2012), others highlight the benefits of living near familiar individuals, including in fitness (Ylönen et al. 1990, Shier and Swaisgood 2012). For example, a higher number of neighbors and familiar neighbors was correlated with greater reproductive success in female great tits (*Parus major*) (Grabowska-Zhang et al. 2011). Benefits in small mammal and avian reproduction and survival appear to be conferred when familiar with conspecifics (Grabowska-Zhang et al. 2011, Shier and Swaisgood 2012, Siracusa et al. 2021); however, whether this occurs in large mammals is unknown. Given previous research showing a matrilineal assemblage structure in this population (Støen et al. 2005), we expected to find that females selected SHR that overlapped related females. Instead, we found that females were indifferent in terms of selection of SHR overlapping relatives. One possibility for why we did not find the expected relationship with relatedness is that kin-recognition is based either on proximity, i.e. adjacent individuals are likely relatives, (Mateo 2004) or familiarity (Tang-Martinez 2001), in which females 'assume' that familiar individuals are related. We suggest that females that were known from the natal period may also exhibit higher tolerance to the settling females. Recent research on North American red squirrels (*Tamiasciurus hudsonicus*), found that familiarity with neighbors resulted in a reduction of time spent on territorial defense and a higher survivability and annual reproduction (Siracusa et al. 2021). The study also did not find a relationship between relatedness and reduced territorial defense or fitness (ibid).

Lastly we found that females select SHR in areas with higher densities that that of their natal ranges, despite the presence of suitable habitat in areas with lower densities. Higher densities of female bears may be a used as a form of social information, such that greater presence of females is representative of suitable areas for survival and reproduction. A similar pattern was found in blue tits (Cyanistes caeruleus), where dispersers with higher reproductive success settled in areas with higher density relative to their natal area (Parejo et al. 2007). The use of social information is particularly relevant during the dispersal process, in which individuals must make settlement decisions with imperfect information (Seppänen et al. 2007). In our population, this indicates that females are settling towards the more densely populated 'core' area than towards the periphery. This trend has important ramifications for future population expansion, in that it is unlikely that females will expand outwards from their current geographical range.

4.2 Familial conflict, settlement distance, and fitness

In our second study, we found some evidence for POC and SC in female settlement patterns. The results of AIC indicated support for four POC models, three within 2 ΔAICc of the top model. For POC, we found that females settled closer to the natal range when their mother had died prior to settlement ($\beta = -0.571$, 95% CI: -1.071 - -0.071, $p = 0.025$). Both 'settlement class' and 'body size' were informative in our SC mode, with one female in a sibling pair settling closer to the natal range than her sister ($\beta = -1.174$, 95% CI: -1.452 to -0.896, $p < 0.001$) and larger females settling closer to the natal range ($\beta = -0.379$, 95% CI: -0.712 to -0.045, $p = 0.026$).

Our fitness results showed a contradictory relationship with distance settled from the natal range- we found that females that settled farther from the natal range were more likely to survive to reproduction ($\beta = 0.586$, 95% CI = 0.033 to 1.140, $p = 0.038$), although lifetime survival was higher for closer-settling females ($\beta = -0.010$, 95% CI = -0.020 to -0.0001, $p = 0.033$).

Our results indicated only partial evidence for POC in the settlement process- that females settled closer to the natal range if their mother had died prior to settlement. This indicates that female offspring are in competition for space use with their mothers, but that this competition does not vary with the mother's age or whether she had a single or multiple female offspring. These results confirm our findings in the first study, which showed that female offspring have greater overlap with their mothers' ranges when the mother died prior to settlement. Patterns in which female offspring compete with their mother for space use has been seen in other species. Columbian ground squirrels (*Urocitellus columbianus*), for example, will settle in their mother's home range if she dies prior to the time of their settlement (Arnaud et al. 2012), and Amur tigers (*Panthera tigris altaica*) preferentially overtake their natal range in the case of the mother dying (Goodrich et al. 2010).

When considered together with the results from the POC models, it appears that familial conflict over space use can be multi-faceted. That is, females may not only compete with their mother for space use, but also with female siblings. This is seen also in red deer (*Cervus elaphus*), where females invest more in the production in sons, possibly as a mechanism of reducing competition with her daughters—whose home ranges overlap her own—and the larger population of related females (Clutton-Brock et al. 1982). In this study, we found a strong pattern in pairs of female siblings in which one sibling of the pair settles closer to the natal range than her sister, on average three times closer. Sibling interactions were shown to have greater influence on dispersal distance than maternal conflict in a study og white-footed mice (*Peromyscus leucopus*) (Jacquot and Vessey 1995). Although we found an effect of body size in a sibling competition models, the effect was weaker in females that settled closer to the natal range. If dominance is involved in determining which sister is forced to disperse farther from the natal range, it might not be closely tied to body size. Other factors, such as agonistic interactions (Drummond 2006) or personality differences (Hudson et al. 2011) might be more influential between siblings. Dispersal patterns are often assumed to be driven by multiple mechanisms (Matthysen 2012) and our study results are in agreement with this assumption.

Our results showed mixed fitness benefits in relation to settlement distance. In terms of lifetime survival, settling closer to the natal range conferred an advantage. Greater survival for resident (versus dispersing) females was also found in North American red squirrels (Martinig et al. 2020). However, females that farther away were more likely to survive to primiparity. These seemingly disparate results reflect previous patterns found in this population. Namely, that females settling farther away begin reproducing sooner than more philopatric females (Støen et al. 2006b), possibly due to reproductive suppression of neighboring females (Ordiz et al. 2008). Females in the population reach primiparity on average at 4.7 years, but the median survival age is only 6 years. This may mean that females settling farther have a better chance of successfully weaning at least one offspring. We did not find a correlation between distance settled and lifetime reproductive success. Cubs in this population are subject to mortality from sexually-selected infanticide, in which immigrating adult males will attempt to kill the offspring of females in order to bring them into a reproductive state (Gosselin et al. 2017, Leclerc et al. 2017). Harvest of male cougars (Puma concolor) induced high enough SSI pressure that population declines resulted, even when females were not removed from the population (Wielgus et al. 2013). Given the high amount of turnover in the population (Frank 2017, Leclerc et al. 2017), direct loss of females via harvest or SSI likely have a larger effect on reproductive success than where a female settles.

4.3 Anthropogenic influences on dispersing and resident males

We found evidence that anthropogenic features were important for selection and movement for dispersing and resident males in our study. The results of the model selection process indicated that the full model (with all habitat and anthropogenic covariates) was the most-supported model at both local and landscape scales for both dispersing and resident males. For the habitat variables, we found that both dispersing and resident males avoided bogs at the landscape and local scales (Figure 3). At a local scale, both dispersers and residents avoided clearcuts, but showed indifference at a landscape scale. Residents showed greater selection for other habitat covariates including for water at the local scale and TRI at both local and landscape scales (Figure 3). Dispersers did not show selection for any anthropogenic covariates at either scale but avoided buildings at the local scale (Figure 3). Resident males showed avoidance for public roads and buildings and selection for forestry roads at both scales (Figure 3). Dispersers increased their movement speed when near buildings, while resident males speed was stable (Figure 3). Nearer to both public and forestry roads, dispersers and residents moved at a fast rate. Movement rates for dispersing and resident males were much faster on forestry roads than public roads (3.26 and 3.54 times, respectively).

In general, resident males showed greater selection and avoidance of habitat and anthropogenic features than dispersing males. Resident males typically selected areas farther from human impact, at both the local and landscape scale, aside from forestry roads, which they selected. This pattern was also seen in Iberian wolves (*Canis lupus signatus*), where residents avoided areas with human disturbance (Rio-Maior et al. 2019). Dispersers, by contrast, were almost always indifferent in terms of anthropogenic features, apart from avoiding buildings at a local scale. The indifference shown by dispersers is suggestive of an individual naïve to novel surroundings and thus takes greater risks when moving through an unknown landscape. Dispersal is an inherently risky process and moving through human-altered landscapes likely exacerbates the risk, as has been documented with American marten dispersing through regenerating forests (Johnson et al. 2009). Aside from anthropogenic features, resident males also selected more rugged terrain at both scales, whereas dispersers exhibited indifference. The most parsimonious explanation of the aforementioned patterns is that resident males are more familiar with their surroundings at both scales and make more informed choices when it comes to selection/avoidance. An alternative reason that dispersing males tend to move through the risky areas that resident males avoid may be an expression of social avoidance behavior. Dispersing males face a mortality risk from the adult resident males whose home ranges they are moving through (Swenson et al. 2001a, Elfström et al. 2014). This puts dispersing males in the difficult position of trying to move through human-influenced novel landscapes while avoiding resident males (Lone et al. 2014).

We found several interesting movement patterns around anthropogenic features amongst resident and dispersing males. While in the vicinity of buildings, dispersing males moved faster. Faster movement in areas typically avoided indicates that they perceive buildings and settlements as risky landscapes that they must move quickly through (Dickie et al. 2020). African lions (Panthera leo) show similar movement patterns, in which they both avoid and move faster through human-dominated landscapes (Oriol-Cotterill et al. 2015). Movement on both forestry and public roads was faster for both life stages. Using the interpretation guidelines set forth by Dickie et. al (2020), when roads are selected for and movement is fast, the individual is likely using it to facilitate movement. Conversely, if the area is avoided and the movement is fast, the individual is likely trying to move quickly through risky habitat. Linear features were reported to facilitate movement of wolves and brown bears in Alberta , but have been shown as risky for elk (Cevus elaphus) (Prokopenko et al. 2016) and European roe deer (Capreolus capreolus) (Passoni et al. 2021). The findings in this study indicate that dispersing males are willing to move through areas that resident males would typically avoid.

Therefore, using the movement tracks of dispersing males is probably more valuable than established male residents for structural connectivity mapping.

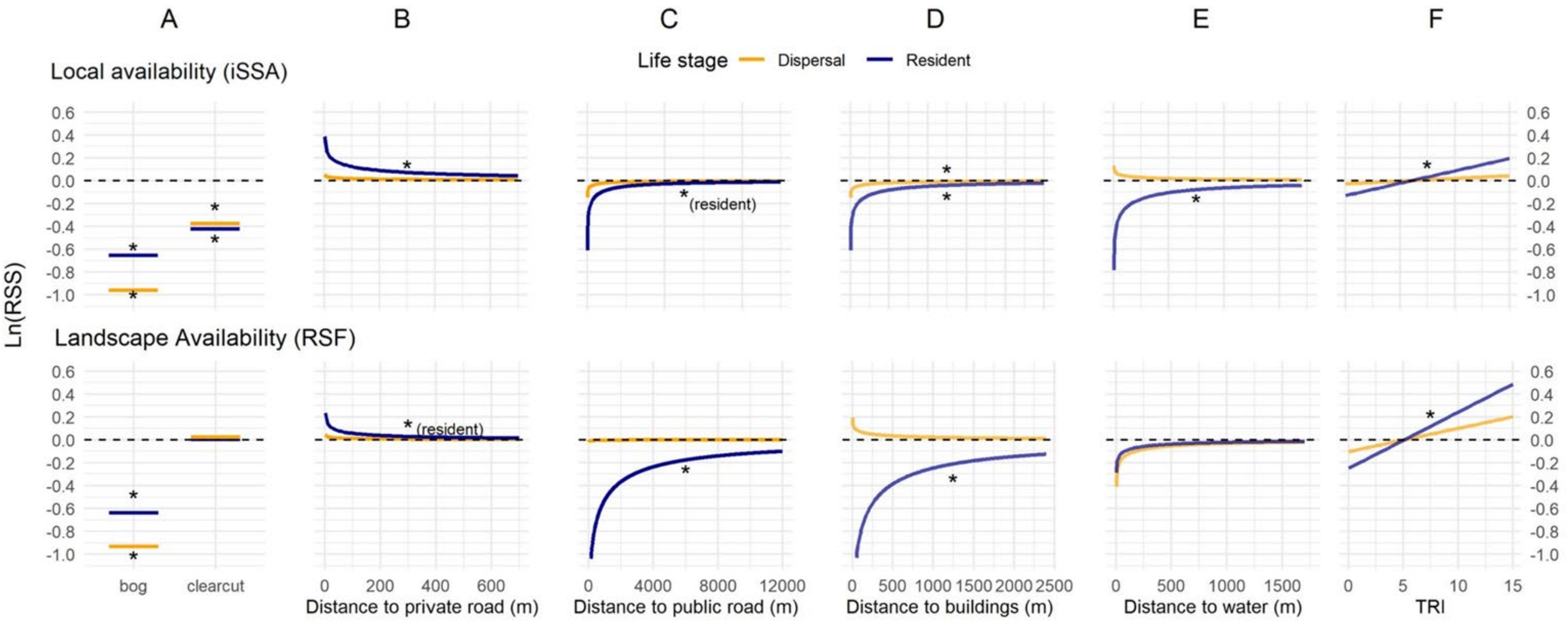

Figure 3. (From Paper 3) Relative selection strength (RSS) for dispersing and resident male brown bears from the inverse-variance weighted linear model. Column (A) is the RSS of staying in the habitat reference category (i.e. not bogs or clearcuts) compared with selecting for either bogs or clearcuts. Columns (B), (C), (D), and E) show the RSS of moving closer towards the features (leftward) vs staying at the same distance across a range of starting distances (x-axis). Column (F) illustrates the RSS of selecting a given TRI value (x-axis) over the mean value (4.19). * indicates covariate was significant for respective 'Resident' and 'Dispersal' models (95% CIs did not overlap zero) for the curve that it is nearest. In cases where placement is not obvious, clarification is given in parenthesis.

5. Conclusion

5.1 Concluding remarks

Our overarching goal was to look at how social dynamics, familial conflict, and anthropogenic features influenced space use and movement, using the brown bear as a model species. The three studies contained in this thesis have provided both insights and challenges in achieving that goal. In our first objective, we aimed to determine what role the social landscape played in females' settlement behavior. That study showed evidence that females are influenced by the social environment when selecting their settlement home ranges in that they prefer to select SHR that overlap their mothers and familiar females. We also found that females will "take over" parts of their mothers' home ranges after the mother's death. This finding supports previous research showing the social awareness of female brown bears (Frank et al. 2017). Females' apparent indifference to settling near relatives casts doubt on previous speculation of kin recognition in this species (Støen et al. 2005, Zedrosser et al. 2007). Preferentially settling near familiar females may still result in matrilineal assemblages if enough of the familiar females are related. Finally, females' preference to settle their home ranges in areas of higher female density has important implications for predicting future space use and gene flow. Chiefly that females will likely continue to settle within the existing population footprint and that males will continue to be the genetic link among Scandinavian populations (Waits et al. 2000, Schregel et al. 2017). The results of our first study suggest that immature individuals are gathering information during their natal period about neighboring females that they later use when selecting a SHR. The means of information gathering by young females on familiar individuals is most likely through olfactory communication (Clapham et al. 2012), although direct interaction with overlapping females is also a possibility.

For our second objective of looking at the influence of familial conflict on settlement distance and subsequent effects on survival and reproduction, we found mixed and contradictory results. Our limited support for parent-offspring competition was evidenced by females settling closer to their natal range after their mothers died, a finding in line with the results of our first study. We found greater support for sibling competition; namely that in pairs of female siblings, one will settle closer to the natal range, while the other settles farther. We also found that body size played a role, but that size was more influential for individuals settling farther away. Our findings support prior research that suggested differential female sibling dispersal in brown bears (Zedrosser et al. 2007). From our investigation on how distance settled influences survival and fitness, we found that females that settled closer to the natal range had greater lifetime survival, as posited in the resident fitness hypothesis (Wiggett and Boag 1992). However, survival does not necessarily mean higher reproduction. In fact, we found that females settling closer to the natal range had a lower probability of surviving to reproduction and found no relationship between distance and mean reproduction success. Delayed primiparity (Støen et al. 2006b) and reproductive suppression (Ordiz et al. 2008) may reduce a female's ability to reproduce before dying and, in a population with high harvest mortality, settling farther might convey a reproductive advantage. Individual or combined effects of harvest and sexually-selected infanticide may disrupt evolutionary patterns (Frank et al. 2017, Frank et al. 2020) that might otherwise be evident. Therefore, anthropogenic effects might be more influential on settlement and fitness than other social and familial factors.

For our final study objective, we investigated how anthropogenic features affects resource selection and movement at two scales (local, landscape) and in two life stages. Our results showed that for both scales and life stages (disperser, resident), human infrastructure influenced resource selection and movement. Dispersers were indifferent towards both landscape features and human infrastructure at the landscape scale, suggesting their general naivety of areas outside their natal range. Resident bears showed more pronounced patterns of selection and avoidance at both local and landscape scales, which reflects their familiarity with their surroundings. The avoidance of buildings by both dispersers and residents reinforces the notion that bears are moving through a 'landscape of fear' (Støen et al. 2015), in which humans pose a legitimate mortality risk (Steyaert et al. 2016). Movement and selection are doubly risky (Lone et al. 2014) for dispersing males who also must avoid adult males on the landscape. We found that male bears in both life stages appear to use forestry roads to facilitate their movement, but that resident males avoid public roads. Dispersers indifference towards public roads indicates that they are moving through risky habitats during dispersal which may increase their mortality risk (Scrafford et al. 2018). Because residents and dispersers exhibit different types of selection, avoidance, and movement patterns, we would not recommend making landscape resistance or structural connectivity maps based on resident bear movement or selection data. A landscape resistance surface derived from dispersing individuals' data is more likely to result in more realistic connectivity pathways (Rio-Maior et al. 2019). Because unique selection and avoidance patterns can occur for different scales (Prokopenko et al. 2016), scale should be considered when addressing functional connectivity of populations and creating resistance surfaces (Zeller et al. 2017).

5.2 Future research

The insights, challenges, limitations, and subsequent questions derived from these studies provides many directions/lines of inquiry for future research. From the first study, an obvious next step would be to examine whether settling near the mother or familiar females provides a measurable fitness benefit. Another potential study might involve looking at how geographic population expansion may be limited by females' preference to settle in more densely-populated "core" areas. Perhaps the most interesting research involves how females are acquiring information on the social environment around them. From this, there are two potential follow-up studies: one using geolocation data to look for instances of direct contact between female bears. The other would require a significant fieldwork component and involves surveying for shared rubbing objects on the landscape and comparison to females' geolocation data for potential overlap.

From the second study, one line of inquiry involves the mechanisms that drive dispersal difference between pairs of female siblings. This type of study would likely involve direct behavioral observations of mothers with her female offspring, admittedly risky and time consuming. A compromise to direct behavioral observation might involve a combination of GPS collar data (collected at a very fin scale, e.g. one fix/minute) and implants which measure physiological components. This type of data may shed light on interactions among the mother and her female offspring at a meaningful resolution and provide physiological data that might reflect agonistic interactions among female siblings. Another potential follow-up study might try to determine whether direct harvest or sexually-selected infanticide have a greater influence on a female’s lifetime reproductive success. This would require a great deal of careful sifting through female reproductive and female/male mortality data as well as inference from movement data. Because of the high harvest-driven turnover in the population, it would be interesting to look at the females with the highest longevity and reproductive success and “reverse engineer” what commonalities they possess and if those might help explain their relative level of success. This type of knowledge would be particular useful in conservation and management. Finally, a frequent wish of researchers working with this population is to conduct a comparative study with a population that is not hunted. However, the amount of data available on protected populations is typically not robust enough to conduct a comparative study yet.

In the final study, the clearest next step would be the development of a landscape resistance surface or least-cost pathway map for male brown bears. This is commonly done in studies that use resource selection functions and step-selection functions. However, as opposed to traditional resource selection and step selection functions, there is no direct pipeline from integrated step selection analysis to resistance surfaces/least-cost pathways. A technique using simulated data is in development, but is currently computationally prohibitive to implement. An alternative would be to use the resource selection function models to produce resistance surfaces at two scales, but without incorporating movement patterns the utility of the product might be limited. A nice follow-up study might compare the dispersers movement with the resident bear(s) whose home range(s) they traverse during their dispersal period. This might help to tease out whether the movement and selection patterns of dispersing males are more influenced by anthropogenic features or avoidance of adult males during their dispersal period.

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Article 1

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Original Article

Social environment shapes female settlement decisions in a solitary carnivore

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How and where a female selects an area to settle and breed is of central importance in dispersal and population ecology as it governs range expansion and gene flow. Social structure and organization have been shown to influence settlement decisions, but its importance in the settlement of large, solitary mammals is largely unknown. We investigate how the identity of overlapping conspecifics on the landscape, acquired during the maternal care period, influences the selection of settlement home ranges in a non-territorial, solitary mammal using location data of 56 female brown bears (*Ursus arctos*). We used a resource selection function to determine whether females' settlement behavior was influenced by the presence of their mother, related females, familiar females, and female population density. Hunting may remove mothers and result in socio-spatial changes before settlement. We compared overlap between settling females and their mother's concurrent or most recent home ranges to examine the settling female's response to the absence or presence of her mother on the landscape. We found that females selected settlement home ranges that overlapped their mother's home range, familiar females, that is, those they had previously overlapped with, and areas with higher density than their natal ranges. However, they did not select areas overlapping related females. We also found that when mothers were removed from the landscape, female offspring selected settlement home ranges with greater overlap of their mother's range, compared with mothers who were alive. Our results suggest that females are acquiring and using information about their social environment when making settlement decisions.

Key words: **dispersal, public information, settlement, social environment, space use.**

INTRODUCTION

How and where a female selects an area to settle and breed is of central importance in dispersal and population ecology (Pulliam and Danielson 1991; Barton 1992; Stamps 2001). After a variable amount of time living in a natal home range (NHR), selection of a settlement area is the final stage in natal dispersal, that is, dispersal before breeding (Bowler and Benton 2005). A common settlement pattern among mammals is for subadult males to disperse and for females to remain philopatric, that is, settle where they overlap their NHR (Waser and Jones 1983). However, even in mammals with general female philopatry it is common for some females to disperse (Lawson Handley and Perrin 2007), and such plasticity in dispersal pattern suggests behavioral control over the settlement process (Benard and McCauley 2008).

Proximate cues in the natal period may influence where individual females settle (Stamps 2001; Benard and McCauley 2008). Natal habitat preference induction is a mechanism whereby individuals use environmental cues from their NHR when searching for settlement areas (Stamps and Davis 2006). Another mechanism is density dependence (Matthysen 2005), that is, females living at higher population densities may be limited in areas available to settle and breed (Fretwell and Lucas 1969; Stockley and Bro-Jørgensen 2011). Kin-based dispersal, that is, females settle in areas away from related individuals to avoid kin competition and thereby increase their inclusive fitness, has also been proposed as a mechanism for female settlement decisions (Cote and Clobert 2010). Conversely, in other social systems females settle where they overlap kin with increased tolerance towards

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related individuals, which may also increase inclusive fitness (Clutton-Brock and Lukas 2012).

The influence of social information, that is, information acquired by observing other individuals interact with the environment (Danchin 2004), on the settlement process is receiving attention as a mechanism influencing settlement patterns (Vercken et al. 2012; Wey et al. 2015). The use of social information for settlement decisions has been described for a variety of taxa (Doligez et al. 2002; Nocera et al. 2006; Robinson et al. 2011; Vercken et al. 2012), but has received less attention in mammals (Valone 2007). This implies that social structure (relationships and interactions among individuals) and social organization (the composition of individuals within an area or group), that is, the social environment, can provide information for individual dispersal decisions (Bowler and Benton 2005; Armansin et al. 2020). For example, conspecific density can be used to assess the quality of a resource or an environment (Dall et al. 2005). In addition, information about the social environment gleaned in the natal period, for example, the presence and location of conspecifics on the landscape (Danchin et al. 2004) or the detection of a female with dependent young (Clobert et al. 2001), can provide naïve individuals with valuable information, for example, on habitat availability or reproductive competition, and reduce uncertainty for their settlement decisions (Danchin et al. 2004). Lastly, the use of information regarding specific female identities allows an individual to gain familiarity with overlapping conspecifics which can reduce 'social resistance' into an area for settlement (Armansin et al. 2020).

Research on the influence of the social environment in mammals is typically conducted on social species (Hare et al. 2014; O'Mara et al. 2014). We use the brown bear (*Ursus arctos*) as model species to investigate if the social environment influences natal dispersal and the selection of settlement home ranges (SHR) in a non-territorial, solitary mammal. Brown bears live solitarily for the majority of their lives aside from the mating period and females rearing offspring. Adult females maintain relatively stable home ranges with extensive spatio-temporal overlap, especially among related individuals (Mace and Waller 1997; Støen et al. 2005). Female brown bears likely exhibit inverse density dependent dispersal, which may result in the formation of matrilineal assemblages, that is, overlapping home ranges of several generations of related females (Støen et al. 2005). Reproductive suppression has been documented in female brown bears, and it has been suggested that related females (Støen et al. 2006b) and neighboring females (Ordiz et al. 2008) influence one another's breeding patterns. After the death of an adult female, other females will shift their home ranges to fill in that vacancy (Frank et al. 2017). This suggests that female brown bears may make decisions on space use and reproduction based on information regarding the social environment. Information gathering from conspecifics may reduce uncertainty in the settlement process and result in an increased chance of successful breeding (Danchin et al. 2001). Brown bears extensively use chemical scent cues (Clapham et al. 2012, 2014; Jojola et al. 2012; Morehouse et al. 2021) and other spoor on the landscape (Sergiel et al. 2017), and scent communication is the most likely means of acquiring information on conspecifics (Revilla et al. 2021). Additionally, information about the social environment may be obtained through direct social interactions with spatially overlapping females. We propose that females acquire information about the social environment during the natal period, such as the identity and density of conspecifics, that is later used in the selection of an SHR.

The primary objective of this study is to investigate if the social environment influences selection of an SHR by a solitary-living mammal, the brown bear. We hypothesized that, amongst all female conspecifics, an individual female's mother would exhibit the highest level of social tolerance towards them. We thus predicted that (P1) females would select SHR that overlapped their mother's home range. However, hunting in the population leads to regular socio-spatial changes (Frank et al. 2017), and a mother may die before a female's settlement decision. We hypothesized that females detect the presence or absence of their mother on the landscape and would use that information when making settlement decisions. Specifically, we predicted that (P2) females whose mothers died before settlement would overlap a greater amount of their mother's home range than females whose mothers were alive in the settlement period. A kin-based socio-spatial structure has been documented in female brown bears (Støen et al. 2005) and we hypothesized that females recognize and show higher social tolerance to kin than non-kin. We thus predicted that (P3) females would select SHR that overlapped related females. The presence of females who are familiar from the natal period (Mateo 2002) may decrease aggressive encounters between neighboring females and improve breeding success (Ylönen et al. 1990; Armansin et al. 2020). We hypothesized that during the natal period females gained familiarity with neighboring females who may be less hostile to a female in the settlement period. We, therefore, predicted that (P4) female bears would select SHR that overlapped with females "known" from the natal period, hereafter "familiar" females. Previous research on female brown bears indicated that density patterns are regulated through social interactions of females and that individuals have the ability to detect local density levels and that reproductive success of primiparous females is higher in lower density areas (Støen et al. 2006a; Zedrosser et al. 2009). We hypothesized that females detect density levels of conspecifics in the natal period and during the selection of an SHR. We, therefore, predicted (P5) females would select an SHR with a density lower relative to the NHR to reduce competition.

MATERIALS AND METHODS

Study area and model species

Our study area covers ~13,000 km^2 and is located in Gävleborg and Dalarna counties, southcentral Sweden (~61°N, 14°E). The terrain is hilly, and Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) are the dominating tree species. The forests are intensively managed, resulting in a mosaic of mixed-aged stands, bogs, and lakes. The human population density in the region is low (Ordiz et al. 2012), but there exists an extensive network of forestry roads (Frank et al. 2015). Bears are hunted in the study area (Frank et al. 2017).

Brown bears are solitary-living and non-territorial carnivores with a promiscuous mating system and extensive overlap of male and female home ranges (Støen et al. 2005; Steyaert et al. 2012). The mating season is from May to July (Steyaert et al. 2012) and females give birth to cubs during hibernation in January (Friebe et al. 2001). Offspring in the Scandinavian population remain with their mothers in the NHR for either 1.5 or 2.5 years until family break up (Van de Walle et al. 2018). Dispersal is a gradual process over a 2–3 year timespan, and up to 54% of the female subadults will settle in areas overlapping their NHR (Støen et al. 2006a). The average age of female primiparity in this population is 5 years (Zedrosser et al. 2009).

Telemetry data and home range estimation

The population in the study area has been continuously monitored since 1985 (Swenson et al. 1994). Very-high frequency (VHF) telemetry data span from 1985 to 2016 and Global Positioning System (GPS) telemetry data from 2003 to 2018 (Dahle and Swenson 2003; Arnemo and Evans 2017). Capture and handling of bears was conducted by permit under Swedish authorities and ethical committees (Uppsala Djurförsöksetiska Nämnd: C40/3, C212/9, C47/9, C210/10, C7/12, C268/12, C18/15. Statens Veterinärmedicinska Anstalt, Jordbruksverket, Naturvårdsverket: Dnr 35-846/03, Dnr 412-7093-08 NV, Dnr 412-7327-09 Nv, Dnr 31-11102/12, NV-01758-14). Relocations from VHF collars were obtained weekly on average and GPS collar data were collected hourly. We inspected VHF locations for outliers and removed locations that occurred beyond the average home range diameter (14 km) from the cluster of locations of a given individual. To minimize location error of GPS relocation data, we removed GPS locations with a dilution of precision (DOP) > 10 from the data (D'eon and Delparte 2005). We then subset the screened telemetry data to the average local active period for bears, 01 May to 30 September (Friebe et al. 2001).

We generated annual 95% kernel utilization distributions (UD) using the R package *adehabitatHR* (Calenge 2006) for each focal bear. A focal bear's NHR was estimated from the UD of its mother in the year before family breakup, as focal bears had not yet received radio collars during this time period. We estimated a focal bear's SHR from its own annual UD two years after family breakup, before primiparity (Zedrosser et al. 2009). We selected two years post family breakup because previous work has shown peak dispersal activity for females in the year after family break up (Støen et al. 2006a) and our goal was to best estimate where females settled. For some focal bears (*n* = 24), telemetry data were unavailable for the second year after family breakup. In these cases, we used the first available year post breakup (from 1 to 4 years) for the SHR. For females with living mothers during the settlement period, we estimated the mother's home range in the focal bear's settlement year. For females whose mothers died before settlement, we estimated the mother's home range in the most recently available year (1–2 years before settlement). We extracted the 95% vertices of each annual UD to generate home ranges. We calculated the centroid of the NHR and SHR of each focal individual.

Between 50 and 80% of female bears in the study area are marked on an annual basis (Bellemain et al. 2005; Zedrosser et al. 2006), but not all marked bears have adequate relocation data for home range estimation. To approximate the home ranges of non-focal adult (≥4 years of age) females (*n* = 1259 bear years), we used varying methods based on the availability of their location data. We used the available location as an approximated "home range" centroid for each year of the adult lifespan (≥4 years of age) for marked females with only a single geolocation, for example, the location of their capture or mortality. For marked females with too few locations to estimate a UD, we obtained the centroid of all available points to serve as the annual "home range" centroid. For females with adequate location data, we estimated the 95% annual UD and obtained a home range centroid. We completed a sensitivity analysis to determine the appropriate buffer size around all non-focal female centroids to create assumed home ranges. We overlapped circular polygons with radii from 6–15 km with female home ranges from our study population with the goal of maximizing home range coverage and minimizing the amount of buffer extending beyond the home range. A buffer size of 10.5 km was large enough for 95% average coverage of all known female home ranges although exceeding home ranges by only 5% on average.

