ORIGINAL RESEARCH

The use of anthropogenic areas helps explain male brown bear movement rates and distance travelled during the mating season

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Abstract

During the reproductive period, mating strategies are a significant driver of adaptations in animal behaviour. For instance, for polygamous species, greater movement rates during the mating season may be advantageous due to the increased probability of encountering several potential mates. The brown bear *Ursus arctos* is a solitary carnivore that lives at low densities, with a polygamous mating system and an extended mating season of nearly 3 months. Here, we hypothesized that male brown bears may show changes in movement patterns and space-use behaviour during their mating season. Using long-term (2002–2013) telemetry data from the Finnish Karelia male population ($n = 24$ individuals; $n = 10\,688$ GPS locations), we first analysed daily movement metrics, that is, speed, net and total distance with respect to the period (mating vs. post-mating) and several environmental predictors. Then, we conducted a step-selection analysis for each of these periods. Throughout the year, male bears selected forested/shrub habitats and increased movement rates near main roads. During the mating season, reproductive needs seem to trigger roaming behaviour in adult males to maximize encounter rates with potential receptive females. However, all movement metrics increased within areas of high human activity, suggesting a bear response to a higher risk perception while using those areas. During the post-mating period, overlapping with the bear hyperphagia and the hunting season, males selected anthropogenic areas farther from main roads and trails, suggesting a trade-off between foraging opportunities and risk avoidance.

Introduction

Most organisms undergo seasonal changes in behaviour (Cooke et al., 2014; Simpson & Balsam, 2016). For instance, during the reproductive period, the diverse needs associated with mating can drive significant changes in animal behaviours (Goodenough et al., 2009). In particular, male mammals exhibit many mating-related behaviours during this period, such as agonistic vocalizations, mate-guarding (associated with a reduction in foraging efficiency), increased territoriality, and roaming behaviour (e.g., Clutton-Brock, 1989; Clutton-Brock & Albon, 1979; Girard-Buttoz et al., 2014; Marino, 2012).

Mammals show a great variability in mating systems (Clutton-Brock, 1989), such as monogamy, that is, males and females bonded to a single partner (Ribble, 1991), polygyny, that is, males mate with multiple females (Clutton-Brock & Albon, 1979), and polygamy/promiscuity, that is, males and females mate with multiple partners (Boonstra et al., 1993). Despite this variation, most mammals are polygynous (Clutton-Brock, 1989), and large ranges and greater movements during the mating season may be advantageous because of the increased probability of encountering several different or asynchronously receptive mates (Clutton-Brock, 1989; Shuster & Wade, 2003). Whereas the reproductive success of females is usually limited by the number of offspring they can produce and rear, that of males, in the absence of parental care, is instead proportional to the number of females with which they mate and successfully fertilize (Clutton-Brock & Harvey, 1978;

Shuster & Wade, 2003). Consequently, roaming widely in search of receptive mates (i.e., roaming-to-mate) is a behaviour exhibited primarily by males in order to improve their fitness (Clutton-Brock, 1989). Several mammalian taxa with a polygynous/promiscuous mating system, and where females range more or less widely and unpredictably (*sensu* Clutton-Brock, 1989), show an increase in their roaming behaviour, including marsupials, rodents, ungulates, and carnivores (e.g., Edelman & Koprowski, 2006; Fisher & Lara, 1999; Foley et al., 2015; Graw et al., 2019). Outside the reproductive season, animals prevalently shift their focus from mating to procuring food, with spacing and the size of male ranges being no longer determined by the availability and spatial distribution of receptive mates but by, for example, the spatial abundance of food (Erlinge & Sandell, 1986).