We obtained telemetry data from 56 dispersing females and 31 unique mothers between 1998 and 2018; each represented in the natal and settlement year by ≥20 VHF (range = 20–151, mean = 80) or ≥1000 GPS (range = 1045–6913, mean = 3543) locations. Local density varied from one to 15 females (mean = 7 ± 4 SD) in the NHR and from zero to 11 females (mean = 5 ± 3) in the SHR (see Table S1 for further variable information).

Defining the social landscape

We identified female focal individuals that had available telemetry data in their natal and settlement years. We overlapped the NHR and SHR of focal individuals with the home ranges of non-focal females in each natal and settlement year (Figure 1). To test for predictions 1 and 3–5, we generated four variables based on the resulting overlap data to represent the social landscape (Figure 1). *Maternal overlap* is a binary yes/no variable of whether or not the home range of the focal bear's mother overlapped their own SHR. This variable is only relevant for focal bears who have living mothers in the settlement year. *Relatedness ratio* in the SHR represents the proportion of related females among all overlapping females. We took tissue and hair samples from captured or dead bears in the population and used 16 microsatellites to genotype 1614 individuals. We constructed pedigrees and used genotypes of individuals to assign relatedness of females (detailed in Frank et al. 2020) with the Lynch–Ritland estimator (Lynch and Ritland 1999). This method allows for the estimation of the coefficient of relatedness using molecular markers. We used a pairwise coefficient of relatedness value of ≥0.125 as the threshold for two females to be related. This threshold includes up to third order relationships such as a great grandmother, aunt, or cousin. If all females overlapping the SHR were unrelated, we assigned zero as the relatedness ratio. We did not include a focal bear's mother in relatedness ratio due to her being represented already in the maternal overlap variable. *Familiarity index* represents females that overlapped the NHR (hereafter "familiar"). We divided the number of familiar females by total females overlapping the focal individual's SHR to generate the familiarity index. If no familiar females overlapped the SHR, we assigned zero. We did not include a focal bear's mother in the familiarity index due to her existing representation in the maternal overlap variable. *Density difference* is the difference in local female density (total number of overlapping females) between the SHR and NHR. Obtaining the difference in density allowed us to incorporate variation in natal density among the focal females, as it represents the change in density from the NHR towards the SHR.

To test prediction 2, that is, the effect of the mother being alive or dead during the settlement period, we overlapped the SHR of the focal female with her mother's HR in the settlement year or most recent available year. We calculated an index of overlap for a focal female's SHR and her mother's HR using the following formula:

$$\left(\mathrm{O_{ij}}/\left(\mathrm{A_i}+\mathrm{A_j}\right)\right)*2,$$

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

Statistical analyses and modeling approach

To address our primary objective, the influence of the social environment in settlement decisions, we used second order resource

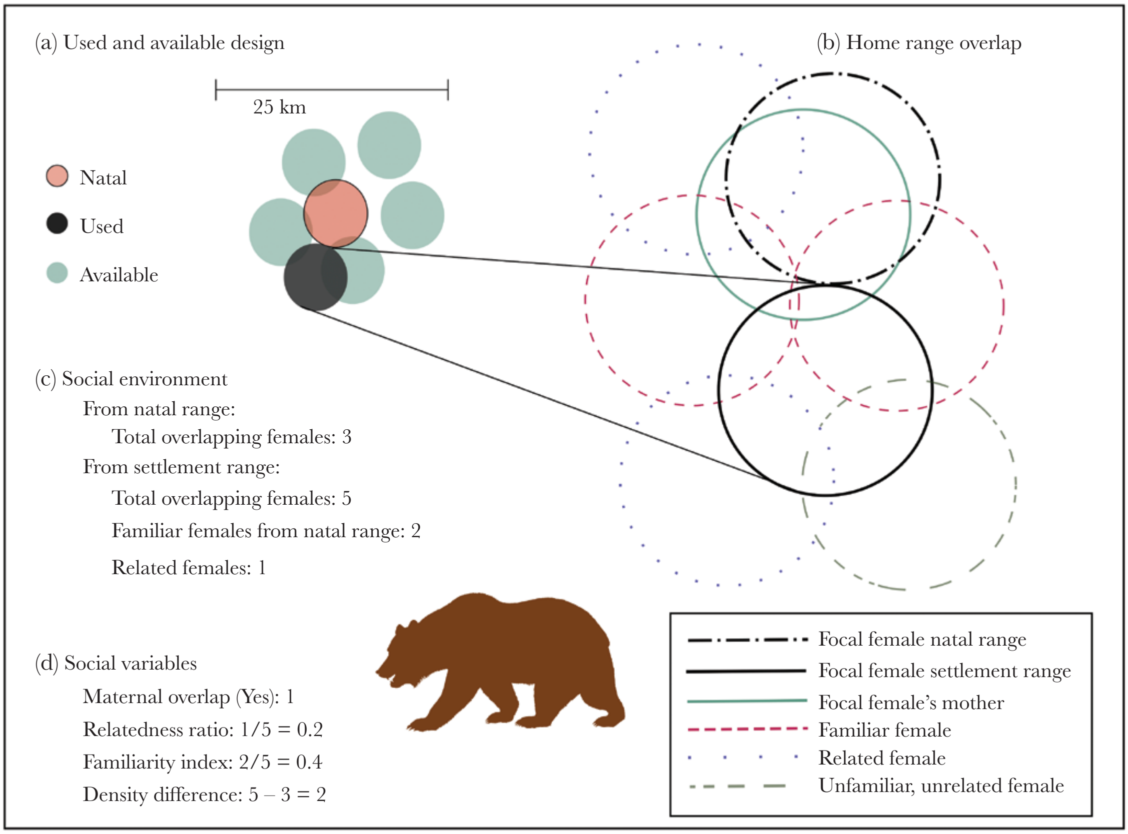

Figure 1

Schematic of how social variables were derived for the study on the influence of social environment on female brown bear settlement home range (SHR) selection. a) Used and available SHR design for the resource selection function. For each used SHR, 5 random available home ranges are created within 25 km of the natal home range. b) A focal female's natal home range (NHR) and each used and available settlement home range were overlaid with the home ranges of all other females on the landscape. c) Social environment variables were extracted based on the overlapping females, including the density (total overlapping females) in the NHR and SHR, the number of related and known females overlapping the SHR, and whether the focal female's SHR overlapped her mother's home range. d) Four social variables (maternal overlap, relatedness ratio, familiarity index, and density difference) were derived based on social environment values extracted in b. Example calculations are given below each (c) and (d).

selection functions (RSF) with a used-available design and an exponential selection function (Manly et al. 2002), which represents selection at the level of individual home ranges (Johnson 1980). The 'used' locations were the set of SHR centroids for the focal females. For each used location, we generated 5 "available" locations representing potential home range centroids where an individual could have settled (Figure 1). We based availability on empirical dispersal distances from the NHR for our focal females (range 1.3–67.7 km). We selected 25 km as the upper limit on availability as this represents the 95% distribution of distances between the NHR and SHR and reflects the average dispersal distance for females in this population (Støen et al. 2006a). We attempted to control for distance by fitting a probability distribution to the dispersal distances and randomly selecting 5 available locations weighted by probability within that buffer using the *spsample* function in the *sp* package (Pebesma and Bivand 2005). We buffered each used and available centroid by 10.5 km to generate a series of used and available SHR polygons from which we extracted our social variables (Figure 1). We used the *glmmTMB* package (Brooks et al. 2017) to fit a logistic generalized linear mixed model with the binary response variable of used (1) and available (0) SHR. As predictor variables, we used *maternal overlap*, *relatedness ratio*, *familiarity index*, *density difference,* and a random intercept for focal individual (focalID). We included an additional random intercept for the number of years since family break up (1–4) to account for variability among individuals. We standardized all continuous predictor variables to have a mean of zero and a standard deviation of one. Due to the importance of habitat features for survival (DeCesare et al. 2014; Matthiopoulos et al. 2015), we initially included the following habitat covariates (measured as percent cover over the home range) in our model: built (anthropogenic) environment, cultivated land, mature forest, young forest, clearcuts, and bogs (see Supplementary S1 for details).

Before modeling, we checked all predictor variables for collinearity by verifying that all variables had variance inflation factors (VIF) < 2. We conducted further analyses investigating the relationship between relatedness ratio and familiarity index because there was potential overlap in those two variables (Supplementary S2). We first fit a base model that included all social predictor variables and no interactions and then sequentially fit the base model containing one interaction term for each combination of predictor variables. We fit only one interaction term per model due to sample size limitations. We did not have a priori hypotheses regarding the relative importance among the social variables, so we fit the base model and fit all possible subsets of the base model using the *MuMIn* package (Bartoń 2018) and ranked them according to Akaike's Information Criterion adjusted for small sample sizes (AICc, Hurvich and Tsai 1995). We retained models within $\Delta\text{AICc} \leq 2$ of the highest-ranked model for further assessment and interpretation (Burnham and

Anderson 2004). We calculated Nakagawa's pseudo R^2 (Nakagawa and Schielzeth 2013) to evaluate goodness of fit and explanatory power. We averaged coefficients and 95% confidence intervals (CI) over the retained model set for each variable. CIs containing zero were considered uninformative (Arnold 2010).

We employed a bootstrapping modeling procedure to assess relative variable importance. For each permutation, we randomly sampled with replacement observations from 90% of the focal bears in the study. In each permutation, we fit the base model and all possible subsets, ranked them via AICc, and retained those with ΔAICc ≤ 2 (Grueber et al. 2011). We then averaged each set of top models and summed model weights by variable, that is, whether a focal variable was contained in the model. After 1000 permutations, we took the mean value of each variable's summed Akaike weight to measure the relative importance among the social variables (Galipaud et al. 2014).

To assess how the mother's presence on the landscape influences settlement decisions, we compared the overlap index between females whose mothers were alive during settlement with those whose mothers died before that period with a Wilcoxon test. One female in each group had overlap values of zero, so we removed them from the analysis to avoid "ties." We performed all statistical analyses in R 3.6.2 (R Core Team 2019).

RESULTS

We did not detect selection or avoidance for any habitat features at the second order scale and model selection showed the highest support for the model containing only social variables (see Supplement S1 for a detailed description on methodology and results from habitat modeling). We did not detect any informative interactions between the predictor variables (Table S2), and the base model received greater support than any models containing an interaction term. We also did not see an effect in the random intercept for a year since the family breakup (Table S3) and the base model received higher support than the model with the additional random intercept.

Two models had ΔAICc ≤ 2; each of the predictor variables appeared in at least one top model (Table 1). Akaike weights of the top models indicated no clear support for a single model, so we present coefficients from the averaged model (Figure 2). Female bears selected for SHR that overlapped mothers ($\beta = 1.03$, 95% CI: 0.3–1.67), familiar females ($\beta = 0.8$, CI:0.44–1.17), and areas with higher density relative to their natal range ($\beta = 0.67$, CI: 0.32–1.03), but were indifferent for overlap with related females ($\beta = -0.19$, CI: −0.52to 0.15). The results of the model bootstrapping procedure indicated that *maternal overlap, density difference,* and *familiarity index* had the highest variable importance (Table 2). In contrast, the CI of *relatedness* ratio contained zero and had the least relative importance in the bootstrapping procedure (Table 2).

Probability of selection for SHR increased with maternal overlap, presence of familiar females, and areas with higher density relative to their natal range, but not for related females (Figure 3). Pseudo R^2 values for the top models indicated that modeling social factors alone explains 27% of variation in second order settlement patterns for female bears (Table 1).

The overlap index between focal females SHR and their mothers' home ranges averaged 0.41 ± 0.23 (range 0–0.83). Females whose mothers died before the settlement year ($n = 20$) had a higher degree of overlap with their mother's last known home range (mean: 0.49 ± 0.24) than females whose mothers were alive ($n = 32$) in the settlement period (mean: 0.36 ± 0.2, $W = 184$, $p = 0.01$, Figure 4).

Table 1

Resource Selection Function model results showing the influence of the social landscape on female brown bear selection of settlement home ranges in Sweden, 1998–2018. Model selection table shows the two most supported models (highest-ranked model and others ΔAICc < 2) plus the null model. Values shown are the degrees of freedom, log likelihood, AICc, ΔAICc, model weight, and Nakagawa's Pseudo R^2 for the marginal (fixed effects) model. Social variable codes are as follows: densDiff = difference in density from SHR to NHR, famIx = familiarity index, matOver = maternal overlap, relRatio = relatedness ratio

Model set	K	logLik	AIC_c	ΔAIC_c	W_i	Pseudo R^2
densDiff + famIx + matOver	5	−131.72	273.62	0.00	0.6	0.27
densDiff + famIx + matOver + relRatio	6	−131.11	274.48	0.86	0.39	0.27
Null model	2	151.39	306.81	33.2	0	0

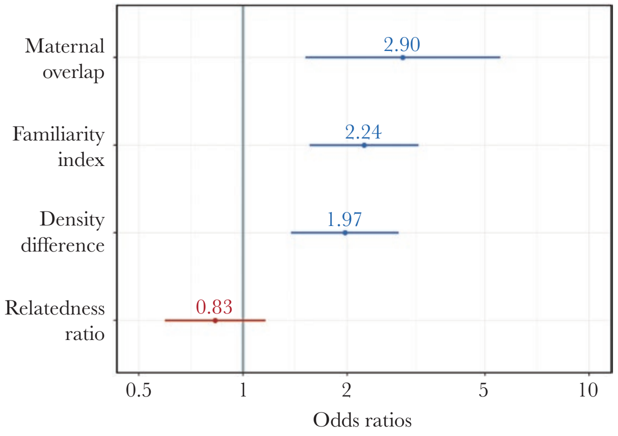

Figure 2

Plot of fixed effect coefficient estimates with 95% confidence intervals (coefficients were exponentiated to derive odds ratios) from a resource selection function averaged model estimating the influence of social variables on female brown bear selection of settlement home ranges in Scandinavia (from 1998–2018). Fixed effects were standardized to a mean of zero and a standard deviation of one. Variables with confidence intervals not overlapping one are considered informative. Exponentiated 95% confidence interval values are 1) maternal overlap (1.51–5.54), 2) familiarity index (1.56–3.22), 3) density difference (1.37–2.82), and 4) relatedness ratio (0.59–1.16).

DISCUSSION

Our study provides evidence that the social environment influences settlement decisions of a large, non-territorial, solitary-living mammal. We found that female brown bears selected SHRs that overlapped their mother's home range (support P1). When mothers were removed from the landscape, that is, through hunting, female offspring selected SHRs with greater spatial overlap of their mother's range, as compared with when mothers were alive (support P2). In contrast, we did not find that females selected SHRs that overlapped related females (no support P3). Instead, females selected SHRs that overlapped familiar females (support P4). Lastly, we found evidence that females used density cues when selecting their SHR, but did not select for lower density areas (no support P5).

We found that the strongest predictor of female SHR selection was overlap with the maternal range. In many mammals, females settle in home ranges that overlap their mother's home range, that is, are philopatric, (Arnaud et al. 2012; Clutton-Brock and Lukas 2012), likely because resource distribution in that area is most familiar and they receive a certain amount of social tolerance from their mother, as suggested by the resident fitness hypothesis (Wiggett and Boag 1992). Studies from small rodents demonstrate clear fitness benefits from philopatry: female bushy-tailed woodrats (*Neotoma cinerea*) who spatially associated with their mothers after independence had increased over-winter survivorship and reduced reproductive failures compared with those that settled in areas lacking their mother (Moses and Millar 1994). Presence of mothers was related to higher survival in female grey mouse lemurs (*Microcebus murinus*), with daughters of present mothers more likely to survive to the breeding season (Lutermann et al. 2006). Familiarity with resources of an area conveys a considerable advantage to an individual establishing an SHR (Waser and Jones 1983), such as foraging spots (Ashbury et al. 2020), or refugia from predators (Gehr et al. 2020). For example, female orangutans (*Pongo pygmaeus*) show high spatial overlap with their maternal range from independence through sexual maturity and benefit from the mother's high social tolerance and the familiarity with foraging locations (Ashbury et al. 2020). Among Ursids, females often select an SHR that overlaps with their mothers (Powell 1987; McLellan and Hovey 2001; Støen et al. 2005). However, tolerance is dependent on a mother's ability to recognize her independent offspring (Waser and Jones 1983). Kin recognition, likely based on olfactory cues (Jojola et al. 2012), has been suggested in our study population (Zedrosser et al. 2007; Swenson and Haroldson 2008). An individual's mother is the most familiar on the landscape other than full siblings. Thus, it is plausible that female brown bears recognize their independent offspring and tolerate home range overlap with them.

Table 2

Results of averaging the top models of the influence of the social landscape on female brown bear settlement home range selection in Scandinavia (between 1998 and 2018). Summary of parameter estimates, standard error, and 95% confidence interval (CI) after model averaging each covariate on probability of use for used and available settlement home ranges. Relative importance of each variable is from their summed Akaike weights. Variable codes are as follows: matOver = maternal overlap, famIx = familiarity index, densDiff = change in density from settlement to natal home range, relRatio = relatedness ratio

Variable	β	SE	CI	Relative importance
matOver	1.03	0.32	0.33–1.67	0.95
famIx	0.8	0.19	0.44–1.17	0.99
densDiff	0.67	0.18	0.32–1.03	0.99
relRatio	−0.19	0.17	−0.52 to 0.15	0.34

Our strongest evidence for the influence of the social environment was the difference in settlement patterns based on whether or not an individual's mother was present and alive on the landscape during the settlement period. If a focal female's mother had died before settlement, the settling female established an SHR with greater overlap of her deceased mother's last known home range.

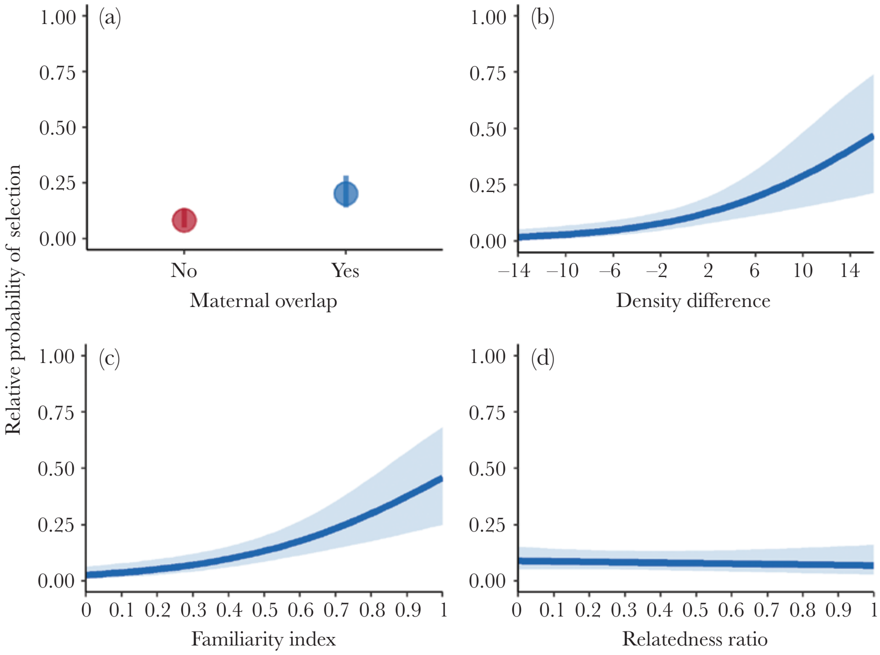

Figure 3

Relative probability of a female brown bear selecting a settlement home range (SHR) dependent on a) overlapping her mother's home range, b) the difference in female bear density in the SHR relative to her natal home range, c) the proportion of familiar (individuals a focal female had natal home range overlap with) to total females overlapping the SHR, and d) the proportion of related females to total females overlapping the SHR. Data are predicted from a resource selection model for the female Scandinavian brown bear population between 1998–2018.

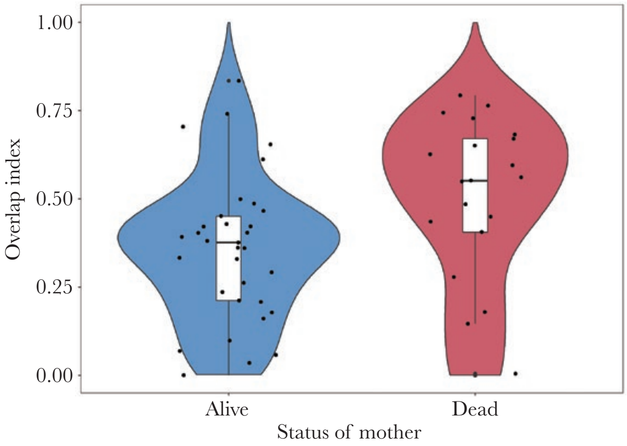

Figure 4

Violin plot showing relationship between the amount of overlap between the settlement home range of a female brown bear and the home range of her mother. The *x* axis indicates whether the mother of the female was alive during the settlement period or had died before settlement. Overlap index values on the *y* axis are between 0 and 1. Mean overlap for females with living mothers was 0.36 (±0.2); mean overlap for females whose mother died before settlement was 0.49 (±0.24).

Conversely, for focal females with living mothers in the settlement period, SHR had less overlap with their mother's range, which indicates a mother-offspring conflict over space (Frank et al. 2017). Similar patterns have been found in solitary rodents (Lutermann et al. 2006; Arnaud et al. 2012; Sakamoto et al. 2015). For example, experimental removal of Japanese wood mice (*Apodemus speciosus*) mothers inhibited natal dispersal in their female offspring, whereby females whose mothers were present dispersed more frequently and longer distances (Sakamoto et al. 2015). In American black bears, females partially overlapped their mother's home range although she was alive, but took over her home range after her death (Powell 1987). Our results suggest a tradeoff in which mothers may limit home range sharing to maximize their own fitness. Parent-offspring conflict theory (Trivers 1974) dictates that conflict is expected between mothers and their independent daughters. A settling female should attempt to maximize her fitness by selecting an SHR with the greatest possible overlap with her mother's range, providing she incurs no related costs. Delayed primiparity of philopatric females has been shown in this population, indicating a potential cost of selecting an SHR overlapping their mother (Støen et al. 2006b). A young female may be compensated for this cost by increased survival and higher future reproduction, possibly due to familiarity with the resources available in their mother's range. Mothers, however, are expected to limit the amount of overlap to any given daughter to increase her inclusive fitness. A mother that allows her independent daughter greater access to the resources in her HR might decrease her own future survival and reproduction (Trivers 1974). It is possible that mothers are tolerating overlap in marginal areas of their home range although maintaining exclusive use of a "core" area, thereby minimizing their fitness costs, however, we did not investigate these characteristics within home ranges.

We further found that familiarity but not relatedness was selected for in SHR and no interaction between being related and familiar. Thus, familiarity alone appears to be a stronger social cue for female bears in settlement decisions. Early associations as juveniles with overlapping females can be important for discrimination of familiar neighbors. Even a short period of association may allow the recognition of familiar individuals, as shown in Grey seals (*Halichoerus grypus*) (Robinson et al. 2015). This highlights the possibility of young individuals gathering information on familiar conspecifics that they can use later in life. In ursids, information about the social environment is most likely obtained via scent cues and olfactory communication (Clapham et al. 2012; Morehouse et al. 2021), but, given females' extensive home range overlap, it may also be gained through direct social contact. Future research should directly investigate the use of scent cues and rates of direct contact by female bears.

The benefits of nearby kin have been well documented (Clutton-Brock 2009; Dobson et al. 2012). However, it is becoming increasingly clear that familiarity with other individuals, independent of their relatedness, may give fitness benefits (Ylönen et al. 1990; Shier and Swaisgood 2012). Higher reproductive success in female great tits (*Parus major*) was correlated with a higher number of familiar neighbors and whether their nearest neighbor was familiar (Grabowska-Zhang et al. 2011). Familiarity with conspecifics appears to confer fitness benefits for both survival and reproduction for birds and small mammals (Grabowska-Zhang et al. 2011; Shier and Swaisgood 2012; Siracusa et al. 2021), but it is unknown if this occurs in large mammals. Further research is needed to determine whether settling near closely related or familiar females provides enhanced fitness for dispersing females.

Two potential mechanisms may explain why females select SHR overlapping familiar females but not related females. The first mechanism is the "dear enemy" effect in which an individual will exhibit reduced aggression towards their familiar neighbors compared with strangers (Temeles 1994). This is mostly seen in territorial species (Rosell and Bjørkøyli 2002; Benten et al. 2020; Vázquez et al. 2020). Bears are non-territorial, but previous research has indicated that aggression may be a mechanism for explaining the socio-spatial patterns exhibited in brown bears (Støen et al. 2005). Intraspecific aggression in brown bears has been reported in several populations across their geographic range (Miller 1985; McLellan 1994; Swenson et al. 2001). If aggressive encounters are reduced by selecting SHR overlapping familiar neighbors, this benefits the focal female. Brown bear females exhibit strong site fidelity and stable home ranges are conducive to establishing familiarity with neighboring females. The second mechanism is through familiarity-based kin recognition, that is, discrimination of kin based on association or familiarity (Tang-Martinez 2001). This alternative to phenotypic kin recognition is location-dependent; if an individual is adjacent, they are likely related (Mateo 2004). Tolerance behavior towards neighboring females can be maintained in populations that exhibit philopatry due to the probability that neighbors are closely related (Waser and Jones 1983). If familiars are also relatives, there could be an increase in inclusive fitness. Due to the generally philopatric nature of female brown bears, related individuals are typically clustered spatially (Støen et al. 2005). Despite the suggestion of kin recognition in our population, our results do not suggest its occurrence among female brown bears, but there is support for individual recognition through prior association.

We predicted that females would detect density differences on the landscape and select SHR in areas of lower density, as suggested by previous research (Støen et al. 2006a); however, we did not find support for that in our study. Although females did appear to respond to density in this study population, contrary to our prediction, they selected SHR in areas with higher density relative to their natal ranges. Females possibly settle in areas with higher female density because it could indicate higher quality habitat. Although male bears may disperse into areas lacking conspecifics

(Zedrosser et al. 2007), this is not seen with females. Additional research investigating the relationship between population density and habitat quality could help shed light on this settlement pattern.

Strikingly, females do not appear to use non-social environmental cues (i.e., habitat types) when selecting SHR at the second order. Human-mediated homogenization of landscapes through large scale forestry in the study area has created consistent cut blocks and regenerating stands (Josefsson et al. 2010). This suggests that important heterogeneity cues for settlement decisions occurs within the social landscape. Changes in the social makeup of this population are largely driven by hunting (Gosselin et al. 2015; Bischof et al. 2018). As adult females are removed from the population via harvest, surviving females will shift their home ranges to “fill in” vacancies left by the deceased female (Frank et al. 2017). This annual variation in the distribution of the population would make sensitivity towards and use of cues regarding the social environment particularly valuable not only for settlement decisions but also when expanding or shifting the home range configuration over time. Our study highlights that the social environment, beyond conspecific presence or density, is an important consideration when describing settlement decisions and dispersal patterns, and that such information is important for solitary-living species.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Supplement S1: deriving and modeling habitat variables in resource selection functions of female brown bear settlement home range selection

Methods

We obtained a 10 m resolution landcover raster, the National Landcover Database (NMD), covering all of Sweden from the Swedish Environmental Protection Agency (Naturvårdsverket 2018). Landcover in the NMD was classified by the Swedish Environmental Protection Agency into 25 thematic classes in three hierarchical levels. Details on the NMD and the classification process can be found at http://www.swedishepa.se/State-of-the-environment/Maps-and-map-services/National-Land-Cover-Database/. We selected six landcover classes of interest for our study: 1) anthropogenic features (built environment), 2) cultivated areas, 3) young forest, 4) mature forest, 5) clearcuts, and 6) bogs.

We overlaid each used and available settlement home range (SHR) polygon (centroids with a 10.5 km buffer) with the landcover raster. We extracted all of the landcover data within the SHR polygon using the 'extract' function in the *velox* package (Hunziker 2018). We used a custom function (which can be accessed at https://mhallwor.github.io/_pages/activities_ExtractingRasterValues) to summarize the amount of each landcover class within the SHR polygon. The result was a dataframe containing the total percent cover of each of the six landcover classes of interest for each used and available SHR.

We added percent cover of each landcover class to our dataframe containing the social variables maternal overlap, relatedness ratio, familiarity index, and density difference that were previously calculated (see main text for details) in each used and available SHR. We import this dataframe below for performing resource selection function modeling and model selection in this supplement.

Load required packages:

```
library(car)
library(glmmTMB)
library(MuMIn)
library(AICcmodavg)
```

Import and prep data:

```
# load data frame containing social and habitat variables

combinedDF <- readRDS("objects/distAdjustHab.rds")

head(combinedDF)
```

```
##   focalID mother used        built         cult matureForest   clearcut
## 1   W0010  W9403    0 0.0011079662 0.0041933951    0.5844815 0.11326936
```

```
## 2   W0010  W9403    0 0.0004824466 0.0008474918    0.5415143 0.08147845
## 3   W0010  W9403    0 0.0009026761 0.0008696514    0.5001504 0.12050909
## 4   W0010  W9403    0 0.0002072877 0.0016876523    0.6635794 0.11157216
## 5   W0010  W9403    0 0.0002017819 0.0013299263    0.6551969 0.11181653
## 6   W0010  W9403    1 0.0004751866 0.0008494649    0.6426707 0.11990849
##   youngForest       bog     famIx  relRatio matOver densDiff
## 1  0.10975652 0.1075296 0.3684211 0.7222222       1        6
## 2  0.18679674 0.1845404 0.2727273 0.3636364       0       -2
## 3  0.15462915 0.2147048 0.2500000 0.4545455       1       -1
## 4  0.04255452 0.1058653 0.2500000 0.6000000       1        3
## 5  0.03469548 0.1159035 0.2857143 0.6923077       1        1
## 6  0.05237144 0.1348704 0.2500000 0.6000000       1        3
```

```r
# standardize continuous variables to mean of zero and standard deviation of one

combinedDF[ , c(4:11,13) ]<- scale(combinedDF[ , c(4:11,13)])

head(combinedDF)
```

```
##   focalID mother used      built       cult matureForest    clearcut
## 1   W0010  W9403    0 -0.3734486 -0.2648155   0.30803922  0.09621241
## 2   W0010  W9403    0 -0.4303277 -0.5497270  -0.05917673 -0.77266548
## 3   W0010  W9403    0 -0.3921158 -0.5478400  -0.41268907  0.29408164
## 4   W0010  W9403    0 -0.4553482 -0.4781854   0.98404243  0.04982609
## 5   W0010  W9403    0 -0.4558489 -0.5086466   0.91240235  0.05650509
## 6   W0010  W9403    1 -0.4309879 -0.5495590   0.80534795  0.27766638
##     youngForest         bog       famIx  relRatio matOver    densDiff
## 1  0.0008776213 -0.46361993  0.09736696 1.5950891       1  1.45939654
## 2  1.5315850141  0.77749239 -0.30902781 0.2401396       0 -0.07356864
## 3  0.8924491631  1.26362381 -0.40554657 0.5836479       1  0.11805201
## 4 -1.3343549496 -0.49044124 -0.40554657 1.1332612       1  0.88453460
## 5 -1.4905056413 -0.32866475 -0.25387423 1.4820543       1  0.50129330
## 6 -1.1393031643 -0.02299268 -0.40554657 1.1332612       1  0.88453460
```

Check predictor variables for collinearity:

```r
vif(lm(used ~ built + cult + matureForest + clearcut + youngForest + bog
       + matOver + relRatio + famIx + densDiff,
       data = combinedDF))
```

```
##        built         cult matureForest     clearcut  youngForest          bog
##     2.860013     3.094965     1.286195     1.401453     1.573142     1.659896
##      matOver     relRatio        famIx     densDiff
##     1.136876     1.122107     1.197251     1.360491
```

built & cult have VIF > 2. All remaining predictor variables have VIF values < 2.