Animal movement and space use can be influenced by various external factors, including food and shelter availability, landscape structure, habitat characteristics, and anthropogenic activities (del Mar Delgado et al., 2010; Martin et al., 2013; Nathan et al., 2008). Landscape and habitat features can particularly impact animal movement behaviour during different times of the year, including the reproductive season. For instance, during this period, male red pandas *Ailurus fulgens* were found to travel longer daily distances while avoiding roads and small-habitat patches with low forest cover (Bista et al., 2021). Additionally, male polecats *Mustela putorius* demonstrated a preference for riparian habitats and ponds, which facilitated their increased movements while searching for mates (Rondinini et al., 2006). In such context, understanding how landscape characteristics can alter animal movement patterns during biologically sensitive periods like mating may have important implications from both management and conservation perspectives, especially within human-modified landscapes (e.g., Martin et al., 2013; Moriarty et al., 2016). Actually, the distribution range of many mammalian species is characterized by high human densities, widespread human activities, and infrastructures, such as urban development and dense networks of transport infrastructures (Morales-González et al., 2020; Penteriani et al., 2020), which cause increased mortality and multiple human-driven disturbances in movements and rhythms of activity (Bischof et al., 2009; Ordiz et al., 2017).

The brown bear *Ursus arctos* is a solitary carnivore that lives at relatively low densities and has an extended mating season lasting for ~3 months from May to July (Swenson et al., 2021, 2023). Moreover, brown bears are polygamous, that is, individuals of both sexes mate a variable number of times with a variable number of partners during a given mating season (Steyaert et al., 2012; Swenson et al., 2021, 2023). Thus, male bear movement behaviour and space-use have the potential to be strictly related to mating needs. To date, however, few studies have directly related movement patterns to male mating behaviour (Dahle & Swenson, 2003a, 2003b; Edwards & Derocher, 2015). Thus, our main aim here is to integrate movement data with remotely sensed environmental data to explore the potential consequences of brown bear mating needs on their movements.

Using long-term telemetry data from the Finnish Karelia brown bear population, we hypothesize that male brown bears may show changes in both movement and space-use patterns during their mating season due to attempts to maximize successful reproduction, that is, finding mates. Thus, we have first derived multiple daily movement metrics (i.e., speed, net and total distance displaced) and analysed them via linear mixed-effects models (LMMs) with respect to the period (mating vs. post-mating) and several predictors describing daily bear habitat use. Second, in order to better investigate how landscape structure affects seasonal bear movement, we have performed a step-selection analysis based on (mixed) conditional logistic regression (Fortin et al., 2005; Thurfjell et al., 2014) for mating and post-mating seasons.

Firstly, we predict that males would show greater daily displacements and faster movements to cover more ground during the mating season compared with the post-mating period to increase the chance of encountering a receptive mate (*prediction 1*). Further, we expect that males would show more risky behaviours during mating than in the post-mating season. Indeed, brown bears usually tend to avoid areas with higher human activity, infrastructure, and consequent disturbance (e.g., de Gabriel Hernando et al., 2020; Martin et al., 2010; Nellemann et al., 2007; Preatoni et al., 2005; Rode et al., 2006), a proxy of risky areas (Morales-González et al., 2020). However, the roaming-to-mate need for males might be stronger than avoidance of sources of human disturbance. Thus, we predict the mating season to have higher movement parameters than the post-mating season, and this is further enhanced by human-derived risk via human presence, activity, and infrastructure (*prediction 2*). Finally, we predict that male bears would use more disturbed habitats, that is, with higher human activity and disturbance, during mating than post-mating (*prediction 3*).

Materials and methods

Study area

Our study area encompassed a large part of central-eastern and southern Finland, covering about 220 000 km² (Fig. 1). The elevation ranges from 100 to 576 m a.s.l., although around 80% of the surface area consists of low-lying land below 200 m in altitude. Forests cover ~75% of the study area: located in the boreal vegetation zone, they are composed mainly of coniferous Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*, mixed with broad-leaved species, such as birches *Betula* spp., alders *Alnus* spp., and European aspen *Populus tremula* (Ahti et al., 1968). The landscape is also characterized by the extensive presence of lakes and wetlands, that is, swamps, marshes, and peat bogs. Human population density averages ~17 inhabitants/km², which is nearly three times lower in eastern Finland compared with southern Finland (https://www.tilastokeskus.fi/tup/suoluk/suoluk_vaesto_en.html). High-traffic roads are scarce throughout the study area, but a developed network of low-traffic roads allows humans easy access to bear habitats (Penteriani et al., 2021). The brown bear population in Finland has increased and expanded during

recent decades, and it has now recovered some degree of connectivity with the Scandinavian population (Kopatz et al., 2021).

Bear captures and movement data collection

From 2002 to 2013, we captured 71 brown bears throughout our study area and Russian Karelia, that is, 115 total captures, with some individuals captured several times (2002: $n = 9$; 2003: $n = 6$; 2004: $n = 13$; 2005: $n = 7$; 2006: $n = 6$; 2007: $n = 7$; 2008: $n = 7$; 2009: $n = 9$; 2010: $n = 17$; 2011: $n = 16$; 2012: $n = 15$; 2013: $n = 3$), but for the purpose of this study,

we used only the GPS locations of adult males within Finland ($n = 10\ 688$ locations, denning period excluded; $n = 24$ individuals; mean number of locations per individual $\pm$ SD $= 427 \pm 347$). However, we decided not to remove bear resting or bed sites (i.e., inactive locations) or short-distance consecutive steps from the analysis for two main reasons: (a) resting or inactivity is part of the bear life and movement strategy of individuals, thus they should not be removed if the aim is to analyse movement patterns in their totality. For example, speed without resting would not really represent the velocity of bear displacements but only a less interesting parameter as bear speed when moving; and (b)
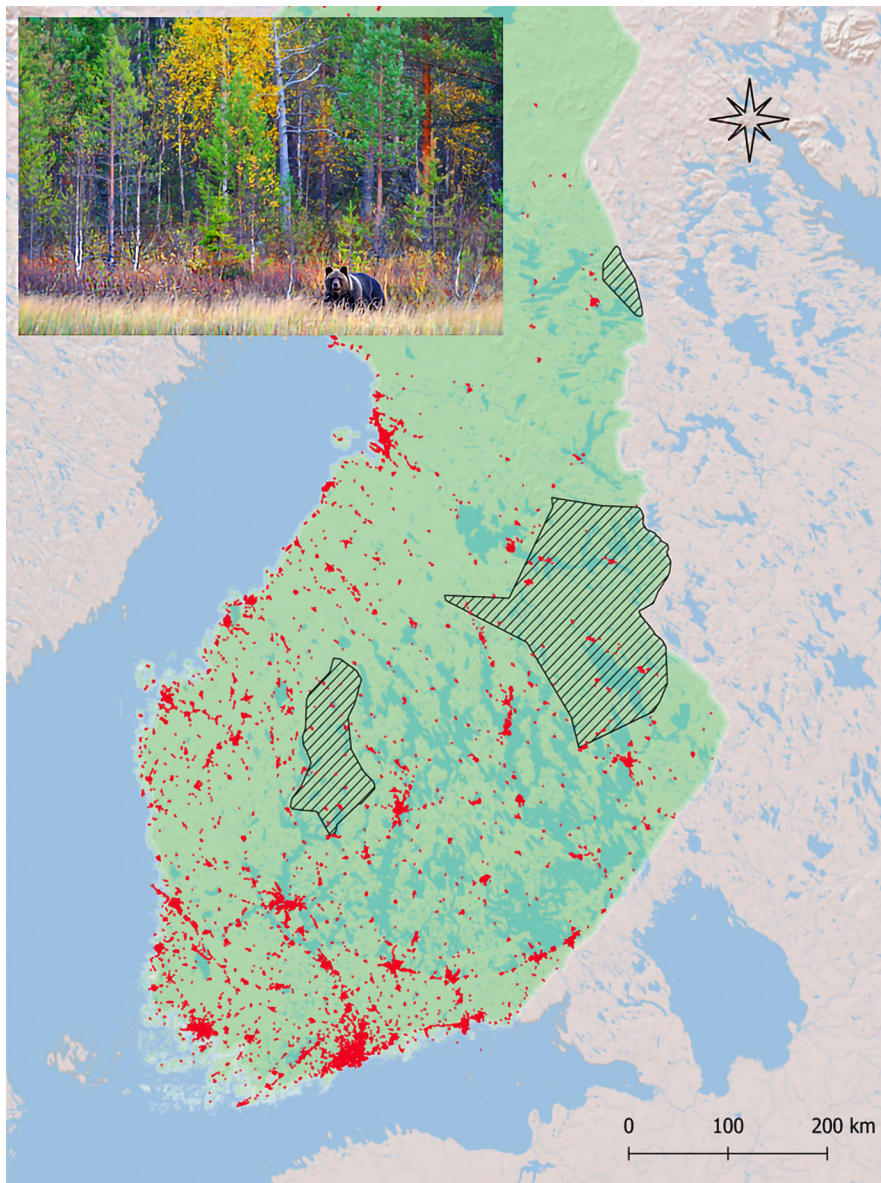