Check for correlation between built & cult:

```r
cor(combinedDF$built, combinedDF$cult)
```

```
## [1] 0.7873743
```

built & cult are too highly correlated to fit in the same model. Variables will be modeled separately.

Fit full model with social and habitat models:

```
combined.rsfA <- glmmTMB(used ~  built +  matureForest + clearcut +
                        youngForest + bog + matOver + relRatio +
                          famIx + densDiff + (1|focalID),
                        family = binomial(),
                        data = combinedDF,
                        na.action = na.fail)
summary(combined.rsfA)
```

```
##  Family: binomial  ( logit )
## Formula:          used ~ built + matureForest + clearcut + youngForest + bog +
##     matOver + relRatio + famIx + densDiff + (1 | focalID)
## Data: combinedDF
##
##      AIC      BIC   logLik deviance df.resid
##      280      322     -129      258      325
##
## Random effects:
##
## Conditional model:
##  Groups  Name        Variance  Std.Dev.
##  focalID (Intercept) 1.257e-09 3.546e-05
## Number of obs: 336, groups:  focalID, 56
##
## Conditional model:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -2.45212    0.28283  -8.670  < 2e-16 ***
## built        -0.13402    0.24764  -0.541  0.58839
## matureForest  0.06486    0.18345   0.354  0.72368
## clearcut     -0.06881    0.19135  -0.360  0.71914
## youngForest   0.38120    0.19994   1.907  0.05658 .
## bog          -0.31810    0.22050  -1.443  0.14912
## matOver       1.00977    0.33582   3.007  0.00264 **
## relRatio     -0.15599    0.17262  -0.904  0.36619
## famIx         0.83097    0.19275   4.311 1.63e-05 ***
## densDiff      0.73993    0.19756   3.745  0.00018 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
# Pseudo R Squared for GLMMs

r.squaredGLMM(combined.rsfA)
```

```
##                   R2m       R2c
## theoretical 0.3127530 0.3127530
## delta       0.1721432 0.1721432
```

```r
combined.rsfB <- glmmTMB(used ~  cult + matureForest + clearcut +
                        youngForest + bog + matOver + relRatio +
                          famIx + densDiff + (1|focalID),
                        family = binomial(),
                        data = combinedDF,
                        na.action = na.fail)
summary(combined.rsfB)
```

```
##  Family: binomial  ( logit )
## Formula:
## used ~ cult + matureForest + clearcut + youngForest + bog + matOver +
##     relRatio + famIx + densDiff + (1 | focalID)
## Data: combinedDF
##
##      AIC      BIC   logLik deviance df.resid
##    278.9    320.9   -128.4    256.9      325
##
## Random effects:
##
## Conditional model:
##  Groups  Name        Variance  Std.Dev.
##  focalID (Intercept) 7.381e-10 2.717e-05
## Number of obs: 336, groups:  focalID, 56
##
## Conditional model:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -2.48805    0.28771  -8.648  < 2e-16 ***
## cult         -0.33436    0.29609  -1.129 0.258801
## matureForest  0.06560    0.18072   0.363 0.716632
## clearcut     -0.04429    0.18760  -0.236 0.813347
## youngForest   0.35675    0.19978   1.786 0.074147 .
## bog          -0.37323    0.22441  -1.663 0.096270 .
## matOver       1.02510    0.33630   3.048 0.002302 **
## relRatio     -0.17442    0.17296  -1.008 0.313246
## famIx         0.82318    0.19354   4.253 2.11e-05 ***
## densDiff      0.71792    0.19757   3.634 0.000279 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```r
# Pseudo R Squared for GLMMs

r.squaredGLMM(combined.rsfB)
```

```
##                   R2m       R2c
## theoretical 0.3391719 0.3391719
## delta       0.1899676 0.1899676
```

Fit model with only habitat variables:

```r
hab.rsfA <- glmmTMB(used ~  built + matureForest + clearcut +
                        youngForest + bog + (1|focalID),
                        family = binomial(),
                        data = combinedDF,
                        na.action = na.fail)
summary(hab.rsfA)
```

```
##  Family: binomial  ( logit )
## Formula:          used ~ built + matureForest + clearcut + youngForest + bog +
##     (1 | focalID)
## Data: combinedDF
##
##      AIC      BIC   logLik deviance df.resid
##    310.6    337.3   -148.3    296.6      329
##
## Random effects:
##
## Conditional model:
##  Groups  Name        Variance  Std.Dev.
##  focalID (Intercept) 5.262e-10 2.294e-05
## Number of obs: 336, groups:  focalID, 56
##
## Conditional model:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)   -1.6598     0.1534 -10.823   <2e-16 ***
## built         -0.2766     0.2120  -1.305   0.1921
## matureForest   0.1105     0.1587   0.696   0.4863
## clearcut      -0.1334     0.1705  -0.782   0.4341
## youngForest    0.2782     0.1801   1.545   0.1223
## bog           -0.4344     0.2018  -2.152   0.0314 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```r
# Pseudo R Squared for GLMMs

r.squaredGLMM(hab.rsfA)
```

```
##                    R2m        R2c
## theoretical 0.04677020 0.04677020
## delta       0.02192748 0.02192748
```

```r
hab.rsfB <- glmmTMB(used ~  cult + matureForest + clearcut +
                        youngForest + bog + (1|focalID),
                        family = binomial(),
                        data = combinedDF,
                        na.action = na.fail)
summary(hab.rsfB)
```

```
##  Family: binomial  ( logit )
## Formula:
## used ~ cult + matureForest + clearcut + youngForest + bog + (1 |      focalID)
## Data: combinedDF
```

```
##
##      AIC      BIC   logLik deviance df.resid
##    308.4    335.1   -147.2    294.4      329
##
## Random effects:
##
## Conditional model:
##  Groups  Name        Variance  Std.Dev.
##  focalID (Intercept) 6.411e-10 2.532e-05
## Number of obs: 336, groups:  focalID, 56
##
## Conditional model:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -1.68537    0.15785 -10.677   <2e-16 ***
## cult         -0.43349    0.24405  -1.776   0.0757 .
## matureForest  0.09226    0.15834   0.583   0.5601
## clearcut     -0.08761    0.16765  -0.523   0.6012
## youngForest   0.24305    0.18027   1.348   0.1776
## bog          -0.47299    0.20527  -2.304   0.0212 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```r
# Pseudo R Squared for GLMMs

r.squaredGLMM(hab.rsfB)
```

```
##                    R2m        R2c
## theoretical 0.07290817 0.07290817
## delta       0.03468707 0.03468707
```

Fit model with only social variables:

```r
soc.rsf <- glmmTMB(used ~  matOver + relRatio + famIx
                   + densDiff + (1|focalID),
                        family = binomial(),
                        data = combinedDF,
                        na.action = na.fail)
summary(soc.rsf)
```

```
##  Family: binomial  ( logit )
## Formula:          used ~ matOver + relRatio + famIx + densDiff + (1 | focalID)
## Data: combinedDF
##
##      AIC      BIC   logLik deviance df.resid
##    274.2    297.1   -131.1    262.2      330
##
## Random effects:
##
## Conditional model:
##  Groups  Name        Variance  Std.Dev.
```

```
##  focalID (Intercept) 7.999e-10 2.828e-05
## Number of obs: 336, groups:  focalID, 56
##
## Conditional model:
##             Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -2.4110     0.2748  -8.774  < 2e-16 ***
## matOver       1.0633     0.3306   3.216 0.001298 **
## relRatio     -0.1804     0.1666  -1.083 0.278703
## famIx         0.8068     0.1850   4.361  1.3e-05 ***
## densDiff      0.6730     0.1807   3.724 0.000196 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
# Pseudo R Squared for GLMMs

r.squaredGLMM(soc.rsf)
```

```
##                   R2m       R2c
## theoretical 0.2687401 0.2687401
## delta       0.1437782 0.1437782
```

Model selection

Check for most supported model from the five models.

```
mList <- list(combined.rsfA, combined.rsfB, hab.rsfA, hab.rsfB, soc.rsf)

aictab(mList)
```

```
##
## Model selection based on AICc:
##
##       K   AICc Delta_AICc AICcWt Cum.Wt      LL
## Mod5  6 274.48       0.00   0.90   0.90 -131.11
## Mod2 11 279.71       5.23   0.07   0.96 -128.45
## Mod1 11 280.80       6.32   0.04   1.00 -128.99
## Mod4  7 308.75      34.27   0.00   1.00 -147.20
## Mod3  7 310.93      36.45   0.00   1.00 -148.29
```

“‘

The model containing only social variables has the highest support.

Conclusion

Modeling habitat variables alone in a resource selection function explains very little variation in female brown bear settlement patterns, as evidenced by the pseudo r squared values of 0.05 and 0.08. Combining habitat variables with social variables in a resource selection function did not result in greater model support; the delta AICc was greater than 5 from the model only containing social variables. Due to the lack of explanatory power and support after including habitat variables, we move forward in our analysis using only social variables.

References

Hunziker, P, 2018. velox: fast raster manipulation and extraction. R package version 0.2.0.9002.

Naturvårdsverket, 2018. National Land Cover Database. http://www.swedishepa.se/State-of-the-environment/Maps-and-map-services/National-Land-Cover-Database/

Table S1. Description of social variables used to evaluate female brown bear selection of settlement home ranges in Sweden, 1998-2018. Statistics are shown for the realized settlement home ranges (SHR; i.e. ‘used’ home ranges from resource selection function). Min = minimum, max = maximum, SD = standard deviation. Maternal overlap is given as the proportion of females that had mothers present on the landscape and had SHR overlapping their mother’s home range (n = 32 present mothers, n = 4 present without overlap, n = 20 absent mothers).

Variable	**Type**	**Min**	**Max**	**Mean**	**SD**
Maternal overlap: Home range of mother overlaps focal female’s SHR	Binary	0	1	0.89	-
Familiarity Index: Proportion of known to total females home ranges overlapping focal females SHR	Continuous	0	1	0.44	0.22
Relatedness Ratio: Proportion of related to total female home ranges overlapping focal females SHR	Continuous	0	0.83	0.3	0.23
Density Difference: Difference in density between focal females SHR and natal home range (NHR) SHR density – NHR density	Continuous	-9	12	0.3	4.41

Table S2. Results from resource selection function models of female Scandinavian brown bear settlement home range selection. Interactions were fit individually due to model convergence issues related to sample size. Interactions are shown in italics and significant p-values (≤ 0.05) are shown in bold. None of the interaction terms in the models were significant and the base model had the lowest AICc value, i.e. was the most supported model. Familiarity index, maternal overlap, and density difference were significant in all models.

Model	**Term**	**β**	**Std Error**	**P Value**	**CI**	**AICc**
Base Model	famIx	0.806	0.185	< **0.001**	0.44 – 1.17	**274.5**
	relRatio	-0.185	0.171	0.279	-0.52 – 0.15	
	matOver	1.063	0.331	**0.001**	0.42 – 1.71	
	densDiff	0.678	0.182	< **0.001**	0.32 – 1.04	
Interaction 1	famIx	0.801	0.185	< **0.001**	0.44 – 1.16	276.5
	relRatio	-0.251	0.278	0.366	-0.8 – 0.29	
	matOver	1.068	0.333	**0.001**	0.42 – 1.72	
	densDiff	0.677	0.182	< **0.001**	0.32 – 1.03	
	matOver:relRatio	0.109	0.355	0.758	-0.59 – 0.8	
Interaction 2	famIx	0.785	0.221	< **0.001**	0.35 – 1.22	276.5
	relRatio	-0.188	0.172	0.275	-0.53 – 0.15	
	matOver	1.045	0.347	**0.003**	0.36 – 1.72	
	densDiff	0.685	0.186	< **0.001**	0.32 – 1.05	
	matOver:famIx	0.057	0.336	0.865	-0.6 – 0.72	
Interaction 3	famIx	0.811	0.187	< **0.001**	0.44 – 1.18	275.8
	relRatio	-0.19	0.172	0.269	-0.53 – 0.15	
	matOver	1.139	0.343	< **0.001**	0.47 – 1.81	
	densDiff	0.851	0.274	**0.002**	0.31 – 1.39	
	matOver:densDiff	-0.279	0.326	0.391	-0.92 – 0.36	
Interaction 4	famIx	0.834	0.198	< **0.001**	0.45 – 1.22	276.4
	relRatio	-0.213	0.185	0.249	-0.57 – 0.15	
	matOver	1.057	0.33	**0.001**	0.41 – 1.7	
	densDiff	0.704	0.194	< **0.001**	0.32 – 1.08	
	famIx:relRatio	0.069	0.173	0.688	-0.27 – 0.41	
Interaction 5	famIx	0.827	0.186	< **0.001**	0.46 – 1.19	275.1
	relRatio	-0.157	0.171	0.36	-0.49 – 0.18	
	matOver	1.064	0.332	**0.001**	0.41 – 1.71	
	densDiff	0.681	0.186	< **0.001**	0.32 – 1.05	
	famIx:densDiff	0.205	0.174	0.238	-0.14 – 0.55	
Interaction 6	famIx	0.809	0.186	< **0.001**	0.44 – 1.17	276.4
	relRatio	-0.166	0.175	0.341	-0.51 – 0.18	
	matOver	1.053	0.331	**0.001**	0.41 – 1.7	
	densDiff	0.714	0.201	< **0.001**	0.32 – 1.11	
	relRatio:densDiff	-0.086	0.195	0.659	-0.47 – 0.3	

Table S3. Results of adding an additional random intercept for year since family breakup in a resource selection function for female Scandinavian brown bear settlement home range selection. The original base model is shown first, with the model containing the random intercept below (Year Model). Variable coefficients (β), standard error (SE), 95% confidence intervals (CI), p-values, and AICc values for each model are presented. Significant p-values are in bold. Variance for the random intercept for year was < 0.001. Standard deviation for the random intercept for year was < 0.001.

Model	**Term**	**β**	**SE**	**P Value**	**CI**	**AICc**
Base Model	famIx	0.806	0.185	**< 0.001**	0.44 – 1.17	274.5
	relRatio	-0.185	0.171	0.279	-0.52 – 0.15	
	matOver	1.063	0.331	**0.001**	0.42 – 1.71	
	densDiff	0.678	0.182	**< 0.001**	0.32 – 1.04	
Year Model	famIx	0.806	0.185	**< 0.001**	0.44 – 1.17	276.6
	relRatio	-0.185	0.171	0.279	-0.52 – 0.15	
	matOver	1.063	0.331	**0.001**	0.42 – 1.71	
	densDiff	0.678	0.182	**< 0.001**	0.32 – 1.04	

Article 2

Hansen, J.E., Hertel, A.G., Frank, S.C., Kindberg, J., Zedrosser, A. 2022. How familial conflict affects home range settlement and fitness in a solitary mammal residing in a human dominated landscape. Manuscript in revision at Animal Behaviour (first submitted 27 May 2022).

Familial conflict affects home range settlement and fitness of a solitary mammal

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ABSTRACT

Familial conflict, including parent-offspring conflict (POC) and sibling competition (SC), occurs when an individual maximizes their access to a limiting resource at the expense of a related individual. The role of familial conflict for competition over space as a limited resource remains relatively unexplored. In this study, we examine how familial conflict affects natal dispersal and settlement decisions of a solitary mammal, the brown bear (*Ursus arctos*), and test whether these settlement patterns covary with fitness. First, we tested whether the distance settled from the natal range was affected by aspects of POC (litter type: single vs. multiple, mother's age, and mother's living status) and SC (near vs. far sibling, body size). We then modeled how distance settled from the natal range influenced three measures of fitness: survival to reproduction, lifetime reproductive success, and lifetime survival. In line with POC, we found that daughters settled twice as far from the natal range when their mother was alive (13 km) than when she was dead (7 km). We found strong evidence for SC such that the 'close' sister settled nearly three times closer than her sibling (near = 6.92 ± 5.4 km, far = 21.3 ± 19.5 km). We found contradictory patterns in fitness outcomes based on settlement distance, such that females settling closer had higher lifetime survival but were less likely to successfully wean at least one offspring. Despite survival advantages gained by settling closer to the natal range, we found no evidence that settlement distance influenced lifetime reproductive success. Annual harvest may disrupt evolutionary processes via hunting of breeding females or through sexually selected infanticide of their offspring, thus increasing difficulties in predicting population growth and geographic expansion.

KEYWORDS

[parent-offspring conflict, sibling competition, reproductive success, dispersal, fitness]

INTRODUCTION

Parent-offspring conflict (POC) is the difference in optimal strategies for maximizing fitness for parents and their offspring (Trivers 1974). In species with only maternal care, a mother is expected to optimize her individual fitness by dividing parental investment equitably amongst her offspring, who are all equally related to her (Parker et al. 2002). However, her offspring are expected to exhibit selfishness and extract more of a given parental resource as they have more to gain from being selfish than from consigning limited resources to relatives (Kilner and Hinde 2012). This selfishness of offspring comes at the expense of their full or half-siblings (Godfray 1995). Further factors contribute to varying levels of POC, including mating system (Macnair and Parker 1978), litter size (Godfray and Parker 1992), number of litters in a lifetime (Parker et al. 2002), age of the mother (Delaney and Janzen 2020), and whether offspring disperse or remain philopatric (Kuijper and Johnstone 2012). Older mothers generally have less residual reproductive value and are expected to provide greater parental resources to offspring than younger mothers (Ronce et al. 1998; Descamps et al. 2007). For promiscuous species, POC is exacerbated by the potential for multiple paternity which reduces the degree of relatedness among siblings (Macnair and Parker 1978) and introduces additional conflict. Sibling competition (SC) is a subform of POC that may occur within or across litters (Parker et al. 2002) whereby one sibling attempts to gain a greater amount of parental investment/resource than their sibling(s) (Kilner and Hinde 2008). It is usually assumed that the larger offspring acts as the dominant sibling and acquires more parental resources (Parker et al. 1989). Inherent in SC is a limited parental resource that siblings are in competition for, with or without a parent present (Parker et al. 2002). Limiting resources may include food and shelter, or features familiar from the natal range (Lawson Handley and

Perrin 2007). In mammal species that exhibit home range overlap, natal range sharing may be another type of parental resource over which POC and SC may arise (Waser and Jones 1983; Lutermann et al. 2006).

Once an individual offspring reaches independence, one of the most important decisions it can make is where to settle on the landscape prior to the onset of breeding (Bowler and Benton 2005), often referred to as natal dispersal (Clobert et al. 2001). In solitary mammals, dispersal is typically sex-biased with males dispersing away from the natal range and philopatric females that settle in areas overlapping the natal range (Greenwood 1980). Female mammals are not strictly philopatric, however, and many species vary in rates of philopatry and dispersal (Karlin and Chadwick 2012; Denomme-Brown et al. 2020; Ducros et al. 2020). In more philopatric species, a clustered grouping of related females may occur, a so-called matrilineal assemblage (Arnaud et al. 2012; Holekamp and Sawdy 2019). This emergent pattern creates conditions where conflict and competition for space use can arise between parent and offspring and among siblings in settlement following independence (Kuijper and Johnstone 2012).

Space use conflict generally arises in POC and SC for access to resources available in the natal range (Starrfelt and Kokko 2010; Kuijper and Johnstone 2012). Greater access to natal range resources is expected to provide a fitness benefit to independent offspring due to known features such as refuge, foraging patches, and familiarity with neighbors (Harris and Murie 1984; Ratnayeke et al. 2002; Piper 2011). The resident fitness hypothesis suggests that resident females enjoy greater fitness than females that disperse due to the familiar resources within their natal site (Anderson 1989). However, resident females also compete with their mothers for limited resources (Wiggett and Boag 1992; Le Galliard et al. 2003), contributing to POC. The success of a mother's independent offspring affects her inclusive fitness (Hamilton 1964), but allowing her independent offspring to settle in or near the natal range introduces competition (Waser and Jones 1983; Kuijper and Johnstone 2012). Alternatively, inducing dispersal, an inherently risky process, may increase her offspring's mortality risk (Bonte et al. 2012) and ultimately reduce the mother's own inclusive fitness.

Studies examining POC and SC typically focus on pre-natal and natal periods (Hudson and Trillmich 2008; Roulin and Dreiss 2012). We use data from an individual-based study running more than 30 years, containing multiple generations of mothers and daughters, to investigate POC and SC in a solitary range-resident mammal, the brown bear (*Ursus arctos*). Our study population lives in a human-dominated landscape, and we investigate POC and SC in the post-natal period and how it may relate to fitness outcomes. The brown bear serves as an ideal model organism for studying POC and SC for several reasons: 1) they are long-lived and females can give birth to many litters in a lifetime, 2) litters may contain single or multiple female offspring, 3) settlement distances of females vary considerably (Zedrosser et al. 2007), and 4) there is a considerable amount of home range overlap among females, including mothers and their independent daughters.

Our first objective is to look for evidence of POC in the distance a female brown bear settles from the natal range. According to POC theory, we expect the following patterns to emerge. Mothers who have more than one female offspring in the same litter experience higher conflict due to increased demands from multiple daughters. Therefore, we predict (P1a) female offspring coming from a litter with multiple females to settle on average further from the natal range than those who were the sole female in a litter. Additionally, younger mothers are expected to have greater conflict with their female offspring due to their higher residual reproductive value compared with older mothers (Descamps et al. 2007). As such, we predict (P1b) that female offspring with younger mothers will settle further from the natal range than those with older mothers. Lastly, parent-offspring conflict ceases when the parent (mother) dies. It follows that (P1c) female offspring with living mothers will settle further from the natal range than those whose mothers have died prior to settlement. Our second objective is to look for evidence of SC in female brown bear settlement. We expect two patterns to emerge if SC for space use occurs in this system: the first is that one of the sisters in a pair will have a larger body size and the second is that one of the sisters will settle closer to the natal range than the other. We predict that (P2a) in a female sibling pair, one sister will settle a home range closer to the natal range and (P2b) larger females will settle closer to the natal range. Our third objective is to determine whether settling closer to the natal range is associated with increased fitness in female offspring, as suggested in the resident fitness hypothesis (Anderson 1989). Given that home range overlap is a cost incurred by the mother, we expect that her female offspring would have higher survival and reproduction as a result (thereby increasing the mother's inclusive fitness). We therefore predict that female offspring that settle closer to the natal range will (P3a) survive to reproduction, (P3b) have greater lifetime reproductive success, and (P3c) have higher lifetime survival. See Figure 1 for a visual description of predictions.

METHODS

Study area and population

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

Brown bears are found across North America, Europe, and Asia, and live solitarily aside from mating or rearing offspring (Steyaert et al. 2012). Female bears in the Scandinavian population typically begin mating around 5 years of age (Zedrosser et al. 2009) and may mate with multiple males during the breeding season (Bellemain et al. 2006). Females give birth while in hibernation (Friebe et al. 2001) to variable-sized litters (mean 2.26, range 1-4, (Gonzalez et al. 2012)). Offspring remain with their mother for either 1.5 or 2.5 years (Van de Walle et al. 2018). Following family breakup, independent offspring settle their own home ranges (Hansen et al. 2022). Virtually all male offspring disperse (Zedrosser et al. 2007) and rates of dispersal vary for female offspring (Støen et al. 2006a). Dispersal for female bears can occur over 2-3 years (Støen et al. 2006a) and concludes when a female settles and begins to breed. Female bears in Scandinavia commonly settle a home range overlapping their natal range (philopatry), but occasionally settle far (up to 90 km) from the natal range (Støen et al. 2006a). Females in this population are primiparous at approximately five years of age (Zedrosser et al. 2009). The greatest source of mortality in the adult population is legal hunting (Bischof et al. 2009). The study population of brown bears has been continuously monitored by the Scandinavian Brown Bear Research Project since 1985. We included marked female bears with known identities and birth/death years in this study, with associated reproduction data from 1986 to 2020. Only the females in any given litter are included in the study, as male offspring disperse on average 119 km from the natal range (Støen et al. 2006a) and do not compete for space with their mother or female siblings.

Predictor and response variables

Radiocollar data from female brown bears was obtained from 1989 to 2020 and comprises both VHF and GPS locations. Details of the capture and collaring procedure can be found in Arnemo and Evans (2017), with ethical permit by Uppsala Ethical Committee on Animal Experiments (Dnr 5.8.18-03376/2020) and capture permit under the Swedish Environmental Protection

Agency (NV-01278-22). Geolocations from VHF were collected once a week and from GPS were recorded hourly. We estimated 95% kernel density annual home ranges for study females and their mothers using the adehabitatHR library (Calenge 2006), then obtained the centroid location of the home range. Natal range centroids for study females were obtained from their mother's home range in the focal female's natal year. Settlement home range centroids were from the study female's home range at four years of age, the age before females typically begin breeding in the study area (Zedrosser et al. 2009). We then measured *distance settled from the natal range* (in km) as the straight-line distance between a study female's natal and settlement home range centroids. We use distance as a proxy for natal range overlap, as the two metrics are highly correlated ($r = -0.81$, $p < 0.001$, $n = 48$) in our study population (Supplement S1). Because density of individuals varies across the landscape, we obtained annual bear density rasters from between 1998 and 2015 derived from non-invasive genetic sampling and the Large Carnivore Observation Index (LCOI), described in Frank et al. (2017) to account for that variation. We overlaid the study female's settlement range over the density rasters and summarized the *average bear density* over that area.

From the reproductive data, we assigned a unique identifier (litter ID) for the litter a study female belonged to. Each litter was then designated as containing a sole female offspring or multiple females, *litter type*. The mother was identified for each litter (mother ID) as well as her age at the birth of the litter, *mother's age*. We then determined whether the study female's mother was alive or dead in the year prior to settlement, *mother's status*. From the litters identified with multiple females, we excluded litters with three or more female offspring and retained pairs of female siblings, assigning each a class, "settled closer" or "settled farther" based on the distance settled from the natal range, *settlement class*. We measured head circumference (cm) as a yearling for study females to represent their *body size* (Zedrosser et al. 2007). For all study females, we determined whether they *survived to reproduction* (successfully weaned at least one offspring) and, if applicable, the total number of offspring that were successfully weaned. For each female that survived to reproduction, we divided the number of offspring weaned by the number of breeding attempts to represent their *lifetime reproductive success*. We created a *lifetime survival* dataset for study females which contained their age at death or oldest known age for right censored living females and the distance settled from the natal range. In addition, we created a survival dataset to get baseline survival information for the entire marked female population.

Statistical Analyses

Prior to analysis, all continuous predictor variables were tested for collinearity and all had a variance inflation factor < 2 (Zuur et al. 2010). All categorical variables were assessed visually with continuous variables for possible collinear relationships. Additionally, continuous predictor variables were scaled by subtracting the mean and dividing by one standard deviation. To investigate potential POC in settlement distances (P1a-c), we fit generalized linear mixed effect models (GLMM) with *distance settled from the natal range* (km) as the Gamma distributed response variable and various candidate models representing predictions P1a-c. For P1a, we fit *litter type* (sole/multiple females); for P1b we included *mother's age*, and for P1c we included *mother's status* (dead/alive). The above predictions are not mutually exclusive, and it is possible that these predictor variables are simultaneously influencing settlement distance, so we fit a model containing all parent-offspring predictor variables and subsets containing unique combinations of each of the predictor variables. We also checked for possible interactions between the predictor variables. We controlled for differences in body size by including the variable *body size* in each parent-offspring model. We ranked our candidate models using AICc and retained the set within 2 ΔAICc of the most-supported model and used model averaging over the retained set for inference (Grueber et al. 2011).

To investigate the effect of sibling competition on settlement distance (P2a-b), we fit a GLMM with *distance settled from the natal range* (km) as the Gamma distributed response variable and included predictor variables *settlement class* (closer/farther) to represent P2a and *body size* for P2b. To investigate the influence of settlement distance on fitness (P3a-c), we fit a logistic GLMM with the response variable *survived to reproduction* (yes = 1, no = 0) for P3a and a zero-inflated Gamma GLMM with *lifetime reproductive success* as the response variable for P3b with *distance settled from the natal range* as the sole predictor variable. To look at survival, we used the survival dataset to fit a Weibull accelerated failure time regression (survival regression) with *distance settled from the natal range* as the predictor variable and age at death or censoring as the response variable. We initially included the term *average density* in models for P1a-c, P2a-b, and P3a-b. We did not detect an effect of *average density* in any of the models (Supplement S2), so it was ultimately excluded from our analysis. A unique *motherID* was included as a random effect term in all models and a unique *litterID* was included as a random effect in the sibling competition models. We used the R package 'glmmTMB' (Brooks et al. 2017) for fitting GLMMs and 'survival' (Therneau and Lumley 2015) to fit the survival regression. GLMMs were assessed for fit and validated using the R package 'DHARMa' (Hartig 2022). All data handling and statistical analyses were done using R version 4.1.2 (R Core Team 2021).

RESULTS

We identified 77 radio-collared females (33 sole, 44 multiple) from 35 mothers with sufficient location data to estimate settlement ranges and distance settled from the natal range at four years of age to include in parent-offspring conflict and fitness models (P1a-c, P3a-c). We found 15 female sibling pairs (n= 30) from 12 mothers with adequate data to estimate settlement ranges and distance settled from the natal range at four years of age to include in the sibling competition model (P2a-b). Median age of survival was 9 years (95% CI: 9-10, range 4-25) for our study population and 6 years (95% CI: 5-9, range: 0-25) for the general marked population of females. Females in the marked population had a survival probability of 0.603 of living to age four (when settlement was measured). See supplementary table (Table S3) for variable descriptions and summary statistics.

Parent-offspring conflict and sibling competition

There were three parent-offspring conflict models within 2 ΔAICc of the most-supported model which contained the variables *litter type*, *mother's age*, *mother's status*, and *body size* (Figure 2). After averaging the set of four models (Table 2), only *mother's status* was informative ($\beta = -0.571$, 95% CI = -1.071 - -0.071, $p = 0.025$), with study females settling closer (alive = 12.9 km, dead = 6.82 km) to the natal range if their mother had died prior to settlement (Table 3). Neither *litter type* nor *mother's age* were informative variables in the averaged model. For sibling competition, we found (Figure 3) that in pairs of female siblings, one of the pair would settle significantly closer (near = 6.92 ± 5.4 km, far = 21.3 ± 19.5 km) to the natal range ($\beta = -1.174$, 95% CI = -1.452 to -0.896, $p < 0.001$). Additionally, we found that larger females had a higher probability of settling closer to the natal range ($\beta = -0.379$, 95% CI = -0.712 to -0.045, $p = 0.026$; Table 2).