Figure 1 The study area is located in central and eastern Finland. The hatched surfaces indicate areas where the GPS locations (2002–2013) of male brown bears ($n = 24$) are distributed. Red surfaces identify anthropogenic areas, as defined by the CORINE Land Cover 2012 (see Table S1). Basemap credits: © 2009 Esri – World Shaded Relief.

because inactive locations are present in both phases (mating vs. post-mating), resting or inactivity would not be contaminating movement analyses.

The details of capture and anaesthetization have been provided in previous studies (i.e., Lamamy et al., 2022; Penteriani et al., 2021). Bears were sexed and weighed, and we extracted the first premolar for age estimation by counting annual cementum layers. Bears were considered adults at the age of 5; males usually reach sexual maturity at 4–5 years, and younger males may still be in a dispersal phase (Støen, 2006). We equipped each individual with a collar carrying a 1.5-kg Global Positioning System (GPS) transmitter (Televilt, Lindesberg, Sweden; Vectronic Aerospace GmbH, Berlin, Germany). The weight of the collars was <0.5–1.0% of adult males (mean ± SD = 212 ± 61 kg). Collars had a pre-programmed *drop-off* mechanism with an average battery life of 1 year. Whenever the mechanism did not work on schedule due to technical flaws, we recaptured the bear to remove the collar. Regardless, we removed all collars before the end of the project in 2014. The capture, handling, anaesthetizing, and collaring of bears met the guidelines issued by the Animal Care and Use Committee at the University of Oulu and permits were provided by the provincial government of Oulu and the Regional State Administrative Agency (OYEKT-6-99, OLH-01951/Ym-23, ESAVI/3229/04.10.07/2013).

The GPS fix rate varied roughly from 1 to 4 h (6–24 locations/day; see also Lamamy et al., 2022; Penteriani et al., 2021, 2022). Signals from the satellite transmitters were recorded by the ARGOS satellite system (https://www.cls.fr/en/cls-group/). We recorded the positional dilution of precision (PDOP) value for all 3-D fixes and the horizontal dilution of precision for 2-D fixes. We excluded all 2-D fixes according to the procedure of D'Eon et al. (2002). While this data-screening method reduces the dataset, it allows for a high detection percentage of large location errors (Bjørneraas et al., 2010).

Digital environmental data

To investigate the characteristics of the landscape where male bears moved, we selected a set of topographic, landcover, and human disturbance variables. All environmental variables were derived from free-downloadable spatial datasets (see Table S1 for all details), converted to raster layers with a spatial resolution of 100 m, and reprojected into a common Coordinate Reference System (i.e., EPSG: 3067 – ETRS89/TM35FIN(E,N) – Finland).

We used a Digital Terrain Model (DTM) to derive a Terrain Ruggedness Index (TRI) using the R package *spatialEco* (Evans & Murphy, 2023). Terrain Ruggedness Index was calculated by taking the square root of the sum of squared differences in elevation of each DTM grid cell to its eight neighbours (Riley et al., 1999). To characterize land use, we subsumed the classification of the CORINE Land Cover 2012 into six categories considered to be relevant for brown bear ecology in our study area: (1) anthropogenic areas, that is, all surfaces altered by humans, including urban areas, man-made

infrastructures, and agricultural areas; (2) mixed-deciduous forest; (3) coniferous forest; (4) natural open areas, that is, grasslands, moors, and all wetland areas; (5) shrubland; and (6) water bodies. Afterward, we transformed each landcover category of interest (i.e., all except water bodies; Barry et al., 2020; Van de Walle et al., 2019) into a binary raster layer, indicating the presence (1) or absence (0) of that category. For all binary layers, we thus calculated the proportion of category occupancy within a circular moving window with a 1300-m radius around every raster grid cell (i.e., proportional coverages). The radius value was chosen based on the average 4-h step length pooled over all individuals (i.e., 1273 meters, see below). As for human disturbance variables, we first reclassified the linear infrastructure network into (1) main roads (i.e., paved roads and from two to four lanes; average density within the study area: 0.25 km/km^2); (2) secondary roads (i.e., paved and unpaved roads with one lane; average density: 1.09 km/km^2); and (3) human trails (average density: 0.06 km/km^2). We then rasterized the shapefile layers and, through proximity analysis, derived the four distance variables (Table S1), that is, distance (in meters) from main roads (DMR), secondary roads (DSR), human trails (DHT), and human settlements (DHS). The processing and calculation of all rasters were carried out with the software R version 4.0 (R Core Team, 2023), QGIS version 3.3 (QGIS Development Team, 2023), and GRASS GIS version 8.2 (GRASS Development Team, 2022).

Linear mixed models for movement metrics

Data preparation: Daily movement parameters

To analyse seasonal variation in movement patterns, we first prepared a consistent dataset by resampling GPS locations at a 4-h fix rate, and we then calculated daily bear trajectories through the R package *adehabitatLT* (Calenge, 2006). To deal with missing data and since we did not have high-resolution environmental data for the neighbouring Russian Karelia (see above and Barry et al., 2020), we only kept complete daily trajectories (i.e., with six locations) within the Finnish territory. Further, we excluded daily trajectories where the daily net distance was zero to deal with days of complete inactivity.

For each retained daily trajectory, we next estimated three movement parameters: (1) daily net distance, the distance travelled between the initial position and the final position on a daily scale; (2) daily total distance, the cumulative sum of the distance between successive relocations on the same daily trajectory; and (3) daily average speed, the daily mean of the step distance (i.e., the displacement between two consecutive relocations) divided by the time interval between consecutive locations. We calculated both net and total daily distance because these might be very different (Austin et al., 2004; Rittenhouse & Semlitsch, 2006). On a daily scale, an individual could actually move even considerably while remaining roughly in the same area, thus ending its daily trajectory close to its initial position. In this case, net displacement will be very short, but the total distance travelled might be very large.

Lastly, for each retained trajectory, we derived the selected environmental variables on a daily scale. We thus extracted the entire set of environmental information at each spatial location and calculated the daily average value for all (quantitative) variables.

Statistical analysis

In a first exploratory step, all environmental variables were screened for collinearity using a Pearson's correlation coefficient threshold of $r > |0.6|$ (Hosmer & Lemeshow, 2000). The only pair of correlated variables was the distance from human settlements with that from main roads ($r = 0.66$); we consequently excluded the distance to settlements variable from the analyses (see below).

For each of the three movement parameters estimated at a daily scale (i.e., daily net distance, daily total distance, and daily average speed), we built a global linear mixed-effects model (LMM) using the R package *nlme* (Pinheiro et al., 2023). Visual analysis of residuals was first performed for each global model to check for model assumptions and the presence of outliers. After the log-transformation of our response variables, model residuals were normally distributed, and we thus fitted the models using a Gaussian distribution. The global model included one of the aforementioned movement parameters as a response variable and the following explanatory variables: (1) season, i.e., mating vs. post-mating season. The mating period was defined from 1 May to 31 July, while the post-mating period was from 1 August to 31 October, when most of the bears enter the den to hibernate. Wild berries, the most important food source during the bear post-mating hyperphagic period in that area, are available onwards late July (Penteriani et al., 2021), making our classification based on a relevant biological break; (2) the previously cited nine predictors of daily habitat use, that is, DHS excluded. All environmental predictors included were standardized (i.e., Z-score normalization) to facilitate the correct interpretation and comparison of parameter estimates (Grueber et al., 2011); and (3) interaction terms between the season and each of the environmental predictors, in order to detect possible differences in characteristics of the landscape where male bears moved between the two periods. Since the number of daily sessions (i.e., a session corresponds to one GPS-tracking day) varied within individuals (mean = 50, range = 3–164) and years (mean = 105, range = 16–303), we included the individual and the year as crossed random effects. Furthermore, in each model, we included the autoregressive correlation structure AR(1) to account for the temporal autocorrelation of daily movement parameters.