Fitness

Our fitness model for a female's probability of surviving to reproduce indicated a positive effect of distance settled from the natal range (Figure 4, $\beta = 0.586$, 95% CI = 0.033 to 1.140, $p = 0.038$), contrary to our prediction. Conversely, our survival regression showed that lifetime survival was higher for females that settle closer to the natal range (Figure 4, $\beta = -0.010$, 95% CI = -0.020 to -0.0001, $p = 0.033$). We did not find an effect of distance settled from the natal range on a female's lifetime reproductive success (Table 3).

DISCUSSION

Our results indicated support for predictions P1c, that female offspring settle closer to the natal range when their mother dies prior to settlement; P2a, that one sister in a sibling pair will settle closer to the natal range; and P2b, that larger females settle closer to the natal range. Additionally, we found support for P3c, that females settling closer to the natal range have higher lifetime survival. We failed to find support for P1a, that sole female offspring settle closer to the natal range or for P2b, that females with older mothers settle closer to the natal range. We also failed to find evidence supporting P3b, that females settling closer to the natal range have higher lifetime reproductive success. Lastly, we found contrary evidence to P3a, such that females settling closer to the natal range are less likely to survive to reproduction.

Familial conflict in space use

We found evidence for POC in female brown bear settlement, i.e. that female offspring will settle closer to the natal range if her mother dies prior to settlement (P1c). This suggests that the death of a mother releases her female offspring from conflict or competition with her (Starrfelt and Kokko 2010). Females of other species have shown similar patterns in settlement. For example, Columbian ground squirrels (*Urocitellus columbianus*) settled within their mother's home range when her death preceded settlement (Arnaud et al. 2012), Amur tigers (*Panthera tigris altaica*) may take over the natal range if their mother dies (Goodrich et al. 2010), and common lizards (*Lacerta vivipara*) disperse more often when their mother is present than when she is absent (Le Galliard et al. 2003). Previous research on our study population also showed greater overlap with the mother's range if she died prior to settlement (Hansen et al. 2022). We did not find support for P1b, that female offspring from older mothers would settle closer to the natal range. A possible reason for this is that annual harvest has resulted in a population skewed towards younger mothers on the landscape (Frank et al.

2017), potentially disrupting any patterns with age that might otherwise exist. A similar pattern was found in a study of American black bear (*Ursus americanus*), where harvest led to a younger population of mothers thereby confounding a potential link between maternal age and dispersal probability (Moore et al. 2014). Thus, while it is possible that older mothers may exhibit lower conflict over space use with their independent female offspring, such patterns are not possible to detect in populations where most females are harvested prior to attaining an advanced reproductive age (Zedrosser et al. 2013; McLellan 2015). Our failure to support P1a may be partially due to greater variation around distance settled in 'multiple' siblings than with 'sole' individuals. A visual comparison (Figure 3b) indicates that sole females settle similar distances to the "closer" sister in sibling pairs, which may help explain the results of our POC models. Other factors in addition to parent-offspring conflict may influence female brown bear settlement patterns. For example, neighboring females on the landscape (the social environment) might exert pressure on settling individuals (Støen et al. 2005; Hansen et al. 2022).

In this population, SC seems to have a clearer influence on settlement distances than POC. We found support for our predictions that between a pair of female siblings, one sibling would settle closer to the natal range (P2a) and that body size was influential in settlement (P2b). A study on white-footed mice (*Peromyscus leucopus*) found that sibling interactions appeared to be more influential on dispersal distances than conflict with the mother (Jacquot and Vessey 1995). If a "dominant" sibling is able to settle near the natal range and her sister is forced to settle farther away, it effectively relaxes competition for space use with the mother and potentially increases inclusive fitness (Cote and Clobert 2010). Viewed from a kin selection perspective, the dispersing sister reduces kin competition by settling away from her philopatric sibling (Cote and Clobert 2010; Waser et al. 2013). We found that body size was found to influence settlement distance in pairs of female siblings, however the effect of body size was greater for the “farther” sister in a pair (Figure 3a). This suggests that size alone cannot explain which sister is able to settle closer to the natal range. Previous research on this study population found that within female sibling pairs, one sibling had closer spatial proximity to the mother, which may have secured a more favorable settlement location in the future (Zedrosser et al. 2007). Future research should investigate other mechanisms that might influence dominance in female sibling pairs, e.g. personality (Hudson et al. 2011) or agonistic interactions (Drummond 2006). It is generally thought that dispersal and settlement are driven by multiple factors (Matthysen 2012) and the results of our study agree with that premise. We have found evidence that settlement distance is under both maternal and offspring control. Although we did not detect density effects in our study, previous research on this population suggests that settlement is at least partially mediated by neighboring females on the landscape (Støen et al. 2005; Hansen et al. 2022). Previous research points to this population as being near or at carrying capacity (Zedrosser et al. 2006), but that was prior to an increase in hunting intensity and subsequent population decline (Gosselin et al. 2015). It is possible that in a population with regular turnover and likely below carrying capacity, conflict and competition for space use is relatively low.

Space use & fitness in a harvested population

For our third objective, we found mixed evidence of resident fitness in our population of female bears. We discovered that females have a clear survival advantage when settling closer to the natal range. However, that advantage does not equate to higher reproduction, either in survival to reproduction or lifetime reproductive success. How can females live longer and not necessarily have higher reproductive output? For example, although they have a greater survival probability, females who settled closer to the natal range had a lower probability of surviving to reproduction, opposite of our prediction (P3a). One potential explanation for this phenomenon relates to a pattern described earlier in this population in which females settling closer to their natal range exhibit delayed primiparity (Støen et al. 2006b), possibly due to reproductive suppression of dominant neighboring females (Ordiz et al. 2008). Given the strong mortality pressure exerted by annual harvest (Bischof et al. 2018), female bears that settle farther and reproduce sooner may have a reproductive advantage over those who experience delayed primiparity. Females settling farther may have the opportunity to pass on their genes at least once before dying. Because the median age of survival in the female population is only 6 years and the average age of primiparity is 4.8 years, females may only have the opportunity to breed once if at all. Due to higher cub loss for primiparous females (Zedrosser et al. 2009), females may survive to primiparity without having successfully weaned offspring. A study of multiple populations of American black bears suggested that dispersal may confer fitness benefits and that plasticity in philopatry/dispersal may be adaptive for female bears (Kristensen et al. 2018).

As predicted, we found that females settling closer to the natal range had higher lifetime survival (supporting P3c). Similarly, a long-term study on North American red squirrels (*Tamiasciurus hudsonicus*) found that resident females lived longer than immigrant (dispersing) females (Martinig et al. 2020). The specific mechanisms leading to higher lifetime survival for female bears that settled closer were not studied but are likely related to familiarity with the landscape. Moving through unfamiliar space was linked to increased risk of predation in ruffed grouse (*Bonansa umbellus*) (Yoder et al. 2004), black-tailed deer (*Odocoileus hemionus columbianus*) (Forrester et al. 2015), and roe deer (*Capreolus capreolus*) (Gehr et al. 2020), indicating that site familiarity provides a survival advantage. Although longevity in female brown bears has been previously linked to higher reproductive success (Zedrosser et al. 2013), we did not find support for our prediction (P3b) that females settling closer to the natal range would have higher lifetime reproductive success. One possible reason for this is the prevalence of sexually-selected infanticide (SSI) in this study population (Bellemain et al. 2006). When a resident male is harvested from the population, a new male will take over his former range and often kill the cubs of resident females which brings females into estrus (Gosselin et al. 2017; Leclerc et al. 2017). Although females traveling with offspring are protected from hunting (Van de Walle et al. 2018), overlapping males in the area are not, leaving cubs vulnerable to male infanticide. For an individual female bear, this can result in many unsuccessful breeding attempts (Swenson et al. 2001), such that longevity does not necessarily correlate with reproductive success. Harvest-driven SSI has been documented in other carnivore populations (Frank et al. 2017), e.g. in South African leopards (*Panthera pardus*), SSI has been shown as the highest cause of mortality in cubs, partially driven by trophy hunting of males (Balme et al. 2013). In a population of cougars (*Puma concolor*), hunting of males induced strong enough infanticide pressures as to show population decline even in the absence of direct removal of adult females (Wielgus et al. 2013). Whether from direct hunting mortality or indirect SSI, constant turnover in the population due to the annual harvest could be disrupting evolutionary patterns that would normally govern reproductive success. Given our contradictory findings of how survival and reproductive success relate to settlement patterns, it is likely that predictions for population management and conservation may be challenging (Jonzen et al. 2003).

CONCLUSION

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

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TABLES

Table 1. Results of models AICc Δ <= 2 from candidate model set of parent-offspring conflict on distance settled from the natal range by female brown bears in Scandinavia. Predictor variables are *litter type* (sole/multiple), *mother's age* (in years), and *mother's status* (dead/alive). *Body size* (head circumference in cm, measured as a yearling) is controlled for in all models. Model selection statistics shown are: df = degrees of freedom, logLik = log likelihood, AICc = AIC value for small sample sizes, Δ = delta AICc, wt = AIC_c weight, Pseudo R^2 = Nakagawa's pseudo R squared for GLMMs (marginal/conditional).

Model	**df**	**logLik**	**AIC_c**	**Δ**	**wt**	**Pseudo R^2**
litter type + mother's status + body size	6	-256.773	526.7	0	0.234	0.13/0.30
mother's status + body size	5	-258.228	527.3	0.56	0.177	0.09/0.29
mother's age + mother's status + body size	6	-257.110	527.4	0.67	0.167	0.12/0.29
litter type + mother's age + mother's status + body size	7	-255.992	527.6	0.86	0.130	0.15/0.31

Table 2. Results of the averaged model (AIC_c Δ <= 2) from a candidate model set of parent-offspring conflict (POC) on distance settled from the natal range in female brown bears in Scandinavia. Predictor variables are *litter type* (sole/multiple), *mother's age* (in years), and *mother's status* (dead/alive). *Body size* (head circumference in cm, measured as a yearling) is controlled for in the model. Results of sibling competition (SC) model showing the relationship between *sibling class* (near/far) and *bodySize* on distance settled from the natal range. Informative variables are shown in bold.

Model	**Term**	**β**	**SE**	**95% CI**	**P-Value**
P1a-c: POC	Intercept	2.501	0.173	2.157 - 2.845	<0.001
	litterType:sole	-0.333	0.204	-0.74 - 0.073	0.108
	motherStatus:dead	-0.571	0.251	-1.071 - -0.071	**0.025**
	motherAge	-0.148	0.105	-0.358 - 0.062	0.167
	bodySize	0.137	0.115	-0.093 - 0.366	0.244
P2a-b: SC	Intercept	2.851	0.241	2.380 - 3.323	< 0.001
	class:near	-1.174	0.142	-1.145 - -0.896	**<0.001**
	bodySize	-0.379	0.170	-0.712 - -0.045	**0.026**

Table 3. Results for resident fitness models representing predictions P3a-c concerning the influence of distance settled from the natal range on fitness of female brown bears in Scandinavia. P3a represents whether the female survived to produce at least one weaned offspring, P3b represents lifetime reproductive success (number of weaned offspring/number of breeding attempts), P3c, represents lifetime survival as measured by survival regression. Informative variables are shown in bold.

Model	**Term**	**β**	**SE**	**95% CI**	**P-Value**
P3a:					
Survived to	Intercept	-0.21	0.247	-0.695 - 0.274	0.394
Reproduction	settleDist	0.586	0.282	0.033 - 1.140	**0.038**
P3b:					
Lifetime	Intercept	0.12	0.109	-0.094 - 0.334	0.271
Reproductive	settleDist	0.073	0.095	-0.113 - 0.258	0.443
Success	ziIntercept	0.318	0.232	-0.137 - 0.774	0.17
P3c:					
Lifetime	Intercept	2.55	0.089	2.380 - 2.728	<0.001
Survival	settleDist	-0.010	0.005	-0.020 - -0.001	**0.033**
	Log(scale)	-0.791	0.099		<0.001

FIGURES

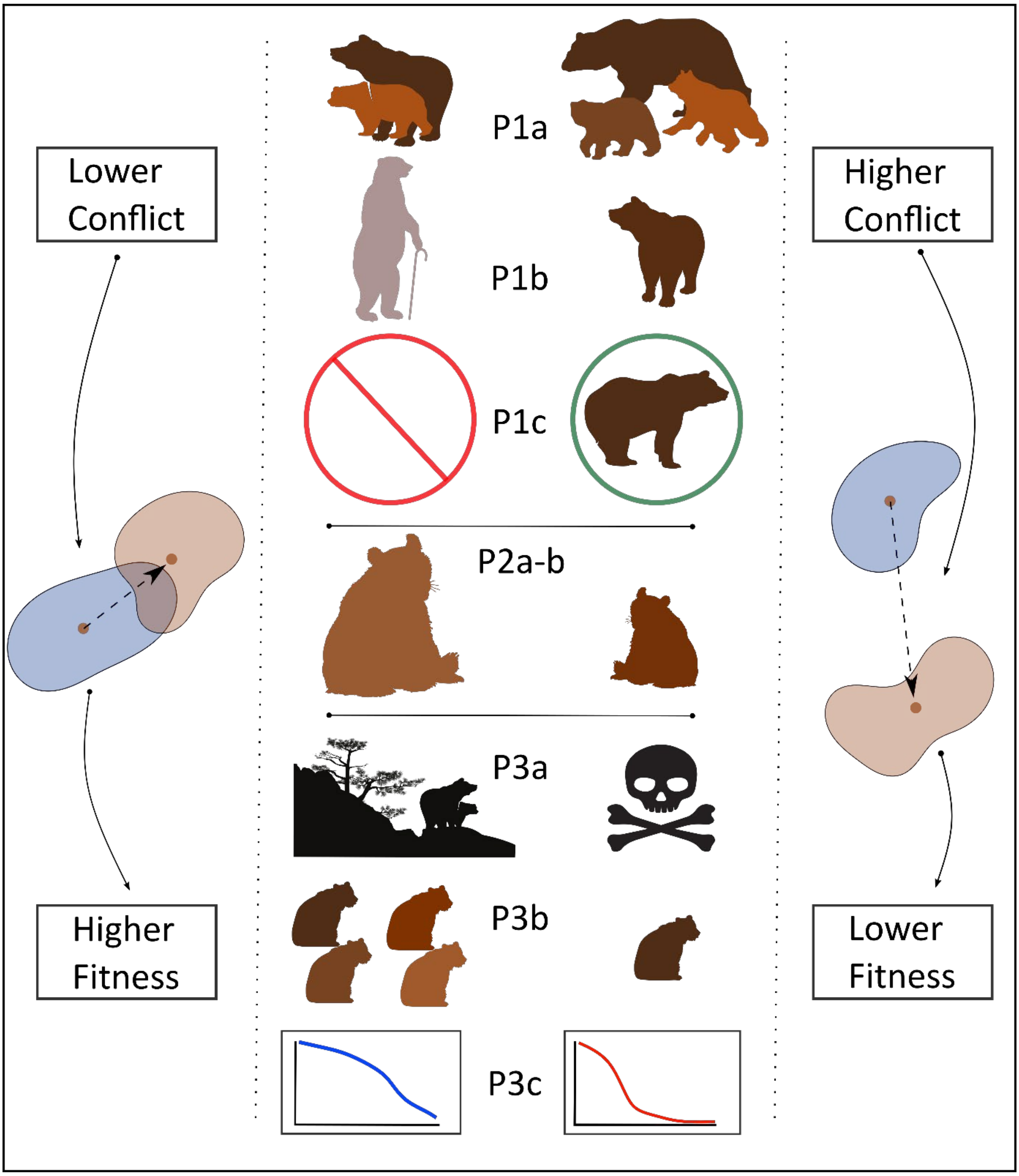

Figure 1. Diagram showing predictions for three objectives in a study of space use and fitness on female brown bears in Scandinavia. Objective one investigates potential parent-offspring conflict on settlement distance from the natal range: P1a) individuals coming from a litter with multiple females will settle farther from the natal range than those who were the sole female in the litter, P1b) female offspring with younger mothers will settle farther from the

natal range than those with older mothers, and P1c) female offspring with living mothers will settle farther from the natal range than those whose mothers have died prior to settlement. Objective two looks at sibling competition in distance settled from the natal range. In a female sibling pair: P3a) one sister in the pair will settle a home range closer to the natal range and P2b) larger females will settle closer to the natal range. Objective three concerns resident fitness, such that females settling closer to the natal range will: P3a) survive to reproduction, P3b) have greater lifetime reproductive success, and P3c) have higher lifetime survival. The natal range is represented in blue and the settlement range is represented in beige.

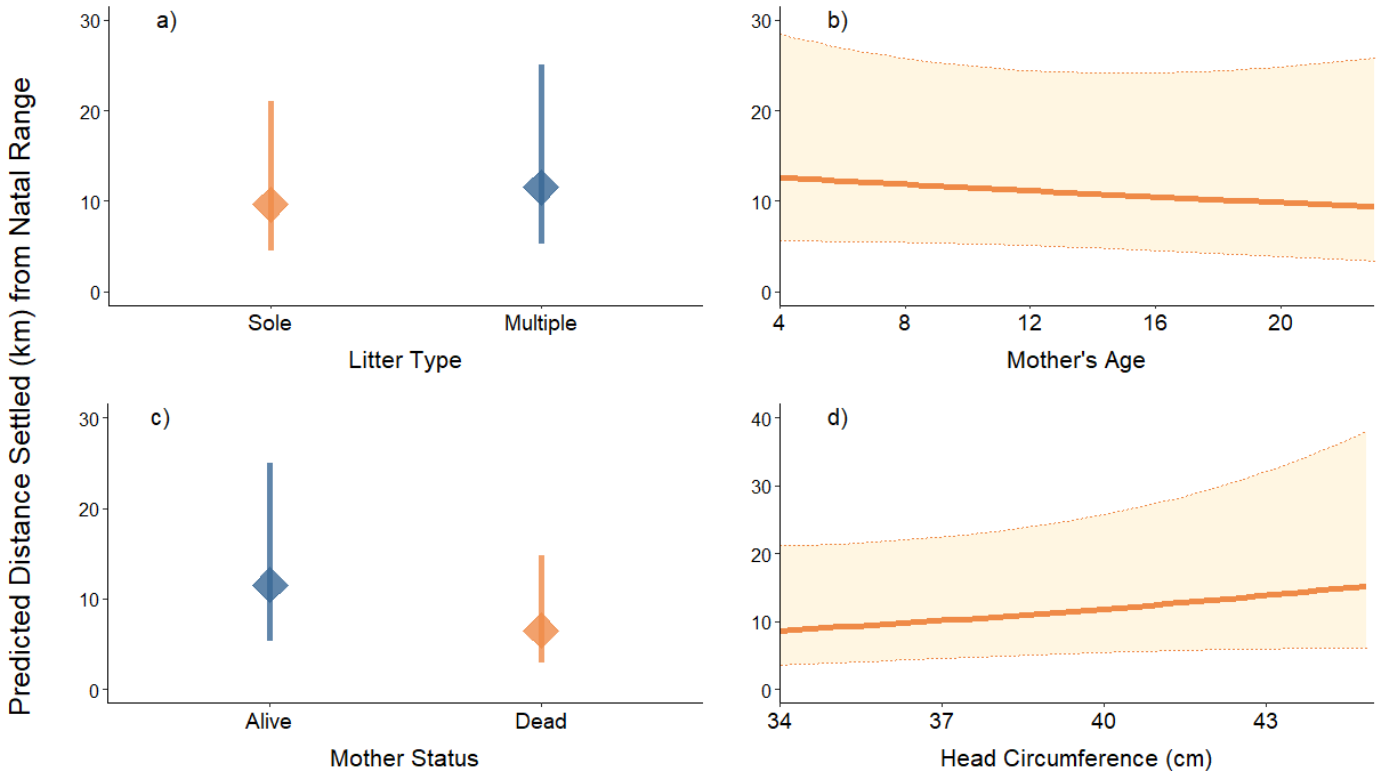

Figure 2. Plot showing predicted distance settled from the natal range by female brown bears in Scandinavia for the averaged parent-offspring conflict model. Predictor variables are: a) *litter type*, b) *mother's age*, c) *mother's status*, and d) is a variable controlling for *body size*, measured as head circumference as a yearling

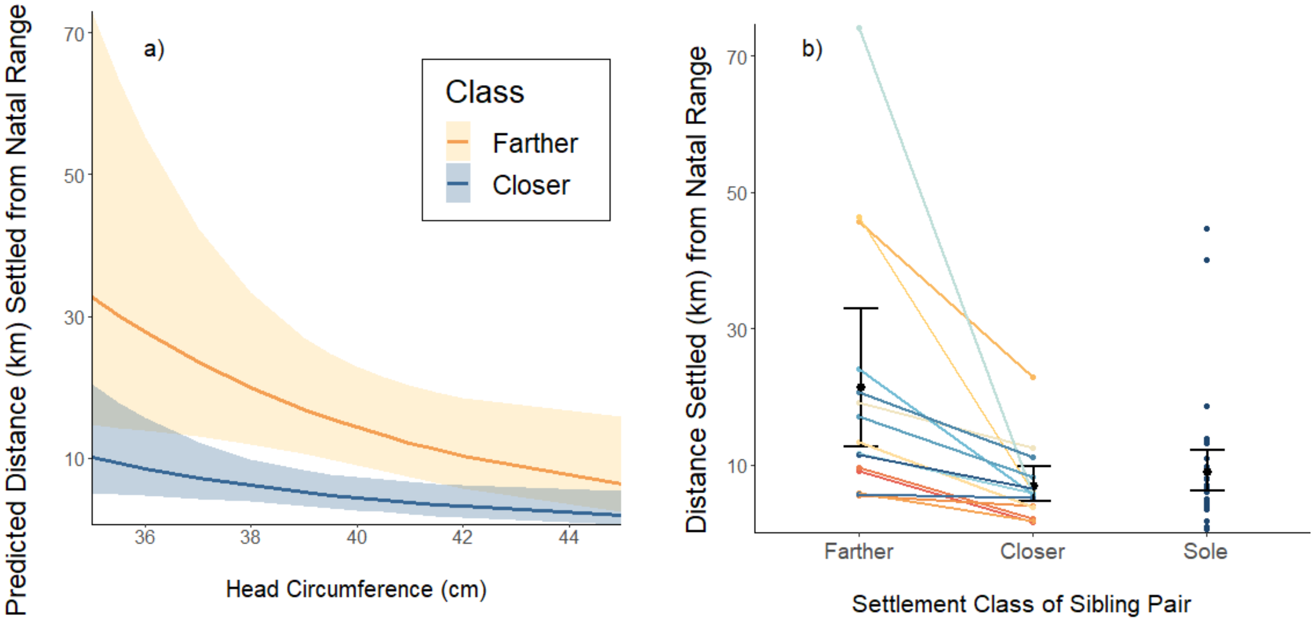

Figure 3. a) Prediction plot for distance settled from the natal range (n = 30) for sibling competition model for female brown bears in Scandinavia. b) Plot showing mean (closer = 6.92 km, farther = 21.3 km) for raw values of distance settled from the natal range by pairs of female siblings classified as settling farther or closer from the natal range. Distance settled from the natal range values of females without a sister (sole = 8.98 km) shown in gray for comparison.

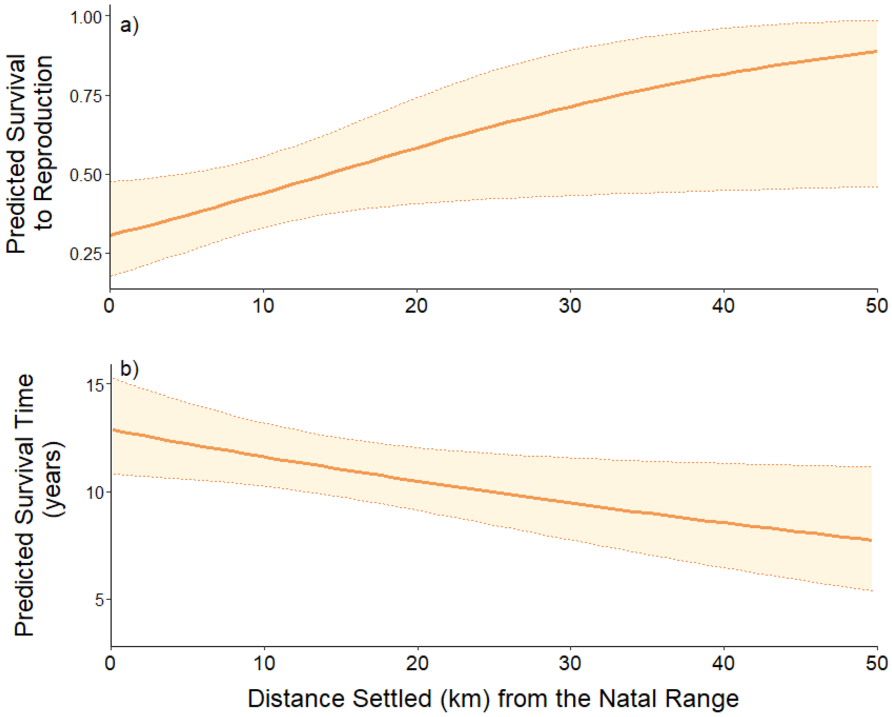

Figure 4. a) Prediction plot for survival to reproduction based on distance settled from the natal range (n = 76) for female brown bears in Scandinavia. Distance settled from the natal range is significant in the model (β = 0.586, 95% CI = 0.033 to 1.140, p = 0.038). b) Prediction from a Weibull accelerated failure time model showing that female bears who settle farther from the natal range (n = 76) have lower lifetime survival than those that settle closer (β = -0.01, 95% CI = -0.02 - -0.001, p = 0.033).

Supplement S1

A comparison of the relationship between natal range overlap and distance settled from the natal range in female Scandinavian brown bears

Hansen et al. 2022

Procedure

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

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

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

Import data:

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

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

Perform Spearman's rank correlation

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

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

References:

Støen, OG., Bellemain, E., Sæbø, S. and JE Swenson. 2005. Kin-related spatial structure in brown bears *Ursus arctos*. Behav Ecol Sociobiol 59, 191–197.
https://doi.org/10.1007/s00265-005-0024-9

Supplement S2. Results of parent-offspring conflict models containing average density

Table 1. Results of alternate models of parent-offspring conflict (P1a-c) and distance settled from the natal range containing the predictive term *average density*.

Model	**Term**	**β**	**SE**	**95% CI**	**P-Value**
P1a	Intercept	2.225	0.135	1.982 - 2.509	<0.001
	litterType	-0.160	0.246	-0.643 - 0.322	0.515
	avgDensity	0.096	0.115	-0.130 - 0.322	0.405
	bodySize	0.161	0.129	-0.093 - 0.415	0.215
P1b	Intercept	2.217	0.106	1.960 - 2.377	<0.001
	momAge	-0.151	0.106	-0.358 - 0.058	0.157
	avgDensity	0.077	0.110	-0.138 - 0.293	0.481
	bodySize	0.187	0.128	-0.064 - 0.437	0.144
P1c	Intercept	2.260	0.117	2.030 - 2.490	<0.001
	motherStatus	-0.396	0.266	-0.917 - 0.125	0.136
	avgDensity	0.139	0.105	-0.066 - 0.344	0.185
	bodySize	0.210	0.133	-0.052 - 0.468	0.116
P1alt-1	Intercept	2.279	0.156	1.924 - 2.536	<0.001
	litterType	-0.012	0.279	-0.560 - 0.535	0.965
	momAge	-0.110	0.126	-0.356 - 0.138	0.388
	motherStatus	-0.306	0.279	-0.852 - 0.240	0.273
	avgDensity	0.097	0.116	-0.130 - 0.325	0.403
	bodySize	0.227	0.133	-0.034 - 0.489	0.088
P1alt-2	Intercept	2.230	0.138	2.025 - 2.567	<0.001
	litterType	-0.121	0.246	-0.603 - 0.360	0.622
	motherStatus	-0.381	0.268	-0.906 - 0.144	0.155
	avgDensity	0.115	0.114	-0.109 - 0.339	0.314
	bodySize	0.222	0.135	-0.043 - 0.487	0.101
P1alt-3	Intercept	2.169	0.145	1.884 - 2.454	<0.001
	litterType	-0.002	0.282	-0.555 - 0.551	0.994
	momAge	-0.150	0.121	-0.387 - 0.087	0.216
	avgDensity	0.077	0.116	-0.150 - 0.305	0.510
	bodySize	0.187	0.129	-0.066 - 0.439	0.147
P1alt-4	Intercept	2.225	0.120	1.991 - 2.460	<0.001
	momAge	-0.111	0.111	-0.330 - 0.107	0.317
	motherStatus	-0.305	0.278	-0.850 - 0.240	0.273
	avgDensity	0.099	0.111	-0.118 - 0.315	0.372
	bodySize	0.227	0.132	-0.031 - 0.484	0.085

Table 2. Alternative model results for sibling competition models (P2a-b) containing average density.

Model	**Term**	**β**	**SE**	**95% CI**	**P-Value**
Distance I: Settlement Class (Near or Far)	Intercept	2.196	0.253	1.700 - 2.692	<0.001
	Class:Near	-0.908	0.148	-1.197 - -0.618	<0.001
	bodySize	-0.286	0.120	-0.521 - -0.051	0.017
	avgDensity	-0.191	0.186	-0.555 - 0.174	0.305

Table 3. Alternative model results for fitness models (P3a-b) containing average density.

Model	**Term**	**β**	**SE**	**95% CI**	**P-Value**
Fitness I: Survival to Reproduction	Intercept	0.145	0.346	-0.534 - 0.823	0.676
	distKM	0.925	0.571	-0.195 - 2.044	0.105
	avgDensity	0.090	0.334	-0.565 - 0.745	0.788
Fitness II: Lifetime Reproductive Success	Intercept	0.102	0.115	-0.124 - 0.328	0.377
	distKM	0.119	0.174	-0.225 - 0.463	0.497
	avgDensity	-0.277	0.159	-0.596 - 0.034	0.081
	ziIntercept	0.000	0.316	-0.620 - 0.620	1.000

Table S3. Description of study variables and summary statistics. Lifetime survival is not included, as it does not have associated summary statistics.

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

Article 3

Thorsen, N.H., Hansen, J.E., Støen, O.-G., Kindberg, J., Zedrosser, A., Frank, S.C. 2022. Human infrastructure influences life stage-dependent movement and habitat selection in a large carnivore. Manuscript, revised and resubmitted to Movement Ecology (initial submission 16 February 2022, resubmitted 07 September 2022).

Movement and habitat selection of a large carnivore in response to human infrastructure differs by life stage

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Abstract

Background: The movement extent of mammals is influenced by human-modified areas, which can affect population demographics. Understanding how human infrastructure influences movement at different life stages is important for wildlife management. This is true especially for large carnivores, due to their substantial space requirements and potential for conflict with humans.