We used the R package *MuMIn* (Bartoń, 2023) to derive from each global model all possible submodels (i.e., with all possible combinations of variables) with relative values of Akaike's information criterion corrected for small sample size (AIC$_C$), AIC$_C$ difference (ΔAIC$_C$), and Akaike weight (wi). Akaike weight of a given model represents the relative likelihood of that model being the best model among the full submodel set (Burnham & Anderson, 2002). Models with a ΔAIC$_C$ < 4 were considered equally parsimonious since the

level of empirical support of such models is still substantial (Burnham et al., 2011; Burnham & Anderson, 2002). Parameter coefficients and the relative importance value (RIV) of each explanatory variable were obtained using the 'natural' model averaging approach on this top model set (Burnham & Anderson, 2002; Grueber et al., 2011). Indeed, averaging the full submodel set, or a large proportion of it, is not recommended because (a) parameter estimates from models with very poor weights are spurious and (b) those sets may include redundant models, such as nested models (Grueber et al., 2011). The RIV of each explanatory variable was estimated by summing the Akaike weights for each model in which a given variable appears (Burnham & Anderson, 2002).

Step-selection analysis for mating and post-mating seasons

Step-selection functions overview

Step-Selection Functions (SSFs) are among the most popular and powerful methods to estimate the use of space and resources by animals moving through a landscape (Fortin et al., 2005; McLoughlin et al., 2010). Basically, SSFs compare environmental attributes of used steps (i.e., linear segments linking two consecutive animal locations) with those of alternative random steps taken from the same starting point, most generally using conditional logistic regression (Thurfjell et al., 2014). In this way, random steps characterize what is available to the animal during its movement, and they are randomly generated from empirical or parametric distributions of step lengths and turning angles; including movement and allowing the data to define the availability sample, SSFs can better investigate the choices made by animals in selecting the resources compared with other approaches (for more details, see Avgar et al., 2016; Thurfjell et al., 2014).

Data preparation: Available steps generation

In order to investigate habitat selection during mating and post-mating season movements, we first calculated the straight-line distance (i.e., step length) between successive locations for all daily trajectories within Finland using the R package *adehabitatLT* (Calenge, 2006). Then, each observed step was matched with 10 random steps that we assumed to be available at each relocation, sharing the same starting point as the observed step but differing in length and/or direction. Since we probably underestimated longer bear displacements because animals most likely do not travel in a straight line during the time gap between successive relocations, we decided to generate available steps as in Forester et al. (2009).

Specifically, the lengths of random steps were drawn through a parametric sampling method, using a negative exponential distribution with a rate parameter $\lambda^{-1} = 2546$ m (i.e., twice the observed mean 4-h step length), and thus an integrated step-selection analysis approach (Avgar et al., 2016). Turning angles for the random steps were instead sampled from a uniform distribution between 0 and 2π. We then extracted the value of environmental variables at the endpoints of each

observed and available step, as we were interested in inferring habitat selection (Avgar et al., 2016; Thurfjell et al., 2014). Finally, all random steps whose endpoints fell outside the Finnish territory were discarded from the availability set (see above).