Methods: We investigated human impact on movement and habitat selection by GPS-collared male brown bears (*Ursus arctos*) in two life stages (residents and dispersers) in central Sweden. We identified dispersers visually based on their GPS locations and used hidden Markov models to delineate dispersal events. We used integrated step selection analysis (iSSA) to infer movement and habitat selection at a local scale (availability defined by hourly relocations), and resource selection functions (RSFs) to infer habitat selection at a landscape scale (availability defined by the study area extent).

Results: Movement of residents on a local scale was facilitated by small forestry roads as they moved faster and selected areas closer to forestry roads, and they avoided areas closer to larger public roads and buildings on both scales. Dispersers were more ambivalent in their response to human infrastructure. Dispersers increased their speed closer to small forestry roads and larger public roads, did not exhibit selection for or against any road class, and avoided areas closer to buildings only at local scale. Dispersers did not select for any features on the landscape, which is likely explained by the novelty of the landscape or their naivety towards it.

Conclusion: Our results show that movement in male brown bears is life stage-dependent and indicate that connectivity maps derived from movement data of dispersing animals may provide more numerous and more realistic pathways than those derived from resident animal data alone. This suggests that data from dispersing animals provide more realistic models for reconnecting populations and maintaining connectivity than if data were derived from resident animals alone.

Keywords: Human disturbance, human-modified, roads, settlements, life stage, home range, dispersal, brown bear, connectivity.

Introduction

Human activity and infrastructure have reduced the movement extent of wildlife globally [1]. Animals are generally sensitive to human infrastructure [2], especially to the creation of linear structures [3], which is commonly reflected in their movement patterns. Maintaining connectivity, i.e. the ease of movement between suitable habitat patches or between populations, within a human-dominated landscape is important to avoid fragmentation of populations and to ensure gene flow [4, 5]. As dispersal contributes to population connectivity and genetic diversity [6], it is crucial to understand how dispersing individuals ("dispersers") respond to human infrastructure and if they respond differently compared with individuals settled within a home range ("residents"). Connectivity is often derived from habitat selection estimates [e.g. 4]. Habitat selection can vary across life stages [e.g. 7, 8], i.e. dispersers compared with residents. Thus, connectivity estimates may differ depending on which life stage the habitat selection estimates are obtained from [8].

Understanding how movement decisions differ by life stage is important for the conservation of species, e.g., for defining potential connectivity and conservation corridors within and between populations [9]. Dispersal can be risky and energetically costly, as it often exposes individuals to unknown environments, especially in human-modified landscapes [10-12] where mortality risk can be higher [13]. This implies that dispersers are either unable to perceive human risk or fail to adjust habitat use or movement in response to human risk due to their naivety [e.g. 14] or they might be more 'tolerant' or 'bold' and traverse risky habitats [15]. In contrast, the home range is familiar to a resident, and risk encountered during movement may be mitigated through spatiotemporal shifts or altered habitat selection based on prior experience [e.g. 16, 17]. This strategy might not be available to naïve dispersers facing unexpected or less predictable, risky features on the human-dominated landscape [18].

Habitat selection, i.e. the disproportionate use of a habitat feature in relation to its availability [19], can be estimated at different spatial scales depending on how availability is defined. Throughout this article we refer to habitat selection on the "landscape scale" when the availability is defined for an area many times the size of an animal's home range, e.g. an entire study area (cf. second order habitat selection [19]). We refer to habitat selection at the "local scale" when the availability is defined over smaller areas or shorter distances (e.g. for step selection functions) that an animal is able to traverse between successive (e.g. hourly) locations (cf. forth order habitat selection [19]). Animals may respond differently to the same covariate depending on the scale of availability [20, 21]. This also applies to human infrastructure, e.g. wolves (*Canis lupus*) avoid gravel roads within their home range but select gravel roads on a local scale [22]. Spatial scale can also be of importance for movement and habitat selection during different life stages, because dispersers navigating a novel landscape will likely only know what is in its immediate surroundings and have less knowledge at a landscape scale.

Here we use the brown bear (*Ursus arctos*) as a model species within a human-modified landscape in Sweden to study the impact of human infrastructure, i.e. roads and buildings, movement and habitat selection at the landscape and local scale during two life stages. Like other large carnivores, brown bears have large home ranges [23] and can travel long distances [24]. There is ample scientific evidence that humans influence brown bear behaviour [e.g. 25, 26, 27], and bears are able to perceive and respond to local context-specific risks [28], but it is unknown how dispersers navigate human-modified environments compared with residents. In this study, we focus on male brown bears in two life stages, dispersers, and residents. We estimate habitat selection and movement at the landscape and local scale and evaluate whether the effect of human infrastructure differs between the two life stages.

We hypothesize (H1) that human infrastructure influence movement of dispersing and resident male brown bears. In support of (H1), we predict (P1) that the most parsimonious model explaining movement and habitat selection for both dispersers and residents will include buildings or roads at one or both spatial scales. We hypothesize (H2) that dispersers will be more naïve or risk-tolerant compared with residents. In support of H2, we predict (P2) that dispersers will show less avoidance of or be closer to buildings and roads compared with residents. We hypothesize (H3) that bears of both life stages will be more sensitive to human infrastructure at the local scale than the landscape scale. In support of H3, we predict (P3) that bears in each life stage will exhibit stronger avoidance of buildings and roads at the local scale compared to the landscape scale.

Methods

Study area and study species

The study area is located in southcentral Sweden (approximately 61° N, 15° E), primarily within Gävleborg and Dalarna counties, spanning ~50,000 km² (Figure 1a). The landscape consists of boreal forest, bogs, lakes, and sparse agricultural land. The intensively managed forest is dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) [29]. Rolling hills comprise the general topography, with steeper and more rugged terrain in the western portion of the study area (elevation range 0-997 m a.s.l.). Human settlement in the area is sparse, with an average of 8.64 inhabitants/km^2 and people tend to live in small villages [30]. There are several larger towns and cities, but urban areas and sub-urban settings contribute to small fractions of our study area and few bears are exposed to this magnitude of human infrastructure. There is an extensive road network, dominated by gravel roads used for forestry. The road density is low in a European context [31] and the traffic volumes are low in a Swedish perspective. Almost all roads are unfenced, only the largest public roads are fenced.

Current brown bear density in the study area ranges from ca 20 to 60 bears per 1000 km^2 [32]. Scandinavian brown bears are subject to high hunting pressure and approximately 70 % of the total mortality is due to legal hunting [32]. They generally avoid humans and their settlements [33]. By way of human infrastructure, brown bears are exposed to mostly roads and buildings in our study area. Male brown bears have large home ranges, on average 800 km^2 [34], encompassing all types of human infrastructure, which they generally avoid [35]. We focused on males because dispersal is primarily male-biased (94%) [36].

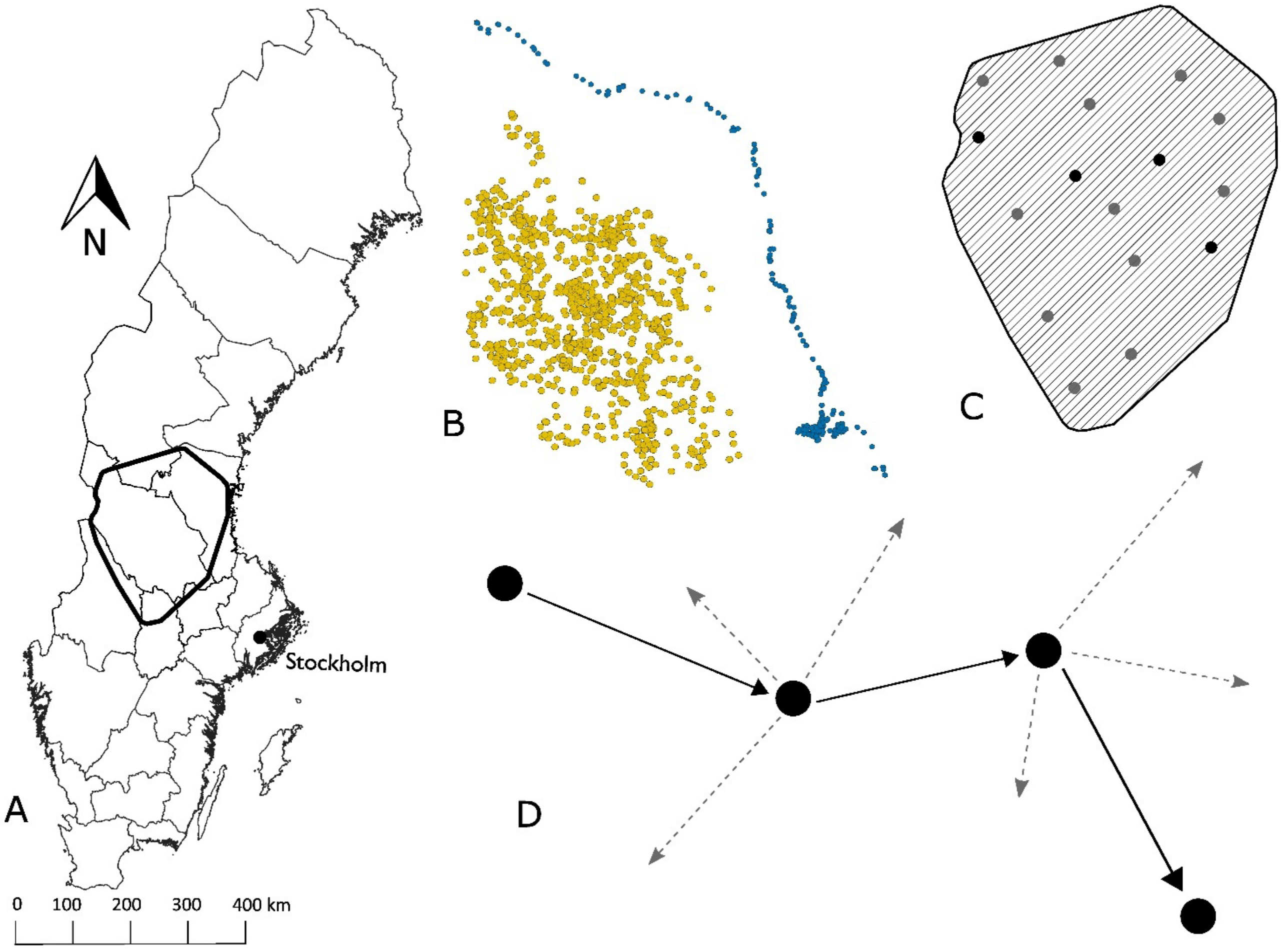

Figure 1. Diagram shows (A) study area within Sweden. (B) Differences between GPS locations of resident (gold) and dispersing (blue) male brown bears. (C) Availability space and sampling design for landscape scale for resource selection function (RSF) where grey dots represent available location and black points represent used. (D) Availability and sampling design for local scale for integrated step selection analysis (iSSA), where grey arrows represent available steps and black arrows represent used steps.

Telemetry data

Brown bears were captured, collared, and monitored from 2007 to 2017 as part of a long-term research project [37]. See Arnemo and Evans [38] for a more detailed description of capture and handling procedures. Capture and handling of bears was conducted by permit under Swedish authorities and ethical committees. Bears were fitted with GPS collars (GPS Plus, Vectronic Aerospace GmbH) with different programming schedules, but all were scheduled to acquire at least one GPS location each hour. All GPS locations were resampled to one location every hour (± 3 min tolerance). We retained only GPS locations with a dilution of precision (DOP) of less than 10 to reduce location error [39]. All GPS locations overlaying water bodies were removed prior to analyses. As our focus was on movement and habitat selection in relation to human infrastructure, we removed locations associated with resting sites (day and night beds) [28]. We defined a bed site as a cluster of GPS locations with a maximum distance of 50 m between any two GPS locations in the cluster, a maximum distance of 30 m between two consecutive GPS locations and at least 5 consecutive locations, i.e., the bear had to spend at least 4 hours in the same location to be defined as a bed site.

Defining dispersing and resident bear-years

We focused only on natal dispersal, i.e. the permanent movement from birth site to first breeding, and will hereafter refer to it as dispersal. We visually examined the GPS tracks of every bear-year, i.e. the unique combination of bear ID and year, to identify bear-years with diagnostic linear tracks typical of dispersal events (Figure 1b). This approach might underestimate dispersal in males that gradually move away from their maternal range over multi-year periods, however, this behavior is difficult to disentangle from home range drift or infidelity [40]. In addition, previous studies have detected high rates (>92%) of male dispersal [36, 41]. We performed 'path segmentation' [42] on movement tracks of bear-years identified with a dispersal event and used hidden Markov models (HMM), a form of state-space modeling [43], to define the transient period of dispersal. Hence, this method identified the onset and end of the dispersal event. For each track, we fit seven HMMs that varied in the number of states and the initial parameters (see supplement S1 for more details on model fitting and structures). We selected the most parsimonious (hereafter 'best') model using Akaike's Information Criterion [44] and used the Viterbi algorithm [45] to classify behaviors from the best model. Based on the classified behaviors, we defined the onset and end for the dispersal period for the bear-years identified as dispersing (supplement S1). Only one dispersal period was defined for each of the bear-years identified as dispersing, and only data from this period for each bear-year was used in the further analysis for dispersers. We used the R package 'moveHMM' [46] for fitting HMMs, model selection, and behavioral classification. Dispersal phases lasted from 21 to 65 days (mean: 43 ± 15) for the 15 males (15 bear-years) defined as dispersing. During their dispersal events, these bears ranged in age from 2 to 4 years old (mean 2.7 years, n = 15).

We defined resident bear-years as all years that a GPS-collared bear had been solitary for at least three years (Figure 1b), and no dispersal event had been detected. Males separate from their mother at 1 or 2 years of age [47] and Støen, Zedrosser [41] showed that 92.3 % of male bears (n = 67) had dispersed by four years of age in the study area, with no observed dispersal events at 4 years of age. Hence, based on our definition of a resident bear-year, we avoided the inclusion of solitary pre-dispersing males, i.e. young males that had left their mother but not dispersed yet, as resident bear-years. We defined an active period between 25 April and 20 August which follows den emergence and precedes the hunting season for brown bears in Sweden. Brown bears in Sweden are known to change their movement pattern after the onset of hunting [48]. For residents, we excluded all data outside this period, and only individuals with GPS locations covering at least 70% of the days during the active period each year for further analysis. For dispersers there were two cases which extended outside this period: one started dispersing 21 April and another whose dispersal ended 22 August. To maximize disperser sample size, we included the six days of data outside the active period for these two individuals. We identified 20 males spanning 46 bear-years that met our resident criteria. The resident bear-years ranged in age from 4 to 21 years old (mean = 9.7 years, n = 45, one with unknown age but classified as adult based on head circumference).

Covariates

We included the following 'core' covariates reported to influence brown bear habitat selection and movement in our analysis: terrain ruggedness index (TRI) [35], clearcuts [49], bogs [50], and distance to water [51, 52]. We calculated TRI from a digital elevation model (25-m resolution) with the R package spatialEco [53] using a 3 × 3 cell moving window. We obtained data on landcover, roads, and buildings from the Swedish Mapping, Cadastral and Land Registration Authority [54]. In Sweden, forestry practitioners must report timber harvesting activities[55], and we used the data for defining clearcuts as logged areas from first cutting up to 10 years [56]. We created a clearcut raster (presence = 1, absence = 0) for each year of the study.

We divided our road data into forestry and public roads. Forestry roads represent the majority of the road network in the study area (mean = 1.27 ± 1.07 km/km^2), which are mainly small gravel roads built for forestry and usually open for the public. Public roads are larger and mostly paved and associated with higher traffic volume (mean = 0.18 km/km^2, SD = 0.45). We included all buildings, the majority of which were houses or cabins (mean density = 10.7 ± 39.4 buildings/km^2). We rasterized all covariates to a resolution of 25 m. We calculated the Euclidean distance from all cells in the raster to the nearest forestry road, public road, and building, for each feature separately. All distance to covariates were log transformed prior to analysis to attenuate covariate effects at longer distances.

Habitat selection and movement analyses

We used exponential resource selection functions (RSF) to estimate habitat selection at the landscape scale (availability defined by the study area extent) [57], and integrated step selection analysis (iSSA) to estimate habitat selection and movement parameters at the local scale (availability defined by hourly relocations) [58]. We used the bear locations excluding bed sites for RSF and iSSA. RSF and iSSA models were fitted at the bear-year level, i.e. one model for each bear-year. The estimates from each model on the bear-year level were later averaged to obtain one population estimate for dispersing individuals and one for resident individuals.

For the RSF, the availability space was defined as the 100% minimum convex polygon of all observed GPS locations for all bear-years buffered by the radius of a circular mean male home range size (r = ~18 km). For each bear-year, we randomly sampled available GPS locations from the availability space with a ratio of 20:1 available-to-use (Figure 1c). The RSF was obtained by fitting a generalized linear model with the glm function in R. The GPS locations were used as the response variable and coded '1' for used and '0' for available.

An iSSA is a form of step selection functions that simultaneously estimate habitat selection and movement parameters [58]. We created "steps" by combining two consecutive GPS locations that were not part of a bed site. An iSSA requires at least two valid consecutive steps, as turning angles need to be calculated and included in model structure. Every step had a duration of 1 hour. An iSSA uses 'local scale availability', i.e. locations to which an animal could possibly have moved to in a given step. Based on the used steps, we calculated step lengths and fitted a gamma probability density function based on maximum likelihood estimation for both life stages combined. We drew 20 step lengths from the fitted gamma distribution for each used step (20:1 available-to-use ratio) and combined them with turning angles drawn from a uniform distribution to generate 'available' steps (Figure 1d). We assigned a unique stepID to each used step and its 20 associated available steps. The available steps represent what was locally available to bears at the starting point of every step. The iSSA was modelled using conditional logistic regression with used (coded as 1) and available steps (coded as 0) as the response variable, and the stepID as the stratum (for matching the used and available steps). Covariates for used and available steps were extracted at the start- and endpoints of the step. The covariates extracted at endpoints are used to infer habitat selection, while the covariates extracted at starting points together with an interaction with step length (or the logarithm of step length) are used to infer movement speed. See Avgar, Potts [58] for a detailed description of iSSA.

Candidate models and model selection

For each RSF and iSSA, we developed candidate models for all dispersers and residents. Each candidate model set contained a model including a set of 'core covariates'. Core covariates account for habitat features which previously have been shown to be important for bear habitat selection and movement. We chose the combination of core covariates as they should cover the most prevalent habitat classes in our study area. The core model was extended with additional covariates representing specific human infrastructure attributes to form competing candidate models. We also included a 'full' model containing all covariates into the analysis (Table 1). RSF and iSSA candidate model formulae were identical, except iSSA models included movement-related covariates (Table 1). For iSSA, we included step lengths (SL) and the natural logarithm of step lengths (lnSL) in all models to capture movement differences between life stages. All covariates were standardized with the formula *(X – mean of X)/standard deviation of X* and checked for collinearity. The highest correlation was 0.30, reported for the variables distance to public roads and distance to buildings.

Table 1. Candidate models used to test the relative importance of forestry roads, public roads, and buildings and habitat selection and movement in male brown bears.

Model	Explanatory covariates
Resource Selection Function (landscape availability)	
Core	clearcut + bog + TRI + Dist.Water
Forestry roads	Core + Dist.ForestryRoads
Public roads	Core + Dist.PublicRoads
Buildings	Core + Dist.Building
Forestry and public roads	Core + Dist.ForestryRoads + Dist.PublicRoads
Forestry roads and buildings	Core + Dist.ForestryRoads + Dist.Building
Public roads and buildings	Core + Dist.PublicRoads + Dist.Building
Full	Core + Dist.ForestryRoads + Dist.PublicRoads + Dist.Building
Integrated Step Selection Analysis (local availability)	
Core	SL[a] + log(SL) + cos(TA[b]) + clearcut_end[c] + bog_end + TRI_end + Dist.Water_end[d] + log(SL):clearcut_start
Forestry roads	Core + Dist.ForestryRoads_end + log(SL): Dist.ForestryRoads_start
Public roads	Core + Dist.PublicRoads_end + log(SL): Dist.PublicRoads_start
Buildings	Core + Dist.Building_end + log(SL): Dist.Buildling_start
Forestry and public roads	Core + Dist.ForestryRoads_end + log(SL):Dist.ForestryRoads_start + Dist.PublicRoads_end + log(SL): Dist.PublicRoads_start
Forestry roads and buildings	Core + Dist.ForestryRoads_end + log(SL): Dist.ForestryRoads_start + Dist.Building_end + log(SL): Dist.Buildling_start
Public roads and buildings	Core + Public roads + log(SL): Dist.PublicRoads_start + Dist.Building_end + log(SL): Dist.Buildling_start
Full	Core + Dist.ForestryRoads_end + log(SL): Dist.ForestryRoads_start + Dist.PublicRoads_end + log(SL): Dist.PublicRoads_start + Dist.Building_end + log(SL): Dist Buildling_start

[a] Step length

[b] Turning angle

[c] "_end" and "_start" denote if the covariate was extracted from the start or the end point.

[d] "Dist" is an abbreviation for "distance-to", and the distance to features were log transformed

We performed model selection for each bear-year for both the RSF and iSSA models. We calculated AIC for all models for each bear-year and calculated the delta AIC from the best model for all candidate models within bear-years. We summed the delta AIC for all the candidate models and considered the model with the lowest mean AIC for each life stage as the best model for that life stage. Note that this may cause the best model to have a mean delta AIC > 0, because that model structure might not be 'best' across all bear-years for a given life stage and scale.

Population level effects

To infer habitat selection and movement responses at the population level, i.e. for dispersers and residents, we averaged the bear-year models using inverse variance-weighted linear modelling [59], following the approach by Dickie, McNay [60]. We fitted inverse-variance linear regression models separately for residents and dispersers and for each RSF and iSSA model set. We used either RSF or iSSA coefficients as response variables and included the mean availability of each variable as an explanatory variable for a given bear-year to control for a possible functional response [61]. We used the inverse of the estimated variance for the coefficients as weights. The availability used in the inverse variance-weighted linear regression models was centered (x - mean of x), to aid in interpretation. The population-level coefficients can be interpreted as the mean coefficient at the mean availability for the males in the population (each for dispersers and residents and for the RSF and iSSA). We interpreted coefficients with 95% CIs overlapping with zero as 'indifferent' and non-overlapping 95% CIs as significant avoidance or selection, or as an effect of the covariate on movement rate [60]. We also recorded the direction of the coefficients for all individual bear-year models and reported the proportion of bear-year models that followed the same direction as the mean of all bear-years in a given life stage. This measure reflects the consistency of individual responses to covariates for each life stage between the local and the landscape scale for the population.

In iSSA, the estimated coefficients for SL, lnSL, and their interactions function as modifiers for the initial estimates of the scale and shape parameters, respectively, in the fitted gamma distribution (used for sampling the available step lengths) on step lengths [58]. For each bear-year, we adjusted the shape and scale parameters of the fitted gamma distribution. We calculated movement rates at the bear-year level by multiplying the adjusted shape and adjusted scale parameters from the gamma distribution. To illustrate changes in movement rates, we calculated movement rates at several levels for each of the focal covariates and kept all other interacting covariates (with lnSL) constant at their mean observed step value.

Movement rates at the population level were obtained by calculating the mean of individual bear-year movement rates across the different levels of a given focal variable and for each life stages separately (iSSA only).

For both RSF and iSSA results, we calculated the relative selection strength (RSS) following Avgar, Lele [62] for all covariates in each analysis. The RSS was calculated based on the population-averaged estimates from the inverse-variance weighted linear models (one for each life stage and availability scale). For step selection functions (iSSA), the ln RSS is a relative measure of how likely the individual is to select a step that ends at location x_1 in relation to a step that ends at location x_2 (the reference location). For “distance to feature” covariates, we calculated the RSS moving one mean step length closer to the feature compared with staying at the same location, and for the other covariates we calculated the RSS of selecting a given feature over the mean of the covariate.

All distance calculations were performed in GRASS 7.2 [63]. We used the ‘amt’ package [64] for iSSA and R 3.6.0 all other statistical analyses [65].

Results

The bed removal procedure removed 28% of the GPS locations, leaving 70 008 GPS locations for statistical analysis (8 012 GPS locations for dispersers and 61 996 GPS locations for residents). The bed removal procedure biased removal of more observations during day (Figure S1). Mean step lengths were 729 m for dispersers and 586 m for residents. Used locations rarely (< 7 %) occurred in bogs and clearcuts (Table 2), and the mean distance to water was 705 m for dispersers and 712 m for residents. There were large differences between dispersers and residents in the mean values of their used locations for human covariates (Table 2). Used locations of dispersers and residents occurred on average 788 and 1186 m from buildings, 3014 and 5213 m from public roads, and 250 and 294 m from forestry roads, respectively.

Table 2. Values for covariates at used locations for brown bears defined as residents and dispersers in Sweden. The values in the table represent population means as calculated from the mean values for each bear year, with the standard error in the parentheses.

Covariate	Residents	Dispersers
Bogs	0.06 (0.03)	0.04 (0.03)
Clearcuts	0.06 (0.01)	0.06 (0.05)
Distance to water	712 (209)	705 (168)
Terrain ruggedness (TRI)	6.03 (1.38)	5.44 (1.47)
Distance to buildings	1186 (232)	788 (261)
Distance to public roads	5213 (2325)	3014 (1458)
Distance to forestry roads	294 (90)	250 (64)

The full models had the lowest mean delta AIC at both spatial scales for dispersers (landscape scale ΔAIC = 0.82, local scale ΔAIC = 2.06) as well as residents (landscape scale ΔAIC = 0.32, local scale ΔAIC = 0.96). The full model scored the lowest AIC for 40% and 20% of the bear-years for the dispersers at the landscape scale and local scale, respectively (Table 3). The full model scored the lowest AIC for 78% and 63% of the bear-years for the residents at the landscape scale and local scale, respectively (Table 3). The four best RSF (landscape scale) models for both life stages contained the covariate public roads, whereas the four best iSSA models (local scale) for both life stages contained the covariate forestry roads.

Table 3. Model selection for dispersing and resident male brown bears of model sets fit using resource selection functions (RSFs) and integrated step selection analysis (iSSA). Mean ΔAIC is the mean ΔAIC for all bear-years during the given life stage (n = 15 for dispersing males and n = 46 for resident males). Minimum AIC tally is the number of times that a given model had the lowest AIC among candidate models within a bear-year and the proportion of the model-specific tally for model sets is given in parentheses.

	Resident		Dispersal	
Model	Mean ΔAIC	Minimum AIC tally	Mean ΔAIC	Minimum AIC tally
Landscape scale (RSF)				
Full	**0.32**	**36 (0.78)**	**0.82**	**6 (0.40)**
Public roads and buildings	21.11	6 (0.13)	6.24	6 (0.40)
Forestry roads and public roads	189.84	0 (0)	20.88	1 (0.07)
Public roads	204.26	0 (0)	26.67	0 (0)
Forestry roads and buildings	536.49	4 (0.09)	33.84	0 (0)
Buildings	556.54	0 (0)	39.46	1 (0.07)
Forestry roads	1019.13	0 (0)	74.65	1 (0.07)
Core	1035.81	0 (0)	81.20	0 (0)
Local scale (iSSA)				
Full	**0.96**	**29 (0.63)**	**2.06**	**3 (0.2)**
Forestry roads and public roads	11.38	7 (0.15)	3.62	3 (0.2)
Forestry roads and buildings	11.47	5 (0.11)	6.74	4 (0.27)
Forestry roads	22.82	2 (0.04)	9.88	2 (0.13)
Public roads and buildings	40.22	2 (0.04)	15.07	0 (0)
Public roads	49.80	0 (0)	17.42	2 (0.13)
Buildings	50.68	1 (0.02)	19.95	0 (0)
Core	61.24	0 (0)	24.57	1 (0.07)

Core covariates

At the population level, dispersers and residents avoided bogs at both spatial scales, showing the same pattern for > 91% of the bear-years in each model (Table 4, Figure S2). Both dispersers and residents avoided clearcuts locally but were indifferent to them on the landscape scale (Table 4, Figure 2). Dispersers and residents were indifferent to distance to water on the landscape scale, but residents selected for distances farther from water at the local scale (Table 4, Figure 2). Dispersers were indifferent to TRI at either scale, however, residents selected for higher TRI at both scales (Table 4). In general, dispersers showed more individual variation and less consistency in their habitat selection towards the core covariates, i.e. a lower proportion of all bear-year estimates conformed to the same direction as the population mean effect, for dispersers compared with residents (Table 4; dispersers: mean of all proportions = 0.59, range = 0.333 – 0.933; residents: mean of all proportions = 0.79, range

= 0.391 – 0.957). Only residents moved faster when their step started in a clearcut (Figure 3d).

Table 4. Average habitat selection and movement rate coefficients for dispersers and residents at the landscape (RSF) and local scale (iSSA). Each bear-year was modelled separately before inverse-variance weighted linear models were run for both dispersers and residents. The proportion columns (‘prop’) give the proportion of the bear-years that had coefficient estimates in the same direction as the averaged coefficient (n = 15 for dispersers and n = 46 for residents). Bolded values indicate that the 95% confidence interval of the coefficients do not overlap zero. “Dist.” is an abbreviation for “distance to”.

		Resident					Dispersal				
category	coefficient name	estimate	CI lower	CI upper	prop	direction	estimate	CI lower	CI upper	prop	direction
Landscape scale (RSF)											
habitat selection	Bog	**-0.638**	**-0.801**	**-0.476**	0.913	avoided	**-0.934**	**-1.318**	**-0.549**	0.933	avoided
habitat selection	Clearcut	0.001	-0.132	0.134	0.391	indifferent	0.023	-0.263	0.310	0.333	indifferent
habitat selection	TRI	**0.049**	**0.032**	**0.066**	0.783	selected	0.020	-0.011	0.051	0.533	indifferent
habitat selection	Dist.Water	0.044	-0.056	0.143	0.478	indifferent	0.063	-0.094	0.220	0.533	indifferent
habitat selection	Dist.buildings	**0.324**	**0.219**	**0.430**	0.913	avoided	-0.028	-0.114	0.059	0.400	indifferent
habitat selection	Dist.ForestryRoads	**-0.042**	**-0.051**	**-0.032**	0.783	selected	-0.008	-0.035	0.019	0.400	indifferent
habitat selection	Dist.PublicRoads	**0.295**	**0.146**	**0.443**	0.870	avoided	0.002	-0.084	0.088	0.533	indifferent
Local scale (iSSA)											
habitat selection	Bog_end	**-0.653**	**-0.727**	**-0.580**	0.935	avoided	**-0.959**	**-1.198**	**-0.719**	0.933	avoided
habitat selection	Clearcut_end	**-0.423**	**-0.520**	**-0.326**	0.717	avoided	**-0.375**	**-0.660**	**-0.090**	0.600	avoided
habitat selection	TRI_end	**0.022**	**0.017**	**0.026**	0.913	selected	0.005	-0.007	0.016	0.600	indifferent
habitat selection	Dist.Water_end	**0.119**	**0.096**	**0.142**	0.957	avoided	-0.020	-0.099	0.059	0.333	indifferent
habitat selection	Dist.buildings_end	**0.060**	**0.021**	**0.100**	0.761	avoided	**0.111**	**0.016**	**0.205**	0.800	avoided
habitat selection	Dist.ForestryRoads_end	**-0.059**	**-0.075**	**-0.043**	0.804	selected	-0.008	-0.054	0.038	0.467	indifferent
habitat selection	Dist.PublicRoads_end	**0.093**	**0.052**	**0.133**	0.826	avoided	0.022	-0.074	0.118	0.800	indifferent
movement	SL	0.000	0.000	0.000	0.674	indifferent	**0.000**	**-0.001**	**0.000**	0.867	faster
movement	log(SL)	-0.010	-0.215	0.195	0.109	indifferent	0.070	-0.277	0.416	0.867	indifferent
movement	log(SL)*clearcut_start	**0.120**	**0.076**	**0.163**	0.826	faster	0.091	-0.033	0.215	0.867	indifferent
movement	log(SL)*Dist.buildings_start	0.008	-0.016	0.033	0.543	indifferent	**-0.032**	**-0.058**	**-0.007**	0.467	faster
movement	log(SL)*Dist.ForestryRoads_start	**-0.071**	**-0.082**	**-0.061**	0.978	faster	**-0.070**	**-0.106**	**-0.033**	0.800	faster
movement	log(SL)*Dist.PublicRoads_start	**-0.022**	**-0.036**	**-0.008**	0.717	faster	**-0.052**	**-0.090**	**-0.014**	0.667	faster

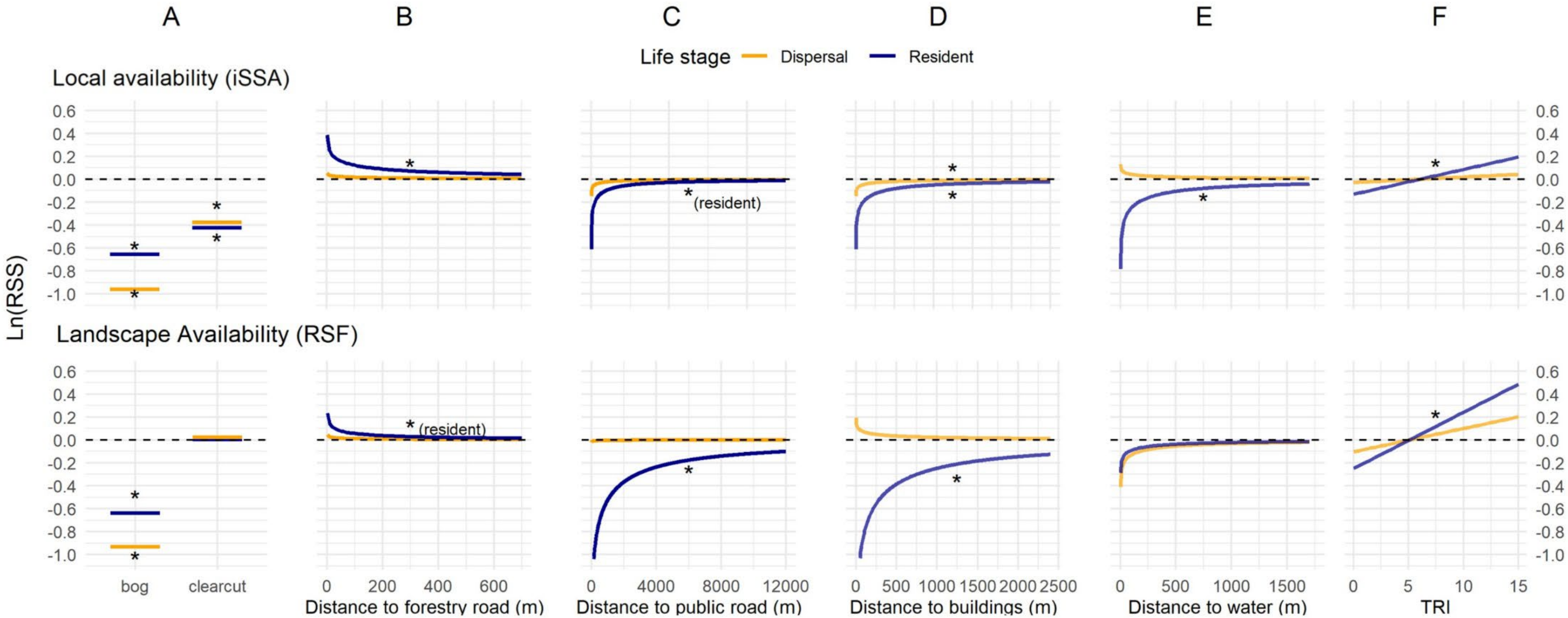

Figure 2. Relative selection strength (RSS) for dispersing and resident male brown bears from the inverse-variance weighted linear model. Column (A) is the RSS of staying in the habitat reference category (i.e. not bogs or clearcuts) compared with selecting for either bogs or clearcuts. Columns (B), (C), (D), and E) show the RSS of moving closer towards the features (leftward) vs staying at the same distance across a range of starting distances (x-axis). Column (F) illustrates the RSS of selecting a given TRI value (x-axis) over the mean value (4.19). * indicates covariate was significant for respective ‘Resident’ and ‘Dispersal’ models (95% CIs did not overlap zero) for the curve that it is nearest. In cases where placement is not obvious, clarification is given in parenthesis.

Human infrastructure

At the population level and across scales, dispersers were indifferent to human infrastructure, except for buildings which they avoided at the local scale. Residents avoided buildings and public roads, and selected forestry roads at both local and landscape scale. Residents did not alter their movement rate closer to buildings, while dispersers moved faster closer to buildings (Table 4, Figure 3c). Both dispersers and residents increased their movement rate closer to forestry roads and closer to public roads (Table 4).

Dispersers and residents moved 551 m/h and 599 m/h, respectively, faster when their step started on a forestry road compared with the movement rate when starting 500 m away from a forestry road (Figure 3a). Similarly, dispersers and residents moved 141 m/h and 169 m/h, respectively, faster when their step started on a public road compared with the movement rate at 500 m away from a public road (Figure 3b). In other words, the change in the movement speed for dispersers and residents was 3.26 and 3.54 times higher, respectively, on forestry roads compared with public roads.

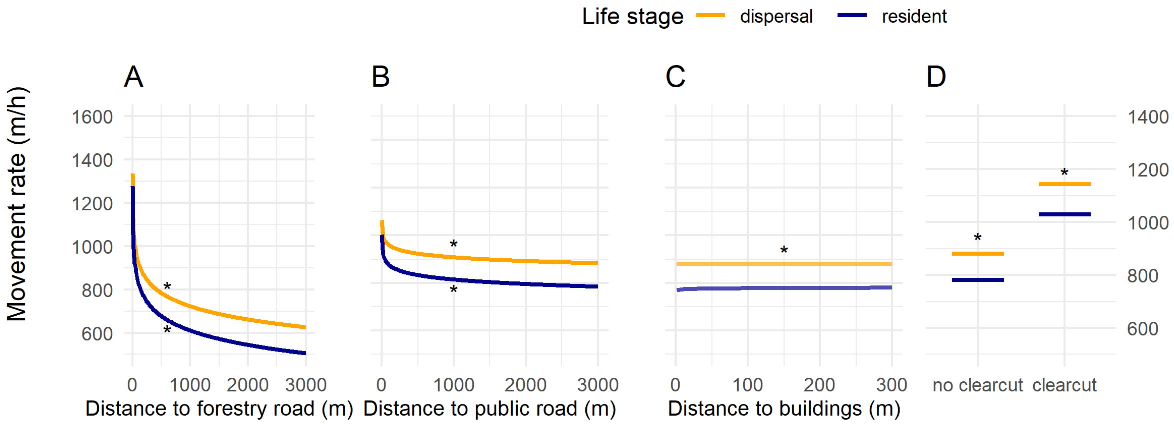

Figure 3. Mean movement rates (in meters/hour) for dispersing and resident male brown bears in relation to (A) distance to forestry roads, (B) distance to public roads with the same range as for forestry roads, (C) distance to buildings, (D) and whether or not the bear started in a clearcut. The focal variable has been varied while all other variables have been kept constant the mean of all used starting points and outside a clearcut for (A), (B), and (C). The asterisks * near 'Resident' and 'Dispersal' curves indicate that respective model estimates were significant (95% CIs did not overlap zero).

Discussion

We found evidence that human infrastructure is important for describing habitat selection and movement (P1 in support of H1) regardless of life stage (i.e. resident or disperser) at both the local and landscape scale, as models containing human infrastructure performed best. However, at the landscape scale, dispersers appeared indifferent towards most landscape features, including human infrastructure (Table 4 and Figure S2). Dispersers were more often indifferent towards human infrastructure at both scales (P2 in support of H2) and did not show the same avoidance patterns of human infrastructure as residents. Dispersers were less sensitive towards human infrastructure on the landscape scale than the local scale, however, this did not apply to residents (P3 partial support of H3). Furthermore, dispersers more often exhibited indifference to human infrastructure in both habitat selection and movement rates.

Human infrastructure appears important for both dispersers and resident at the local scale and the landscape scale (H1). At the local scale, dispersers and residents avoided buildings, and dispersers moved faster closer to buildings suggesting they are perceived as risky habitat. The lack of increased movement rate closer to buildings by residents might be due to residents generally being farther away from buildings. Both dispersers and residents moved faster when closer to public and forestry roads. Whether a road facilitates or impedes movement is likely dependent on the traffic volume [66]. This was presumably the case in our study area, as residents appeared to treat public roads as risky habitat (avoiding and moving faster), whereas they used the smaller forestry roads for travel (selecting and moving faster). The forestry roads are assumed to generally have low levels of human activity, and even lower at night when bears moved more (Figure S1). Mortality risk for bears along all roads during our study period was likely low, as traffic accidents do not account for a large proportion of mortality [<2%; 67] and our study ended before the onset of the hunting season, after which roads have an additive effect on hunting success [68]. Movement facilitation in relation to linear features, such as roads, has also been observed for brown bears in other areas [60], while treating public roads as risky has been reported for other species [69, 70]. Dispersers were indifferent in terms of habitat selection for either road type and traveled faster near both, indicating that public and forestry roads may potentially serve as risky features [71] or as facilitators of movement [72] during dispersal. This indifference might be explained by the dispersers lack of information on where to find roads, or large variation in the population of dispersers where some avoid roads while others may select for them.

Although the best models at the landscape scale contained human infrastructure for both life stages (support of H1), dispersers were mainly indifferent to human infrastructure. They also used habitat closer to human infrastructure compared with residents. This is in support of H2, i.e. dispersers are either more naïve or risk-tolerant to human infrastructure. In contrast, residents were sensitive to human infrastructure and avoided both public roads and buildings at both availability scales. Hence, we suggest that naivety or risk-tolerance plays a prominent role in the behavior of dispersers when navigating novel landscapes. Dispersal is often considered risky due to movement through novel landscapes [73], and human-derived risks can have an additive effect beyond what is 'normally expected' by animals when weighing the decision whether to disperse and where to go [13]. In contrast, the assumption that residents are more familiar with their home ranges and dispersers must navigate novel terrain, is supported by the residents' avoidance of potential human-derived risk at both local and landscape scales.

Alternatively, areas with lower human mortality risk might not be preferred by dispersers, due to increased intraspecific mortality risk or competition from larger, adult males [74, 75], which would effectively sandwich dispersing males between two sources of mortality risk [sensu 76], i.e. humans and conspecifics. This is also consistent with our core covariate findings, i.e., residents selected for rugged terrain, while dispersers did not. Similarly, clearcuts and bogs are open habitats in which bears have less cover from human detection [77]. Such habitats were avoided by both dispersers and residents at the local scale, indicating a similar avoidance of potential human-derived risk in these open or semi-open habitat types. Dispersing males in other large carnivores, such as African lions (*Panthera leo*) [8], African wild dogs (*Lycaon pictus*) [78] and gray wolves [7], depict a similar pattern with weaker or no avoidance of human infrastructure. Lack of avoidance of human infrastructure may be driven by the attempt to avoid of larger males. However, it could also be explained by the dispersing individual's inability to detect these features at relevant distances. Similarly, the lack of selection for landscape features preferred by older males, e.g. the lack of selection for rugged terrain by dispersers, may also be explained by the dispersing males not knowing where to find these features when moving through the landscape. This is supported by dispersers not selecting for any features on any of the scales. Alternatively, adult male habitat selection may emerge from learning, i.e. adjusting from being a dependent with its mother to that of an adult male.

Our selection of covariates might be more applicable toward residents, as it is based on the literature where more information is available for residents compared to dispersers. However, dispersers likely consider and respond to similar habitat features as residents, even though responses may differ. This is supported by our results, as the full model was best for both life stages and candidate models had identical sorting based on the mean ΔAIC and at both spatial scales (Table 4). We attribute the higher proportion of non-significant coefficients in the disperser models to higher individual variation among dispersers. The more risk-tolerant or naïve behavior in dispersers [7, 8] combined with a high level of individual variation may be important to maintain structural and functional connectivity between populations, as bolder or more risk-tolerant individuals [79] may disperse more effectively through human-modified landscapes. At the same time, this also implies that areas important for connectivity with a high human footprint may experience higher levels of human-bear conflict with implications for functional connectivity, unless carefully designed mitigation strategies are adopted [80].

We found partial support of H3, that the scale of availability influences how sensitive bears are towards human infrastructure, as only dispersers were more selective at the local scale compared with the landscape scale (P3). This is in contrast to what has been observed in pronghorn antelopes (*Antilocapra americana*) which showed stronger avoidance at the landscape scale than the local scale during migration [81], illustrating the existence of different strategies for which spatial scale animals avoid human infrastructure. Furthermore, dispersing brown bear males more often treated human infrastructure indifferently in habitat selection and movement rates at the local scale (Table 4). In our study area, bears are intensively hunted annually [upwards of 10% of the population; 82], putting them into contact with human-derived risk virtually everywhere in the study area, and bears modify their behavior to minimize human predation risk [17, 48, 83, 84]. Hence, resident bears likely select areas where human impact is low [35] and further reduce potential encounter rates with humans through behavioral changes on local spatial scales and temporally [28, 48]. As dispersers were more exposed to human infrastructure, they are potentially also more exposed to higher human predation risk. Indeed, hunting mortality of males compared to females appears to be higher at the onset of dispersal in this bear population [68, 85], which could partially be due to male-biased dispersal [41], increased risk-taking or tolerance during dispersal, and the inability of dispersing males to adequately recognize and adjust to novel human-derived mortality risk.

Conclusions

Our study highlights that life stage can influence how individuals respond to human landscape features across scales. The key to attaining reliable connectivity models is the recognition that animal dispersal decisions and movement patterns are life stage dependent. Our findings suggest that risk-tolerant or naïve dispersers might use movement pathways that more risk-averse or habitat-familiar residents would avoid. As a result, landscape resistance or connectivity maps derived from dispersal movement data may provide more numerous as well as more realistic pathways than those derived from resident movement data alone [86-88]. At the same time, the increased risk-tolerance or naivety in dispersers has the potential to exacerbate human-bear conflicts in important connectivity areas. Hence, identifying these areas early on from connectivity maps can help to mitigate human-bear conflict. The differences in scale-specific decisions between dispersers and residents provide the foundation for understanding functional connectivity of a population, in which animals disperse and establish a home range for subsequent reproduction [89]. Attaining individual-based dispersal data on large carnivores is costly but informative, particularly in human-dominated systems where coexistence has been touted as not only possible, but imperative on some level for large carnivore persistence [90-92].

Declarations

Ethics approval and consent to participate

Permits for collaring brown bears were given by the Swedish authorities and ethical committees (Uppsala Djurförsöksetiska Nämnd: C40/3, C212/9, C47/9, C210/10, C7/12, C268/12, C18/15. Statens Veterinärmediciniska Anstalt, Jordbruksverket, Naturvårdsverket: Dnr 35-846/03, Dnr 412-7093-08 NV, Dnr 412-7327-09 Nv, Dnr 31-11102/12, NV-01758-14).

Consent for publication

Not applicable

Availability of data and materials

The datasets used and analysed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Authors` contributions

AZ, JEH, NHT, OGS and SF conceived the idea. JEH, NHT and SF organized the data and did the statistical analysis. NHT lead the writing of the manuscript with significant contributions from JEH and SF. JK contributed to project administration, capture and collaring of bears. AZ, JK and OGS secured funding. All authors contributed significantly through comments and edits on the manuscript.

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Supplement S1

Human impact on life stage dependent movement in male brown bear (Ursus arctos)

Step-by-step documentation for HMM fitting procedure

In this supplement, we go step-by-step through the fitting procedure of hidden Markov models for an individual male bear, W0612, and the selection of dates for the dispersal process.

Load required packages:

```
library(moveHMM)
library(doBy)
library(ggplot2)
library(plyr)
library(plotly)
```

Importing and prepping the data

Import geolocations* from one male bear (W0612)

```
W0612 <- readRDS("C:/Users/jeh/Documents/USN-PhD/Analysis/Bear_Movement/Trajectory_Splitting/W0612_anon

# subset to active season, 01 April - 01 October

W0612 <- subset(W0612, format(GMT.date,'%m%d')>='04-01' & format(GMT.date, '%m%d')
                <= '10-02')
```

Create a ‘move’ object from geolocations. This will calculate distance traveled between each step as well as turning angles of movement.

```
W0612Move <- prepData(W0612, type = "UTM", coordNames = c("x1", "y1"))
```

We keep only steps that are separated by an hour. This prevents unrealistic step lengths and turning angles from being included in the modeling procedure.

```
# copy to a new object called "W0612Reg"

W0612Reg <- W0612Move

# get time differences between each step

W0612Reg$diffHour <- difftime(W0612Move$GMT.date[1:length(W0612Move$GMT.date)] ,
```

```
                              W0612Move$GMT.date[2:length(W0612Move$GMT.date)])

# keep only times that are separated by an hour

W0612Reg <- W0612Reg[W0612Reg$diffHour >= -1 & W0612Reg$diffHour < 2, ]

# remove column for time difference

W0612Reg$diffHour <- NULL
```

Fitting HMMs

In the following section, we fit three models with two behavioral states, representing short and long movement patterns. Each set of initial parameters are different, which increases the chance of finding the global maximum (citation).

Fitting a hidden Markov model to movement data requires four starting parameters specified for n behavioral states. The first parameter is mean step length distance, mu. The second is the standard deviation for each mean, sigma. The third parameter is the mean turning angle, angleMean. The final parameter is kappa, concentration of the turning angle.

The first set of initial parameters were chosen by looking at summaries of the step lengths and turning angles, histograms and density plots. The second set of initial parameters were "wider" (smaller/larger) values than the first set. The initial parameters for the third model were the estimated parameters from the previous model.

There is no exact science behind the selection of initial parameters, but [practical guidance] (https://cran.r-project.org/web/packages/moveHMM/vignettes/moveHMM-starting-values.pdf) is available.

The model specification is as follows:

fitHMM(move_object, number of behavior states, initial parameters, theoretical distribution for step lengths, theoretical distribution for turning angles)

We selected the gamma distribution for the step lengths and the vonMises distribution for the turning angles.

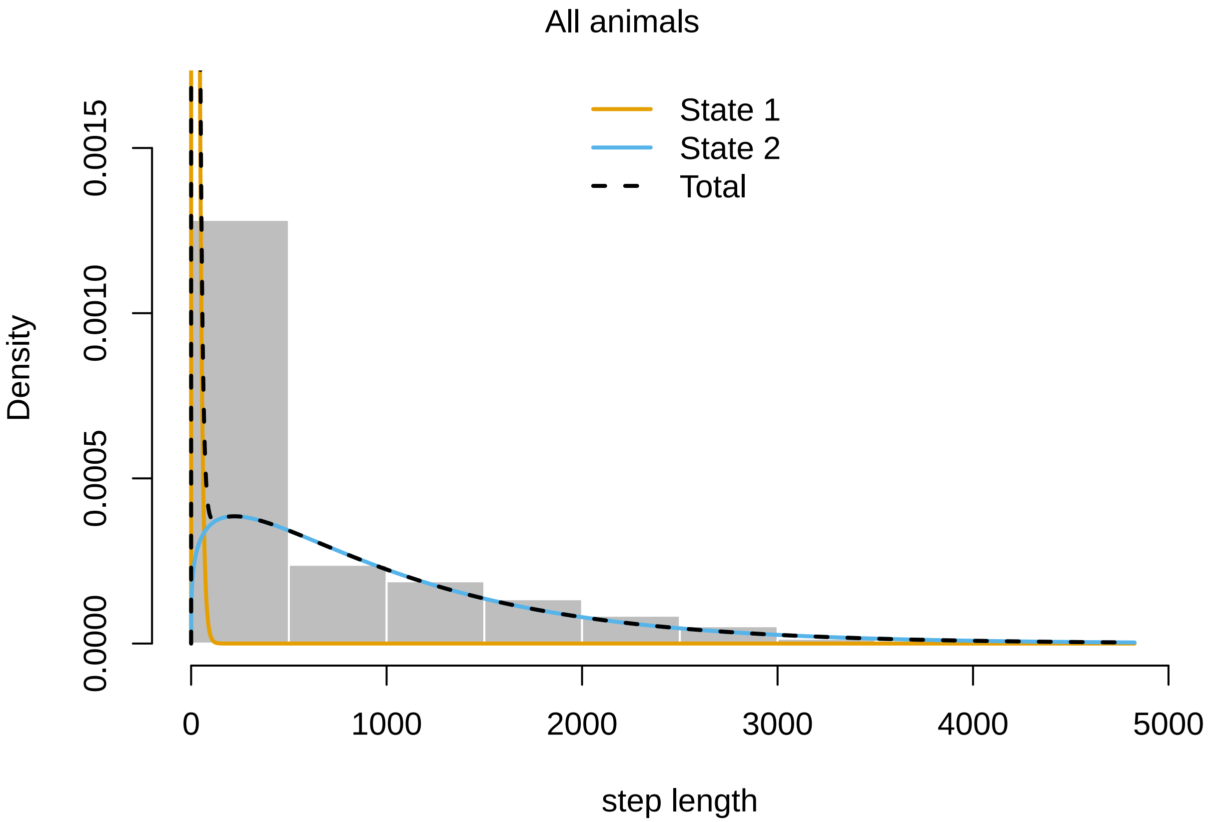
```
# first set of initial parameters

mu2a <- c(10, 1000)
sigma2a <- c(20, 2000)
angleMean2a <- c(pi, 0.005)
kappa2a <- c(0.2, 2)
stepPar2a <- c(mu2a, sigma2a)
anglePar2a <- c(angleMean2a, kappa2a)

# fit the first 2-state HMM

W0612_2a <- fitHMM(W0612Reg, nbStates = 2, stepPar0 = stepPar2a, anglePar0 = anglePar2a,
                   stepDist = "gamma", angleDist = "vm")
W0612_2a
```

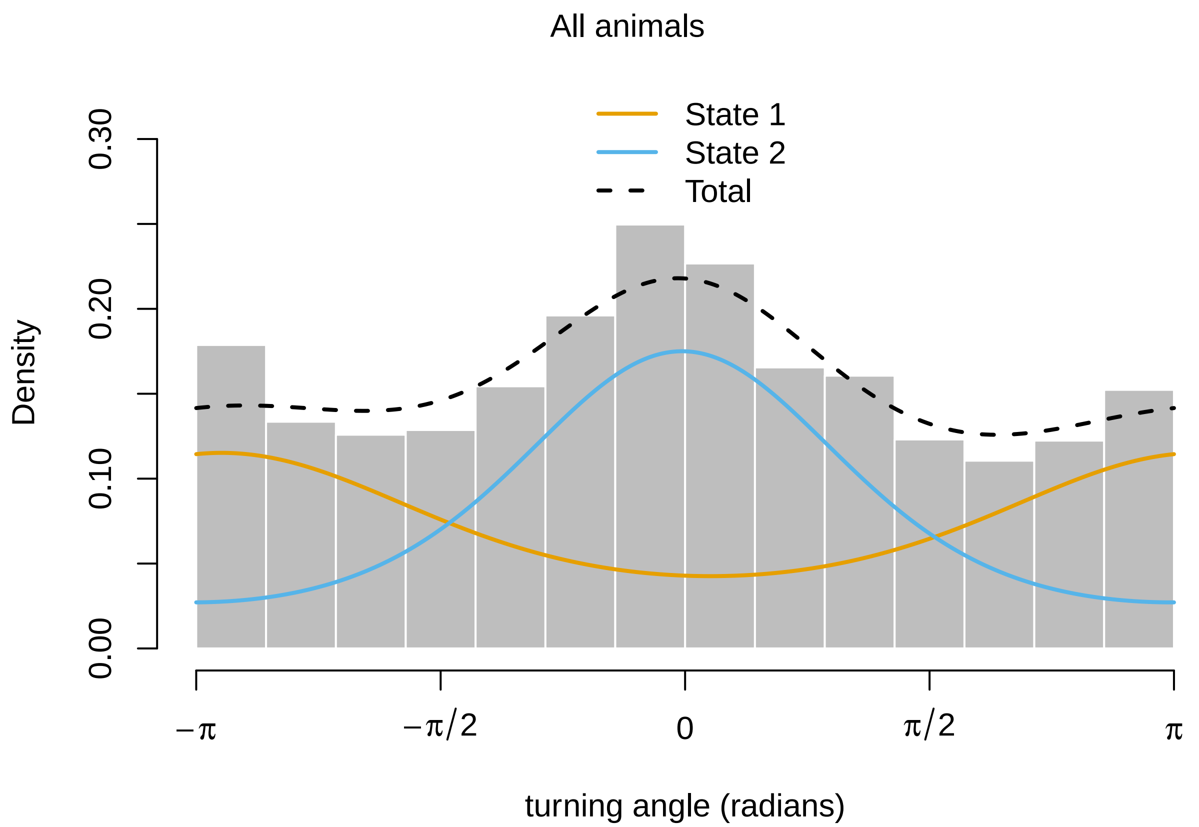
```
## Value of the maximum log-likelihood: -26234.64
##
## Step length parameters:
## ----------------------
```

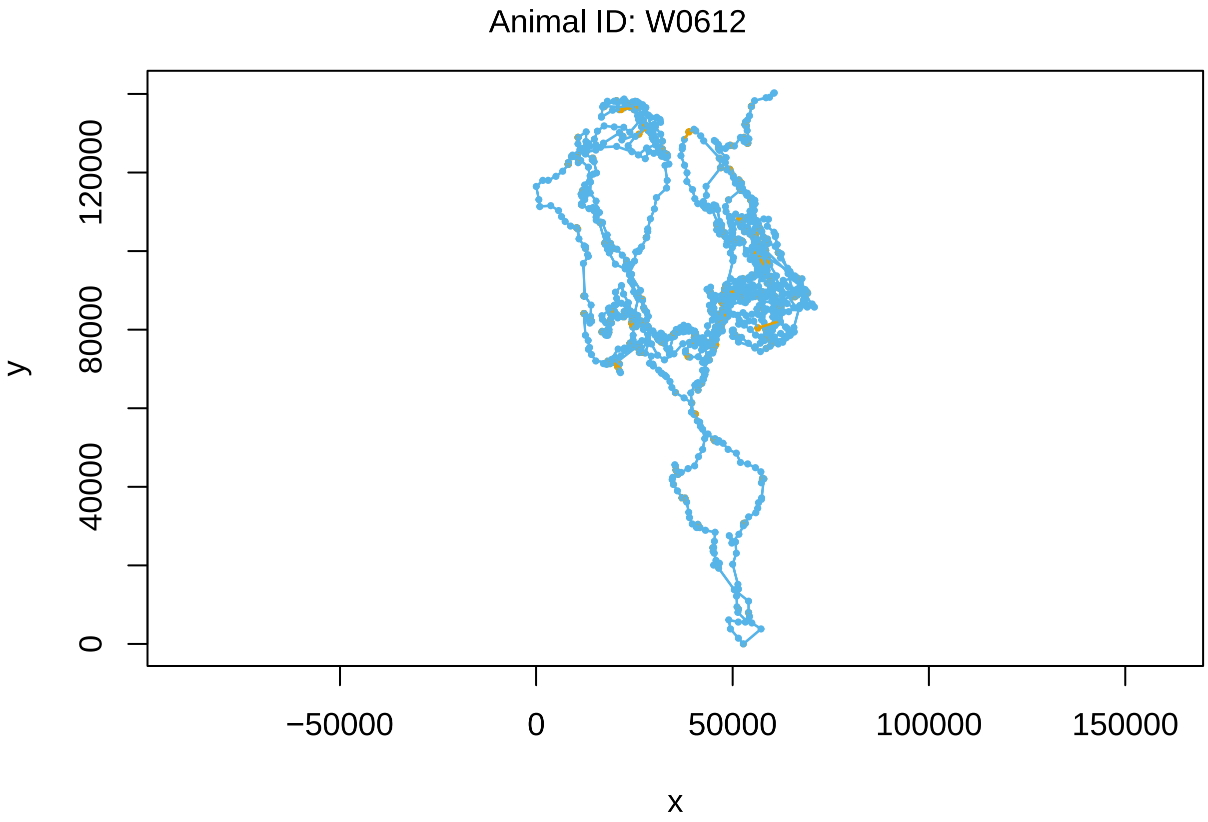
```
##       state 1   state 2
## mean 17.00918 1042.0373
## sd   14.02674  924.3737
##
## Turning angle parameters:
## ------------------------
##                  state 1     state 2
## mean          -2.9787585 -0.01945528
## concentration  0.4975304  0.93201121
##
## Regression coeffs for the transition probabilities:
## --------------------------------------------------
##              1 -> 2    2 -> 1
## intercept -1.281184 -1.476296
##
## Transition probability matrix:
## -----------------------------
##           [,1]      [,2]
## [1,] 0.7826513 0.2173487
## [2,] 0.1859875 0.8140125
##
## Initial distribution:
## --------------------
## [1] 1.154684e-06 9.999988e-01
```

```
# calculate confidence intervals and plot the fitted model results

W0612_2_a <- CI(W0612_2a)
plot(W0612_2a, plotCI = TRUE)
```

```
## Decoding states sequence... DONE
```


All animals
State 1
State 2
Total
Density
0.0000
0.0005
0.0010
0.0015
0
1000
2000
3000
4000
5000
step length


All animals
State 1
State 2
Total
Density
0.00
0.10
0.20
0.30
−π
−π/2
0
π/2
π
turning angle (radians)