Statistical analysis

We built one iSSF model for the mating period and one for the post-mating one (defined above) using mixed conditional logistic regression (Duchesne et al., 2010; Fortin et al., 2009) with the R package *mclogit* (Elff, 2022). The model structure was as follows: (1) used (coded as 1) and available (coded as 0) steps as binary response variable; (2) each used step with its associated random steps as the stratum (i.e., for matching the used and available steps); (3) terrain ruggedness, landcover variables, distance from main roads, secondary roads, and human trails as environmental predictors; (4) step length as a predictor variable, to reduce bias in estimates of model coefficients (Avgar et al., 2016; Forester
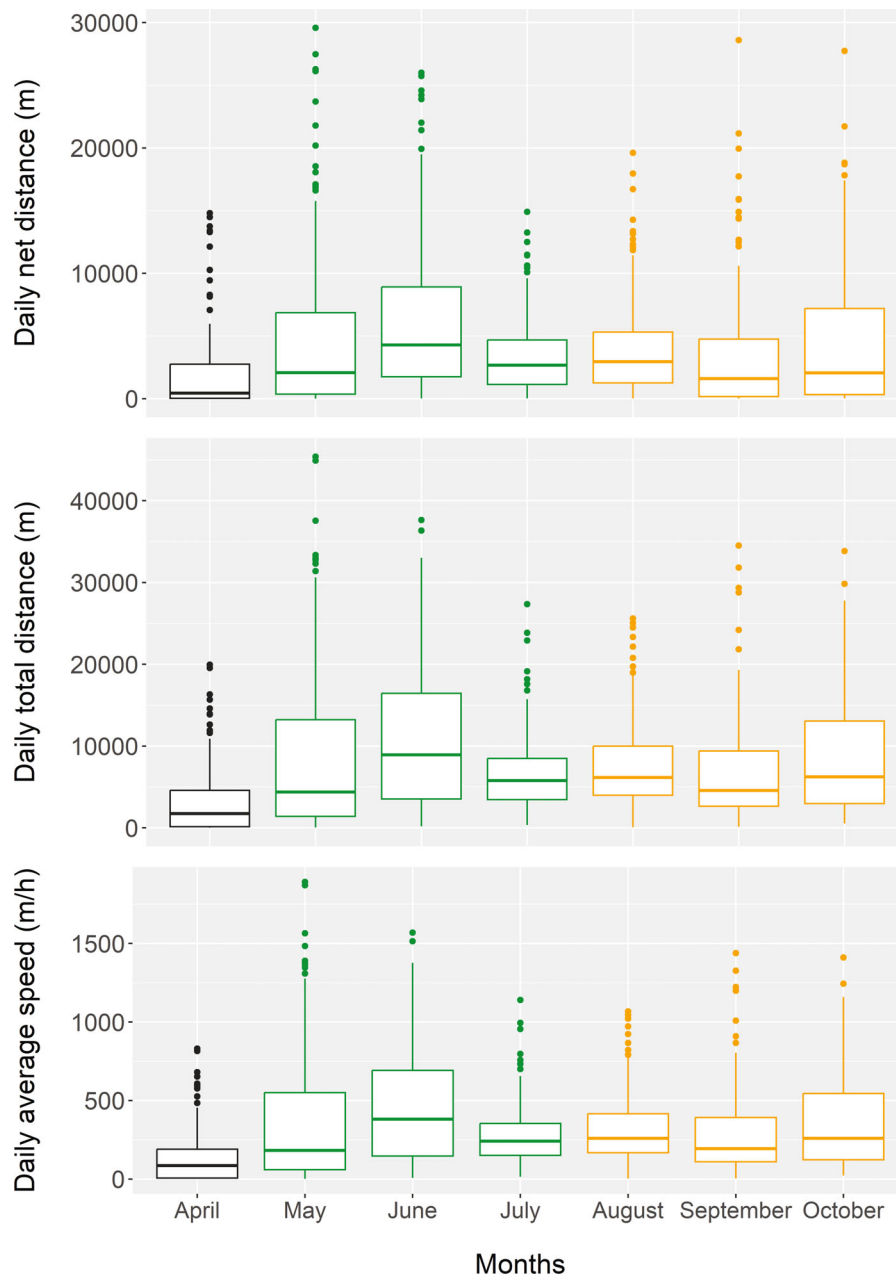

Figure 2 Monthly box plots for each daily movement metric (net distance, total distance and speed) highlighted differently depending on the season (green = mating; orange = post-mating). Values for April are also presented (in black), in order to show the increase in metrics at the onset of mating season (see text for details).