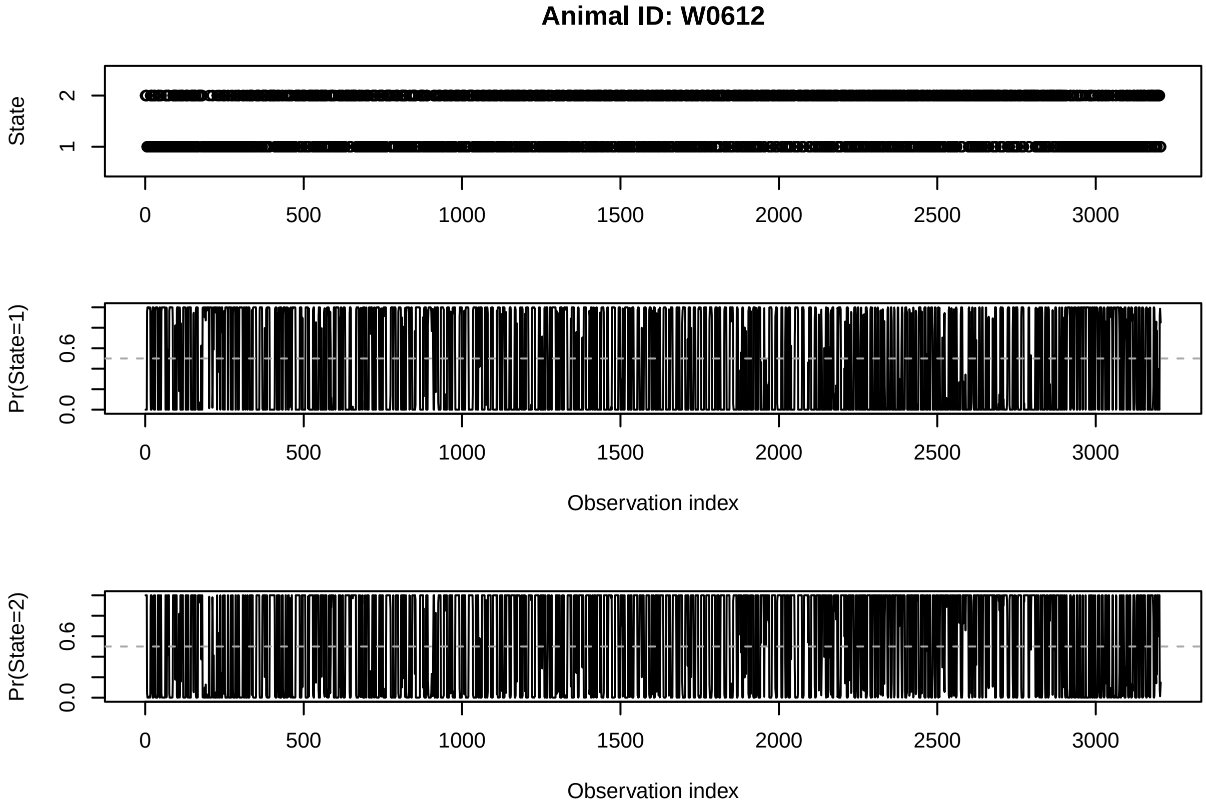
The Viterbi algorithm (Zucchini and MacDonald 2009) assigns probable behavioral states to each step. The plotStates function returns a plow showing the probability of being in a particular state at each observation index location (step).

```
head(viterbi(W0612_2a), n = 20)
```

```
##  [1] 2 2 2 2 2 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2
```

```
plotStates(W0612_2a)
```

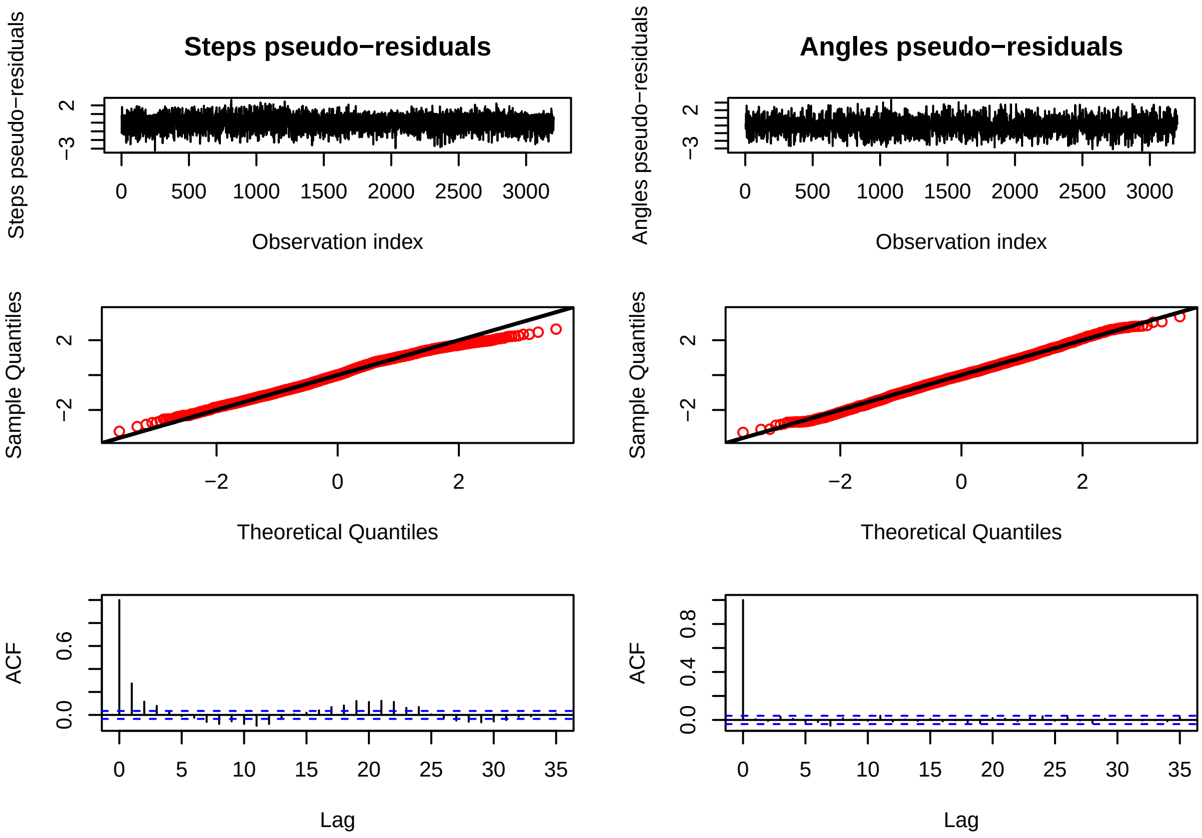
```
## Decoding states sequence... DONE
## Computing states probabilities... DONE
```



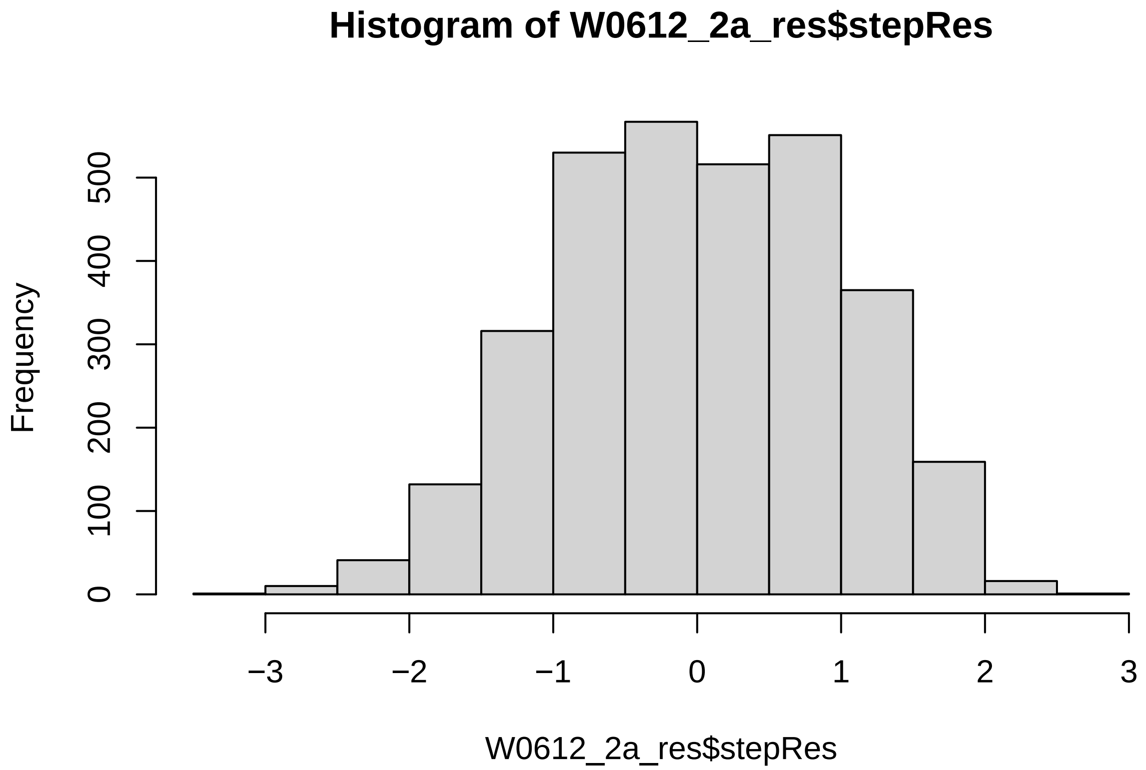
The final step of the process is to look at the residuals to assess the fit of the model to the data. Plotting the model object directly will show the time series, qq-plots, and sample ACF functions of the pseudo-residuals for steps and turning angles. We also produced histograms of the pseudo-residuals for step lengths and turning angles.

```
plotPR(W0612_2a)
```

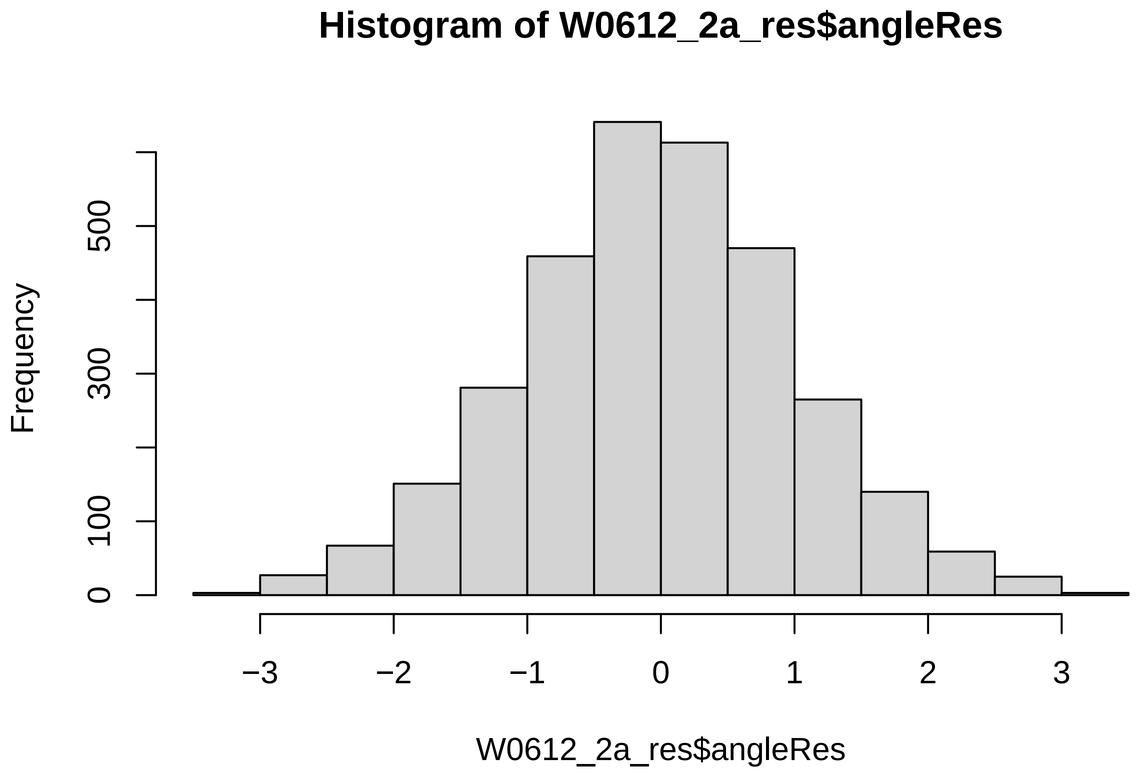
```
## Computing pseudo-residuals... DONE
```



```r
W0612_2a_res <- pseudoRes(W0612_2a)
hist(W0612_2a_res$stepRes)
```



```
hist(W0612_2a_res$angleRes)
```



We fit the remaining two models with different initial parameters.

```
# second set of parameters (wider values)

mu2b <- c(5, 2000)
sigma2b <- c(8, 1000)
angleMean2b <- c(pi, -0.005)
kappa2b <- c(0.1, 1)
stepPar2b <- c(mu2b, sigma2b)
anglePar2b <- c(angleMean2b, kappa2b)


# fit the second 2-state HMM

W0612_2b <- fitHMM(W0612Reg, nbStates = 2, stepPar0 = stepPar2b, anglePar0 = anglePar2b,
                   stepDist = "gamma", angleDist = "vm")
W0612_2b
```

```
## Value of the maximum log-likelihood: -26234.64
##
## Step length parameters:
## ----------------------
##       state 1   state 2
## mean 17.00917 1042.0356
## sd   14.02674  924.3724
##
```

```
## Turning angle parameters:
## ------------------------
##                  state 1     state 2
## mean          -2.9787801 -0.01945568
## concentration  0.4975309  0.93201136
##
## Regression coeffs for the transition probabilities:
## --------------------------------------------------
##              1 -> 2    2 -> 1
## intercept -1.281185 -1.476297
##
## Transition probability matrix:
## -----------------------------
##           [,1]      [,2]
## [1,] 0.7826515 0.2173485
## [2,] 0.1859874 0.8140126
##
## Initial distribution:
## --------------------
## [1] 4.445916e-07 9.999996e-01
```

```
# third set of parameters (estimated parameters from previous model)

mu2c <- c(17, 1042)
sigma2c <- c(14, 924)
angleMean2c <- c(-2.98, -0.02)
kappa2c <- c(0.5, 0.93)
stepPar2c <- c(mu2c, sigma2c)
anglePar2c <- c(angleMean2c, kappa2c)


# fit the third 2-state HMM

W0612_2c <- fitHMM(W0612Reg, nbStates = 2, stepPar0 = stepPar2c, anglePar0 = anglePar2c,
                   stepDist = "gamma", angleDist = "vm")
W0612_2c
```

```
## Value of the maximum log-likelihood: -26234.64
##
## Step length parameters:
## ----------------------
##       state 1   state 2
## mean 17.00917 1042.0380
## sd   14.02674  924.3724
##
## Turning angle parameters:
## ------------------------
##                 state 1    state 2
## mean          -2.978775 -0.0194565
## concentration  0.497498  0.9320255
##
## Regression coeffs for the transition probabilities:
## --------------------------------------------------
##              1 -> 2    2 -> 1
```

```
## intercept -1.281186 -1.476288
##
## Transition probability matrix:
## -----------------------------
##           [,1]      [,2]
## [1,] 0.7826515 0.2173485
## [2,] 0.1859887 0.8140113
##
## Initial distribution:
## --------------------
## [1] 8.609635e-06 9.999914e-01
```

Results of the 2-state modeling indicated a poor fit of step lengths in the model. We continue with fitting a 3-state model with the following behaviors: resting, foraging/short-distance movement, and directed, long-distance traveling.

Fitting of the 3-state HMM is the same as for a 2-state except that we have three values for each parameter that represent the behavioral states. Initial parameter values for the 3-state HMMs were chosen as follows:

1. Educated guess based on step length and turning angle summaries.
2. Creating three equal bins for the distributions.
3. From a combination histogram-density plot in ggplot2.
4. The estimated parameters from the previous model.

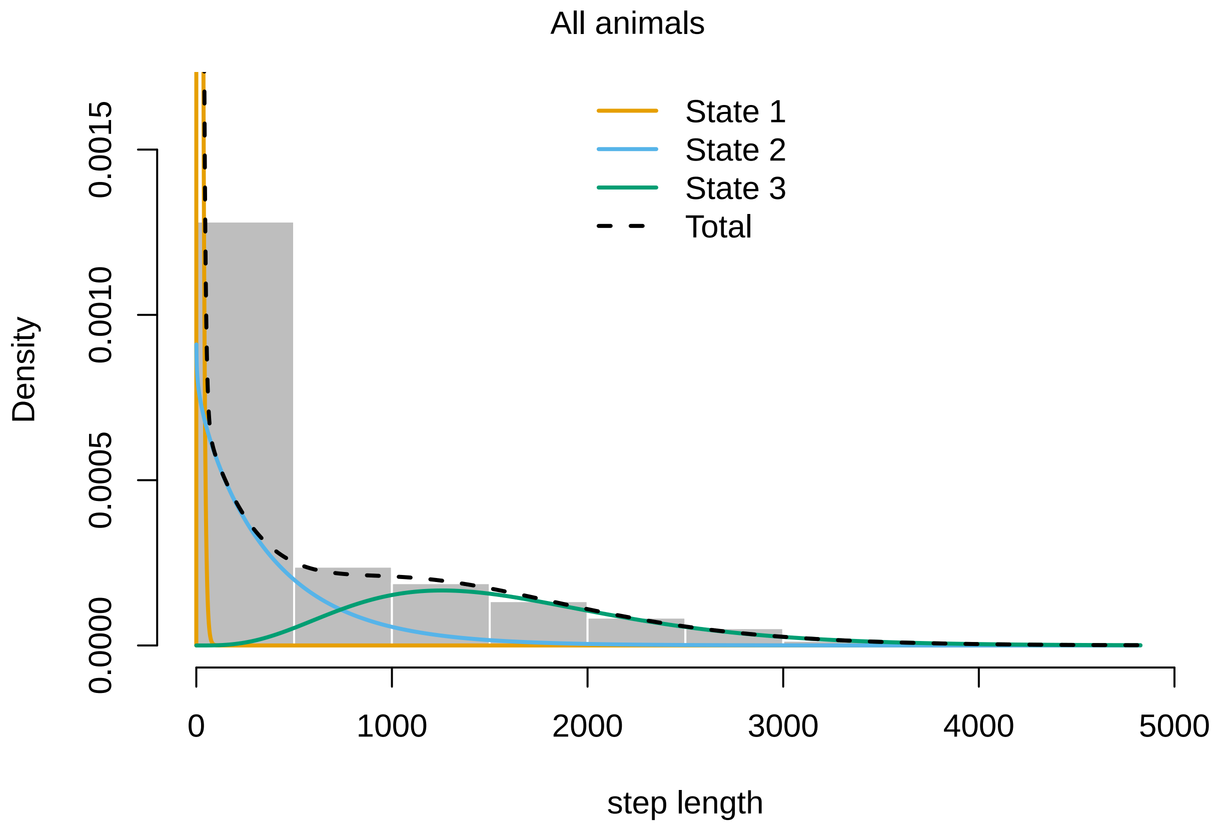
```
# initial parameters for 3-state model

mu3a <- c(4, 200, 3500)
sigma3a <- c(5, 300, 1500)
angleMean3a <- c(pi, 0.005, 0.05)
kappa3a <- c(0.1, 0.5, 1)
stepPar3a <- c(mu3a, sigma3a)
anglePar3a <- c(angleMean3a, kappa3a)


# fit the first 3-state HMM

W0612_3a <- fitHMM(W0612Reg, nbStates = 3, stepPar0 = stepPar3a, anglePar0 = anglePar3a,
                   stepDist = "gamma", angleDist = "vm")
W0612_3a
```

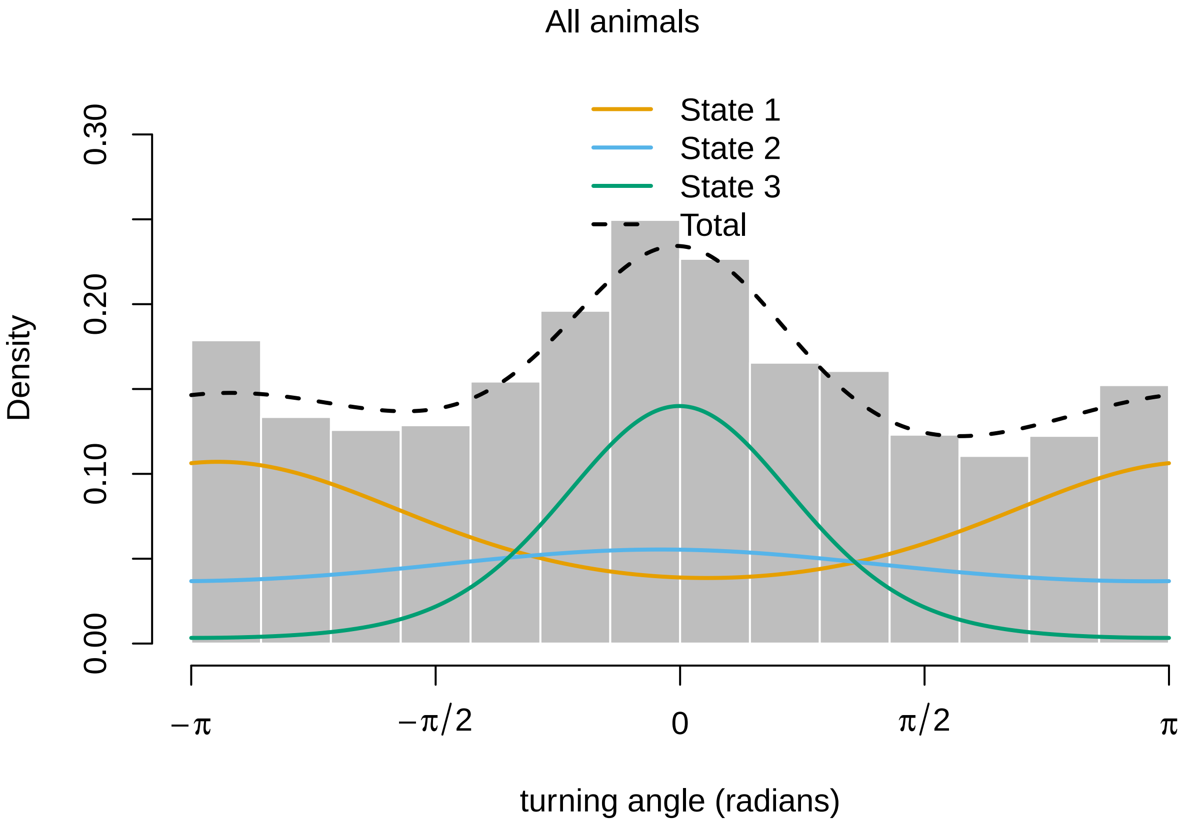
```
## Value of the maximum log-likelihood: -25864.43
##
## Step length parameters:
## ----------------------
##       state 1  state 2   state 3
## mean 13.87421 388.2844 1604.8023
## sd   10.06471 396.6112  749.0172
##
## Turning angle parameters:
## ------------------------
##                  state 1    state 2      state 3
## mean          -2.9698675 -0.1243276 -0.005814789
## concentration  0.5097004  0.2057111  1.868910436
```

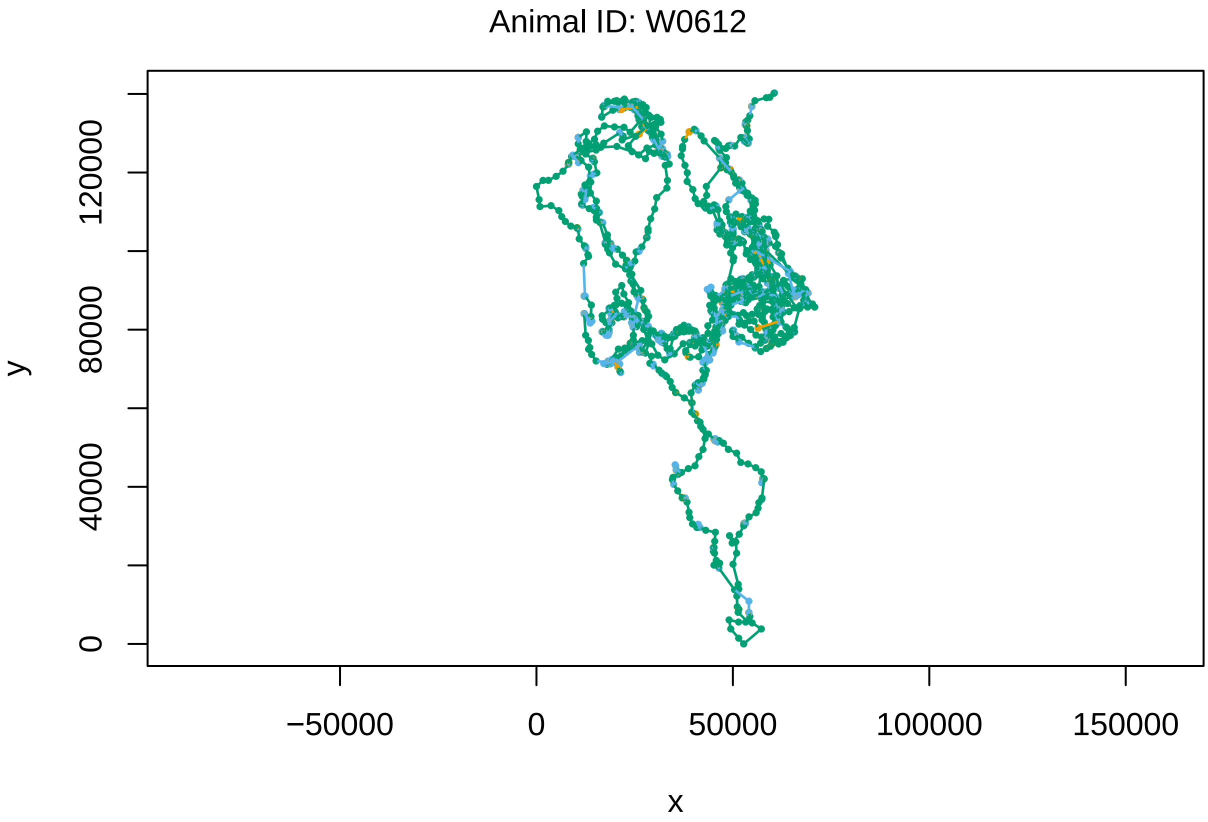
```
##
## Regression coeffs for the transition probabilities:
## --------------------------------------------------
##               1 -> 2    1 -> 3     2 -> 1     2 -> 3    3 -> 1    3 -> 2
## intercept -1.289126 -3.098643 -0.6737897 -0.9160029 -2.426462 -1.161481
##
## Transition probability matrix:
## -----------------------------
##             [,1]      [,2]       [,3]
## [1,] 0.75721904 0.2086225 0.03415843
## [2,] 0.26691251 0.5235909 0.20949663
## [3,] 0.06304459 0.2233685 0.71358691
##
## Initial distribution:
## --------------------
## [1] 1.873944e-06 9.999981e-01 3.746110e-09
```

```
# calculate confidence intervals and plot the fitted model results

W0612_3a_CI <- CI(W0612_3a)

plot(W0612_3a, plotCI = TRUE)
```

```
## Decoding states sequence... DONE
```




All animals
State 1
State 2
State 3
Total
Density
0.00
0.10
0.20
0.30
−π
−π/2
0
π/2
π
turning angle (radians)



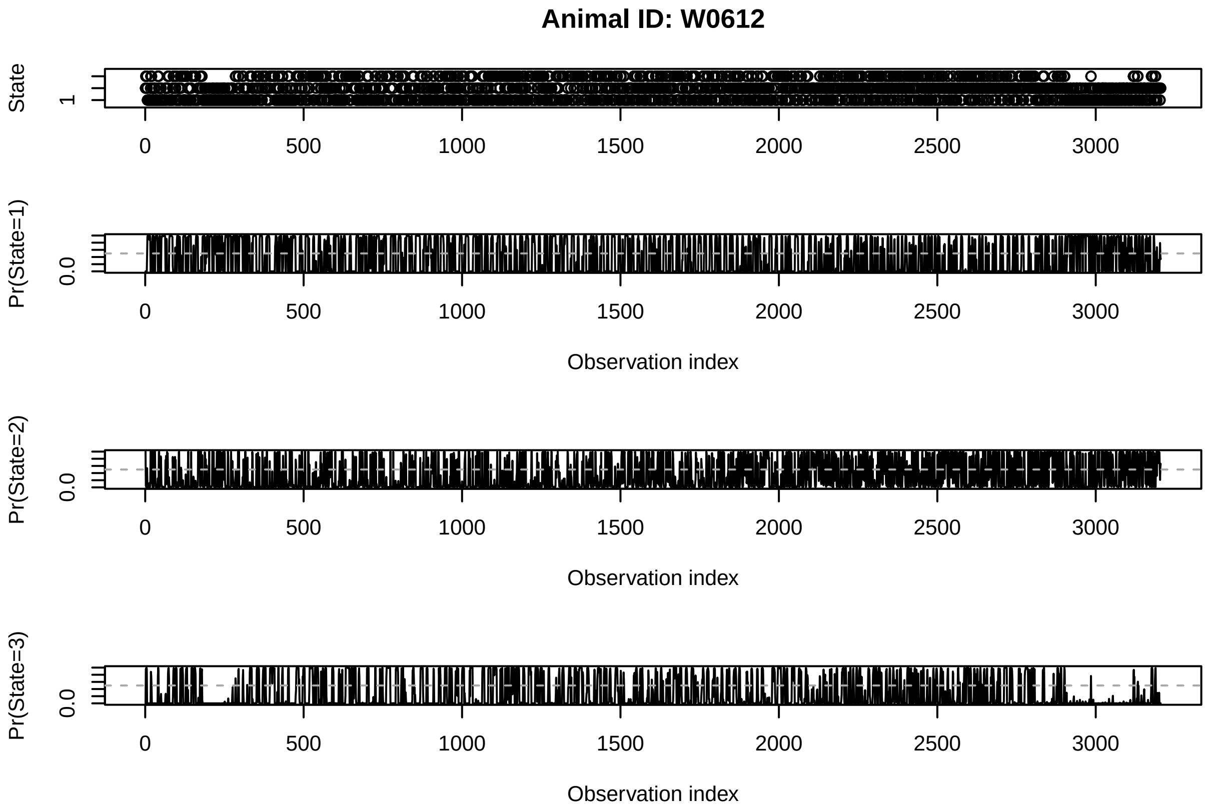
As before, we use the Viterbi algorithm to classify the states for each step.

```
head(viterbi(W0612_3a), n = 20)
```

```
##  [1] 2 3 3 3 3 2 1 1 1 1 1 1 1 1 1 1 2 3 3 3
```

```
plotStates(W0612_3a)
```

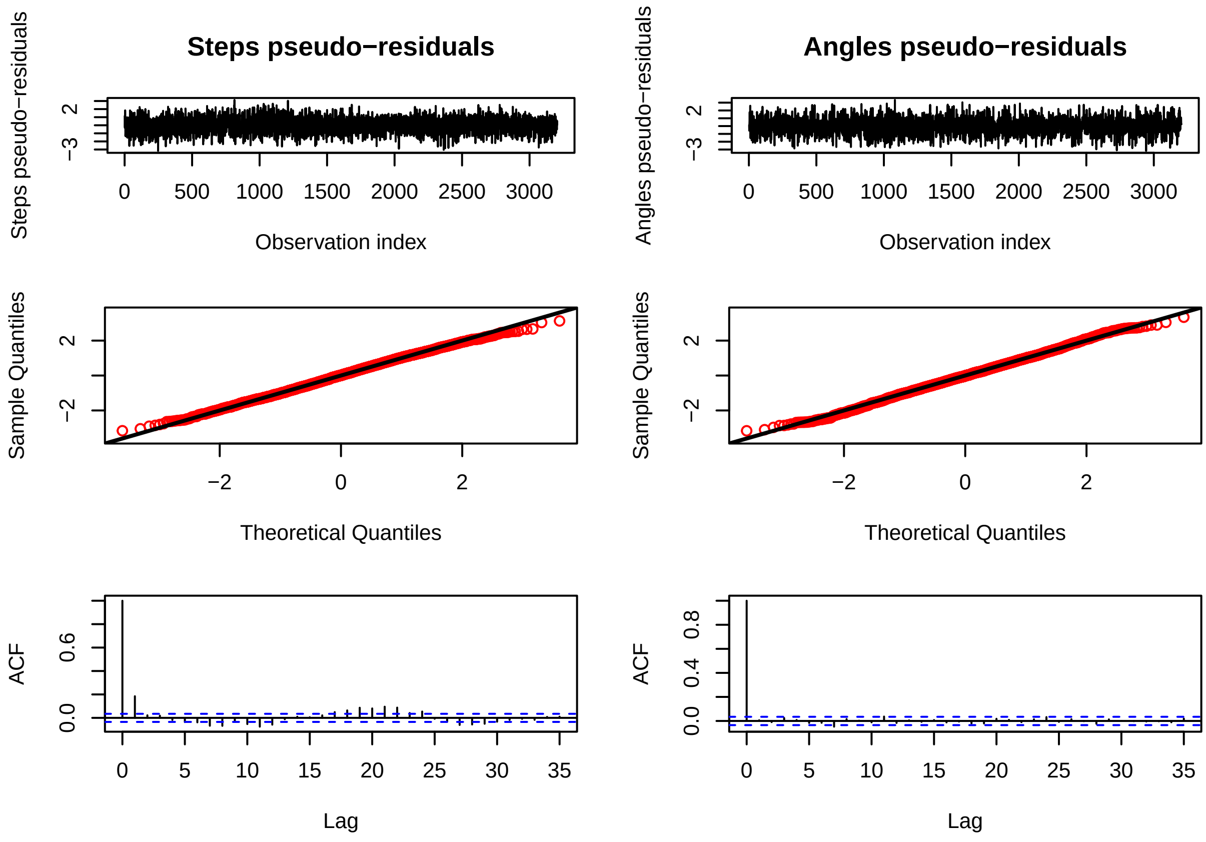
```
## Decoding states sequence... DONE
## Computing states probabilities... DONE
```



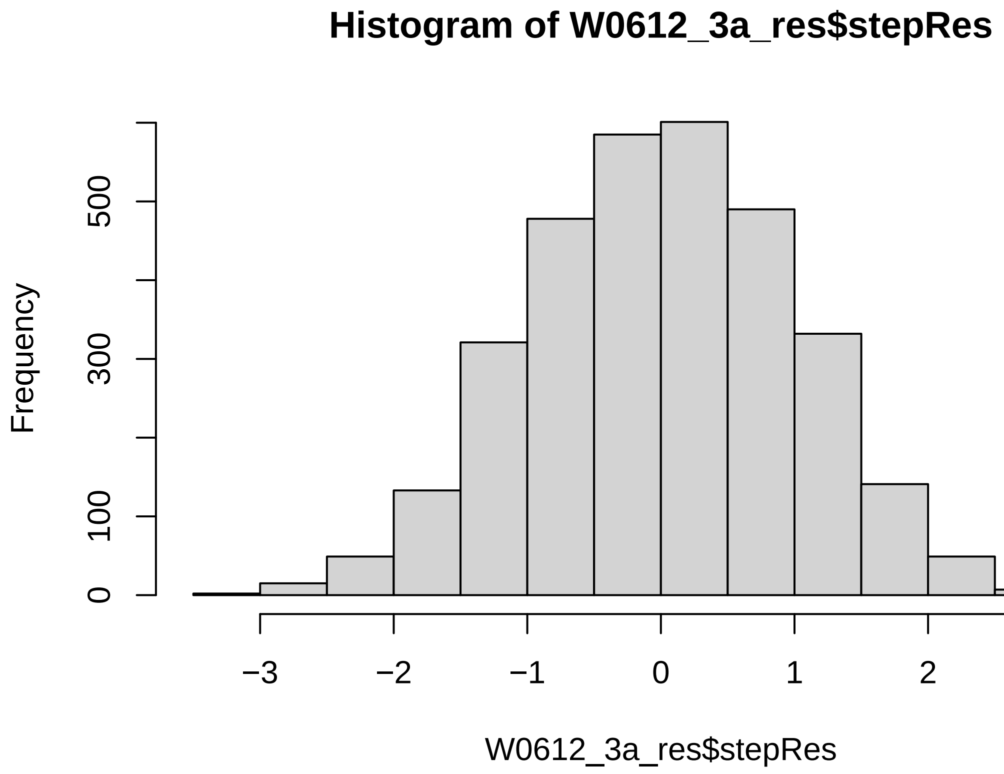
Inspect the pseudo-residuals for model fit.

```
plotPR(W0612_3a)
```

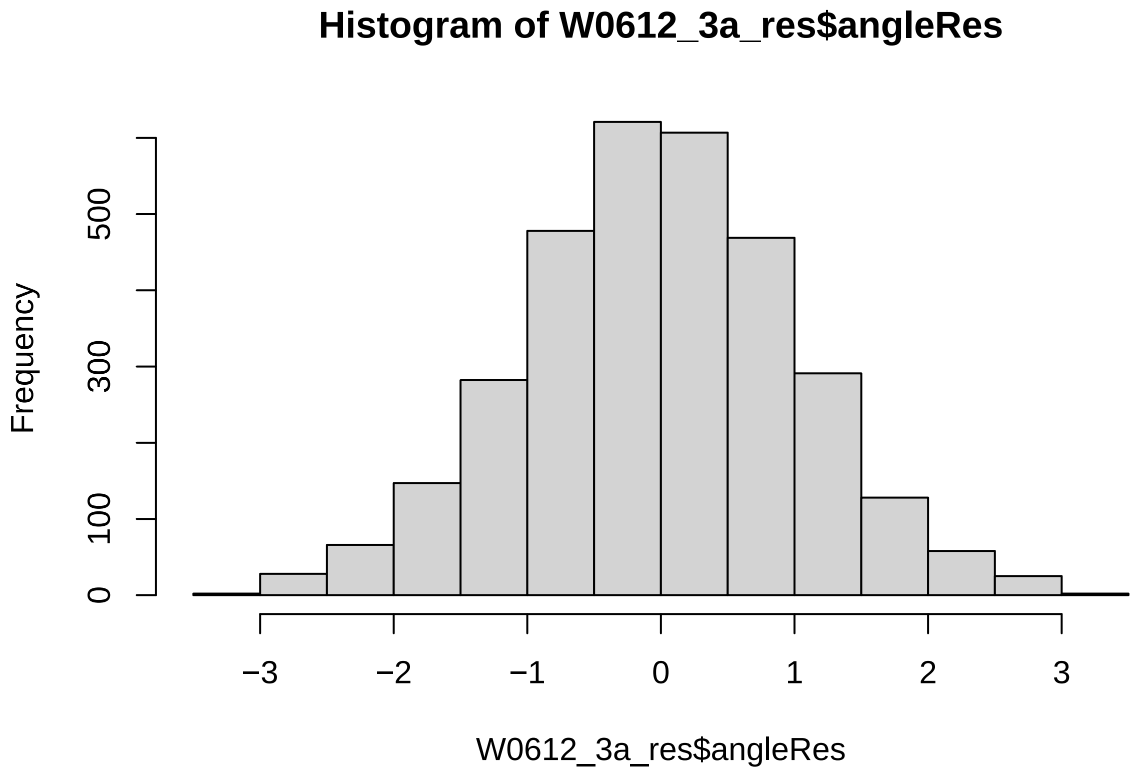
```
## Computing pseudo-residuals... DONE
```



```
W0612_3a_res <- pseudoRes(W0612_3a)
hist(W0612_3a_res$stepRes)
```



```
hist(W0612_3a_res$angleRes)
```



Fit the remaining three 3-state HMMs.

```
# second set of parameters (from equal binning)

mu3b <- c(10, 300, 2000)
sigma3b <- c(5, 150, 750)
angleMean3b <- c(pi,-0.005974, 1.57)
kappa3b <- c(1, 1, 1)
stepPar3b <- c(mu3b, sigma3b)
anglePar3b <- c(angleMean3b, kappa3b)

# fit the second 3-state HMM

W0612_3b <- fitHMM(W0612Reg, nbStates = 3, stepPar0 = stepPar3b, anglePar0 = anglePar3b,
                   stepDist = "gamma", angleDist = "vm")
W0612_3b
```

```
## Value of the maximum log-likelihood: -25864.43
##
## Step length parameters:
## ----------------------
##       state 1  state 2  state 3
## mean 13.87423 388.2872 1604.803
## sd   10.06474 396.6137  749.017
##
## Turning angle parameters:
```

```
## -------------------------
##                  state 1    state 2      state 3
## mean           -2.969865 -0.1243188 -0.005815661
## concentration  0.509698  0.2057129  1.868911138
##
## Regression coeffs for the transition probabilities:
## ----------------------------------------------------
##             1 -> 2    1 -> 3     2 -> 1     2 -> 3    3 -> 1    3 -> 2
## intercept -1.28913 -3.098652 -0.6737915 -0.9160046 -2.426423 -1.161484
##
## Transition probability matrix:
## -----------------------------
##           [,1]      [,2]       [,3]
## [1,] 0.7572199 0.2086219 0.03415817
## [2,] 0.2669122 0.5235913 0.20949646
## [3,] 0.0630469 0.2233675 0.71358556
##
## Initial distribution:
## ---------------------
## [1] 5.665121e-07 9.999994e-01 6.391494e-10
```

```
# third set of parameters (from histogram-density plot in ggplot2)

mu3c <- c(25, 500, 1500)
sigma3c <- c(30, 300, 750)
angleMean3c <- c(pi,-0.005974, 1.57)
kappa3c <- c(0.5, 0.75, 1)
stepPar3c <- c(mu3c, sigma3c)
anglePar3c <- c(angleMean3c, kappa3c)

# fit the third 3-state HMM

W0612_3c <- fitHMM(W0612Reg, nbStates = 3, stepPar0 = stepPar3c, anglePar0 = anglePar3c,
                   stepDist = "gamma", angleDist = "vm")
W0612_3c
```

```
## Value of the maximum log-likelihood: -25864.43
##
## Step length parameters:
## ----------------------
##       state 1  state 2   state 3
## mean 13.87423 388.2859 1604.8017
## sd   10.06474 396.6122  749.0182
##
## Turning angle parameters:
## -------------------------
##                   state 1    state 2      state 3
## mean           -2.9698641 -0.1243471 -0.005813025
## concentration  0.5096999  0.2057083  1.868919615
##
## Regression coeffs for the transition probabilities:
## ----------------------------------------------------
##              1 -> 2    1 -> 3     2 -> 1     2 -> 3    3 -> 1    3 -> 2
## intercept -1.289134 -3.098638 -0.6737932 -0.9159935 -2.426424 -1.161486
```

```
##
## Transition probability matrix:
## -----------------------------
##            [,1]      [,2]       [,3]
## [,1] 0.75722019 0.2086212 0.03415866
## [2,] 0.26691128 0.5235903 0.20949839
## [3,] 0.06304689 0.2233671 0.71358598
##
## Initial distribution:
## --------------------
## [1] 1.291640e-05 9.999870e-01 6.550713e-08
```

```
# fourth set of parameters (the estimated parameters of the previous model)

mu3d <- c(14, 388, 1605)
sigma3d <- c(10, 397, 749)
angleMean3d <- c(-2.97,-0.124, -0.006)
kappa3d <- c(0.51, 0.21, 1.87)
stepPar3d <- c(mu3d, sigma3d)
anglePar3d <- c(angleMean3d, kappa3d)

# fit the fourth 3-state HMM

W0612_3d <- fitHMM(W0612Reg, nbStates = 3, stepPar0 = stepPar3d, anglePar0 = anglePar3d,
                   stepDist = "gamma", angleDist = "vm")
W0612_3d
```

```
## Value of the maximum log-likelihood: -25864.43
##
## Step length parameters:
## ----------------------
##       state 1  state 2   state 3
## mean 13.87421 388.2857 1604.8032
## sd   10.06471 396.6125  749.0181
##
## Turning angle parameters:
## ------------------------
##                  state 1    state 2      state 3
## mean          -2.9698623 -0.1243197 -0.005814957
## concentration  0.5096991  0.2057115  1.868915061
##
## Regression coeffs for the transition probabilities:
## --------------------------------------------------
##              1 -> 2    1 -> 3     2 -> 1     2 -> 3    3 -> 1   3 -> 2
## intercept -1.289122 -3.098663 -0.6737882 -0.9159975 -2.426431 -1.16148
##
## Transition probability matrix:
## -----------------------------
##           [,1]      [,2]       [,3]
## [1,] 0.7572189 0.2086233 0.03415775
## [2,] 0.2669125 0.5235901 0.20949745
## [3,] 0.0630464 0.2233683 0.71358529
##
## Initial distribution:
```

```
## --------------------
## [1] 2.255205e-06 9.999977e-01 4.853313e-09
```

Model selection and assigning behavioral states to steps

We use Akaike's Information Criterion (AIC) to determine which model has the best fit to the data.

```
AIC(W0612_2a, W0612_2b, W0612_2c, W0612_3a, W0612_3b, W0612_3c, W0612_3d)
```

```
##      Model      AIC
## 1 W0612_3b 51768.86
## 2 W0612_3a 51768.86
## 3 W0612_3d 51768.86
## 4 W0612_3c 51768.86
## 5 W0612_2b 52491.27
## 6 W0612_2a 52491.27
## 7 W0612_2c 52491.27
```

All 3-state models have an equally good fit, so we arbitrarily select the final model as the "best" model.

```
# store behavioral states in new data column for best model

W0612Reg$state <- viterbi(W0612_3d)

# extract date from GMT.date into individual date column

W0612Reg$date <- as.Date(W0612Reg$GMT.date)

# get step length and turning angle means for each behavior state

bxStepMeans <- aggregate(step ~ state, W0612Reg, mean)
bxStepMeans
```

```
##   state       step
## 1     1   13.69453
## 2     2  371.89280
## 3     3 1618.44929
```

```
bxTurnMeans <- aggregate(angle ~ state, W0612Reg, mean)
bxTurnMeans
```

```
##   state       angle
## 1     1 -0.16628247
## 2     2 -0.01961102
## 3     3  0.01435323
```

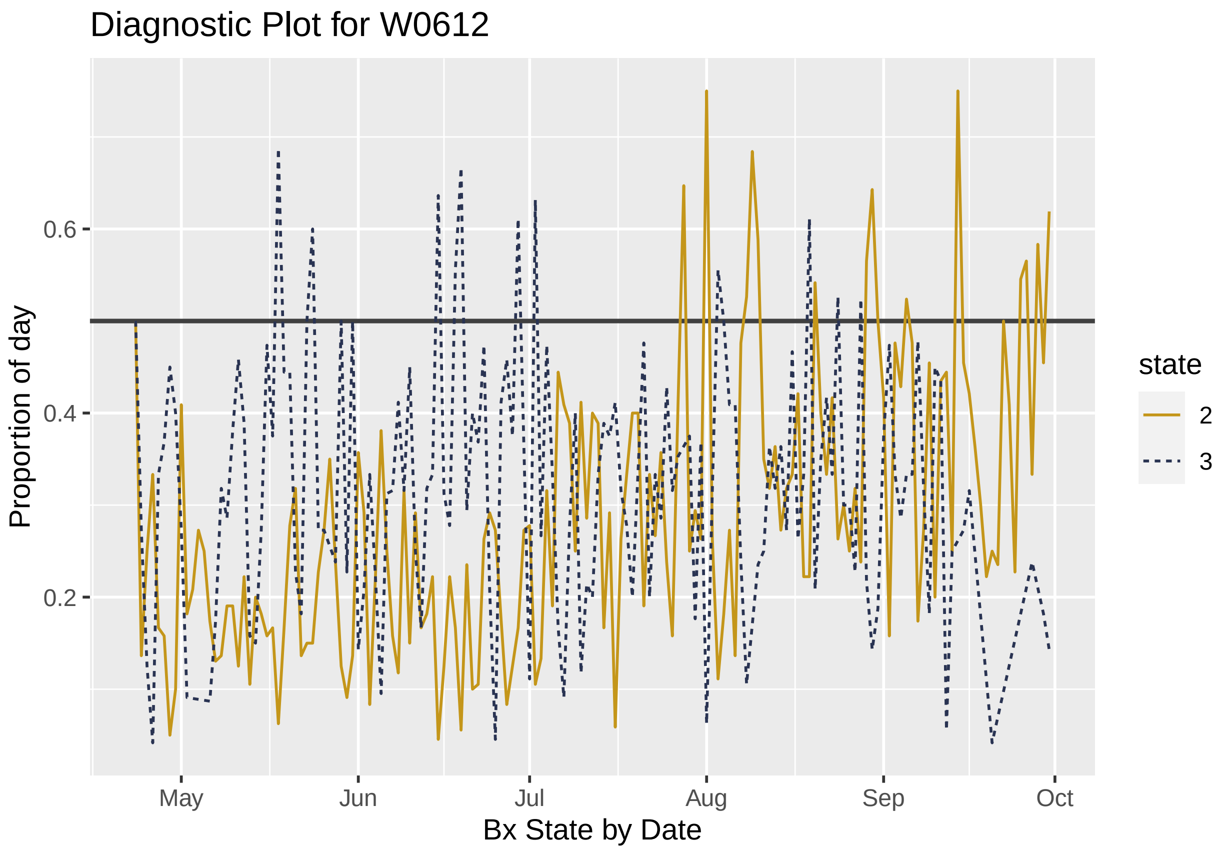
Diagnostic plotting of behavioral states

We constructed a dataframe that summarizes the states per day before plotting.

```
allBx <- summaryBy(state ~ date + state + ID, FUN=length, data = W0612Reg)

prop <- function(x) x/sum(x)

allBx <- ddply(allBx, "date", transform, share = prop(state.length))

allBx$state <- as.factor(allBx$state)
```

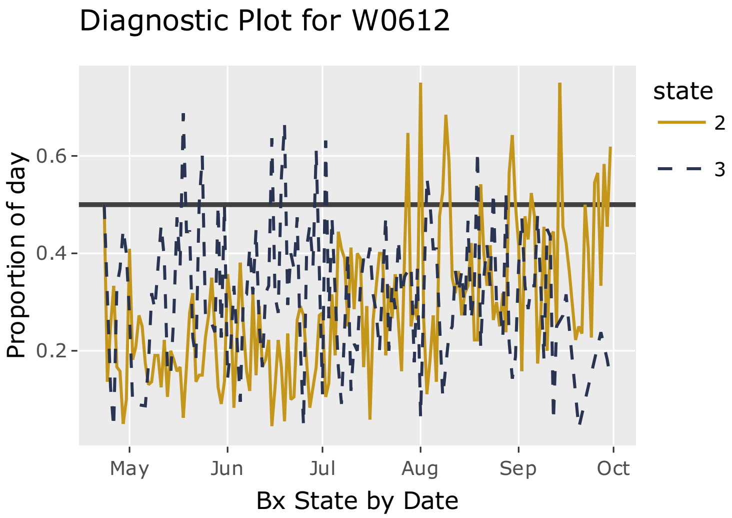
We plot the data in ggplot to look at how the proportion of time in each state changes over time. We look only at the second and third behavioral states, as resting is not important in determining whether or not dispersal is occurring.

```
bxPlot <- ggplot(allBx, aes(x=date, y=share, group=state, colour=state)) +
  geom_hline(yintercept = 0.5, linetype = "solid", color = "grey25", size = .8) +
  geom_line(aes(linetype = state), subset(allBx, state != "1")) +
  scale_color_manual(values = c("#C4961A", "#293352")) +
  xlab("Bx State by Date") +
  ylab("Proportion of day") +
  ggtitle("Diagnostic Plot for W0612")

bxPlot
```



```
# interactive plot in plotly

ggplotly(bxPlot)
```

```
## Warning: `gather_()` was deprecated in tidyr 1.2.0.
## Please use `gather()` instead.
## This warning is displayed once every 8 hours.
## Call `lifecycle::last_lifecycle_warnings()` to see where this warning was generated.
```



Find the dates where the individual spends at least half of the day in the third behavior, representing a dispersal state.

```
dates <- allBx[allBx$state == "3" & allBx$share >= 0.5, ]
dates
```

```
##           date state    ID state.length     share
## 2   2009-04-23     3 W0612            1 0.5000000
## 74  2009-05-18     3 W0612           11 0.6875000
## 89  2009-05-23     3 W0612           10 0.5000000
## 92  2009-05-24     3 W0612           12 0.6000000
## 106 2009-05-29     3 W0612           12 0.5000000
## 112 2009-05-31     3 W0612           11 0.5000000
## 157 2009-06-15     3 W0612           14 0.6363636
## 166 2009-06-18     3 W0612           10 0.5555556
## 169 2009-06-19     3 W0612           12 0.6666667
## 199 2009-06-29     3 W0612           11 0.6111111
## 208 2009-07-02     3 W0612           12 0.6315789
## 302 2009-08-03     3 W0612           10 0.5555556
## 305 2009-08-04     3 W0612           11 0.5000000
## 349 2009-08-19     3 W0612           11 0.6111111
```

```
## 364 2009-08-24     3 W0612           10 0.5263158
## 376 2009-08-28     3 W0612           11 0.5238095
```

The final step was completed in the geographic information system (GIS) software, QGIS. We looked at a shapefile of the geolocations classified by behavior states. Based on the plots, date summaries, and inspection in QGIS, we selected 29 April - 02 July as the dates the individual was dispersing.

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* geolocations have been anonymized; their spatial relationships remain unchanged

References

Zucchini, W. and MacDonald, I.L. 2009. Hidden Markov Models for Time Series: An Introduction Using R. Chapman & Hall (London).

Supplemental information

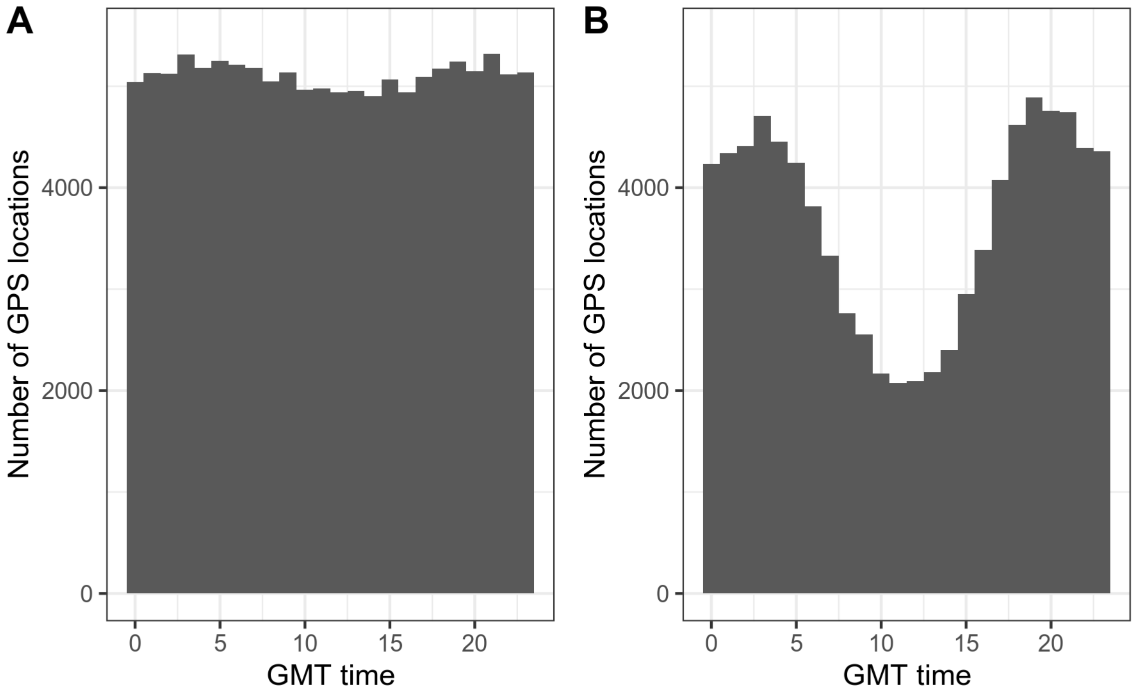

Figure S1. The number of GPS locations at given hours of the day prior to bed removal (A) and after bed removal (B).

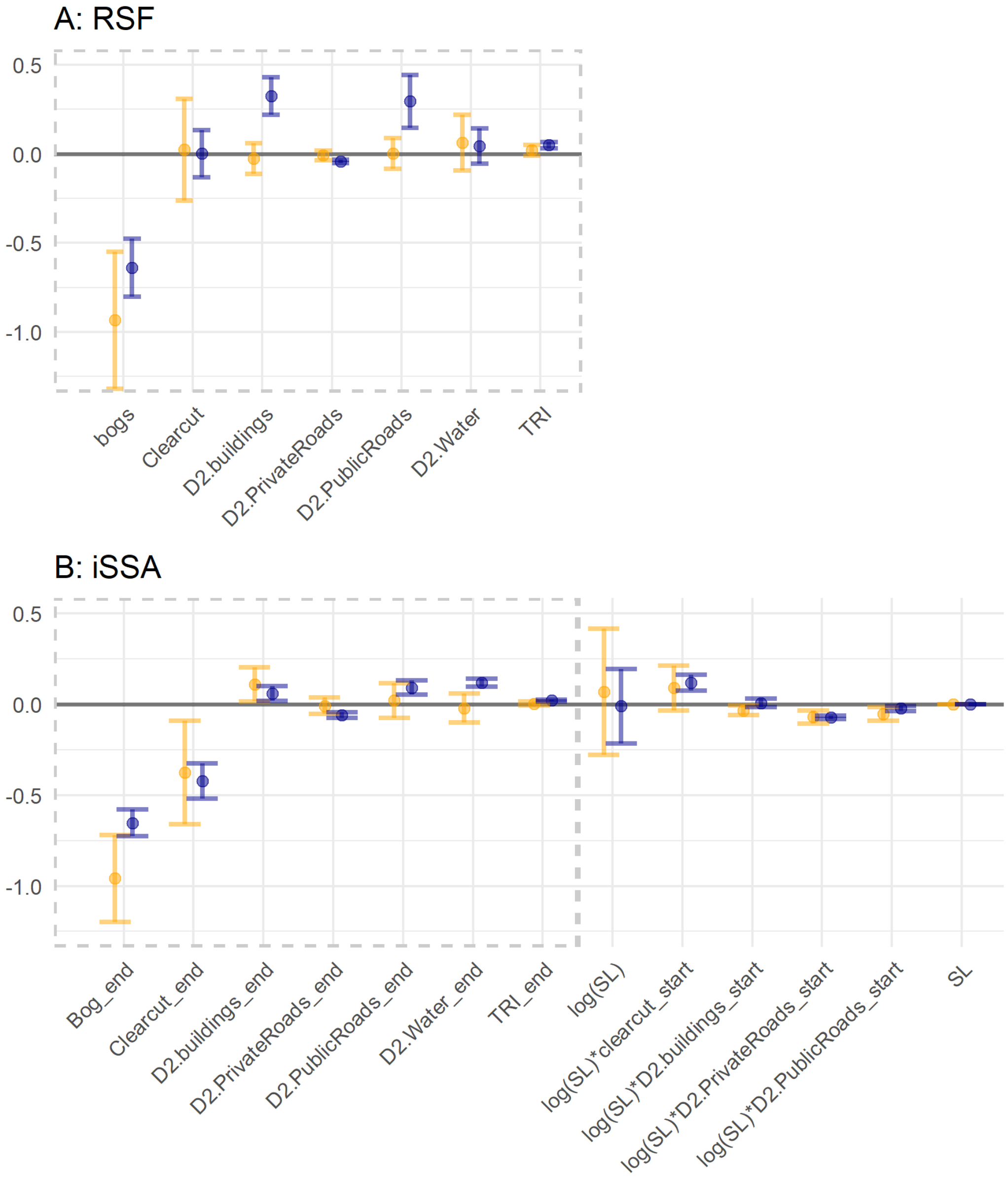

Figure S2. Coefficient plots from resource selection functions (A) and the integrated step selection analysis (B). Yellow color indicate dispersing males and blue color indicate resident males.

Table S1. The mean availability coefficient for the weighted linear models calculating the population estimates. Significant coefficients are indicated in bold and indicate a functional response, i.e. that the effect of the covariate variates with the availability. "D2." is an abbreviation for "distance to".

		Resident			Dispersal		
			95% Confidence interval			95% Confidence interval	
category	coefficient (response)	mean availability (coefficient)	low	high	mean availability (coefficient)	low	high
Resource Selection Function (global availability)							
habitat selection	Bog	31.418	-61.067	123.902	-102.111	-238.085	33.863
habitat selection	Clearcut	1.909	-18.175	21.993	43.935	-18.430	106.301
habitat selection	D2.Buildings	-4.356	-15.618	6.907	-3.759	-10.895	3.377
habitat selection	D2.ForestryRoads	-0.102	-0.752	0.547	-0.179	-1.936	1.579
habitat selection	D2.PublicRoads	4.708	-9.805	19.221	-3.168	-9.237	2.901
habitat selection	D2.Water	-8.026	-25.098	9.047	-3.862	-23.778	16.055
habitat selection	TRI	0.063	-0.546	0.673	0.065	-0.783	0.913
Integrated Step Selection Analysis (local availability)							
habitat selection	Bog_end	-0.729	-2.932	1.475	0.214	-5.224	5.652
habitat selection	Clearcut_end	**8.221**	**4.026**	**12.416**	**19.160**	**8.428**	**29.891**
habitat selection	D2.Buildings_end	0.021	-0.137	0.179	0.099	-0.061	0.260
habitat selection	D2.ForestryRoads_end	0.062	-0.016	0.139	-0.002	-0.208	0.205
habitat selection	D2.PublicRoads_end	**0.168**	**0.080**	**0.256**	-0.083	-0.215	0.049
habitat selection	D2.Water_end	0.067	-0.018	0.152	0.298	-0.123	0.719
habitat selection	TRI_end	-0.001	-0.005	0.003	**0.013**	**0.003**	**0.022**
movement	log(SL)	-0.024	-0.048	0.001	0.009	-0.005	0.022
movement	log(SL)*clearcut_start	-0.621	-2.150	0.908	1.193	-1.437	3.824
movement	log(SL)*D2.Buildings_start	**-0.121**	**-0.215**	**-0.027**	**-0.074**	**-0.121**	**-0.027**
movement	log(SL)*D2.ForestryRoads_start	0.034	-0.015	0.083	-0.010	-0.173	0.154
movement	log(SL)*D2.PublicRoads_start	-0.007	-0.034	0.021	**-0.057**	**-0.110**	**-0.004**
movement	SL	0.000	0.000	0.000	0.000	0.000	0.000

Doctoral dissertation no. 150
2023

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Dissertation for the degree of PhD

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Jennifer Eve Hansen

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