Table 1 Summary statistics of movement parameters and environmental variables, both derived at a daily scale

	Mean ± SD		Median		Range	
	Mating	Post-mating	Mating	Post-mating	Mating	Post-mating
Movement parameters						
Net distance (m)	4519 ± 5203	3895 ± 4505	2793	2410	2–29 587	3–28 603
Total distance (m)	8330 ± 7826	7577 ± 6079	5970	5751	41–45 382	52–34 520
Speed (m/h)	351 ± 329	317 ± 254	252	241	2–1890	2–1438
Environmental variables						
Terrain ruggedness index	2.49 ± 1.37	2.56 ± 1.49	2.22	2.14	0.45–15.49	0.33–9.84
Anthropogenic areas (0–1)	0.02 ± 0.03	0.04 ± 0.05	0.01	0.03	0.00–0.21	0.00–0.33
Mixed-deciduous forest (0–1)	0.12 ± 0.07	0.16 ± 0.08	0.12	0.15	0.01–0.32	0.01–0.43
Coniferous forest (0–1)	0.63 ± 0.10	0.60 ± 0.12	0.63	0.62	0.23–0.84	0.19–0.86
Natural open areas (0–1)	0.06 ± 0.06	0.04 ± 0.05	0.05	0.02	0.00–0.29	0.00–0.28
Shrubland (0–1)	0.13 ± 0.05	0.13 ± 0.04	0.13	0.13	0.04–0.31	0.03–0.32
Distance to settlements (m)	23 295 ± 13 874	18 866 ± 11 492	17 012	14 864	2734–44 557	940–44 501
Distance to main roads (m)	6950 ± 4897	5595 ± 4425	5441	3818	251–22 261	540–19 662
Distance to secondary roads (m)	695 ± 436	662 ± 349	565	568	89–2797	139–2825
Distance to trails (m)	37 152 ± 19 555	31 987 ± 18 355	31 147	27 920	4607–94 069	2786–93 417

Values (mean ± SD, median and range) are presented separately for mating (May to July) and post-mating (August to October) seasons.

et al., 2009). Again, all predictors were standardized (see above); and (5) individual and year as random slopes (i.e., a mixed-effects model), to account for variation among individuals and years (Fieberg et al., 2021; Muff et al., 2020). Since we believed that our model was biologically informed anyway (i.e., we did not add any potentially unnecessary terms), and as more complex formulations of the model (e.g., including interactions) gave some convergence issues (e.g., Fieberg et al., 2021; Muff et al., 2020), we decided to use the results from that model to make inferences. We processed and analysed all data in R version 4.0 (R Core Team, 2023).

Results

According to the results of LMMs, male brown bears moved over longer daily net distances during the mating season compared with the post-mating season, even if they did not show greater daily total distances or higher daily average speed (Fig. 2; see Table 1 for summary statistics and Table 2 for parameter estimates of LMMs). However, during the mating season, all three daily movement parameters increased in areas characterized by human presence, activity, and infrastructure, while only the net distance increased within shrublands (Table 2). In addition, independently of the period, male bears covered greater daily distances at a higher speed in proximity to main roads, but their speed did not increase when close to secondary roads (see also Table S2 for the global model results).

Based on parameter estimates from iSSF models (Table 3), during the mating period, male bears selected coniferous and mixed-deciduous forests, as well as shrubbery habitats (Fig. 3). During the post-mating season, male bears continued to select forests and shrubs, but also anthropogenic areas and open areas, while avoiding close proximity to main roads and human trails (Fig. 3; Table 3).

Discussion

As expected (*prediction 1*), we found evidence that male brown bears from Finnish Karelia covered greater per-day net distances in the mating than in the post-mating season, but we did not detect a significant season effect for the daily total distance and average speed. Additionally, the observed patterns for daily movement metrics supported our *prediction 2*, revealing faster/greater displacements of bears within anthropogenic areas during the mating season than post-mating. Since human presence and activity are supposed to be higher in those areas (Morales-González et al., 2020), this finding may suggest that adult males in the mating season prioritized the search for mates over avoiding human disturbance. Lastly, the results of the step-selection analysis supported our *prediction 3* only partially: while male bears avoided disturbed habitats closer to roads and trails only during the post-mating season, they also showed a selection for anthropogenic areas during that period.

By examining the monthly trend of daily movement parameters (Fig. 2), there appeared to be a yearly variation in their value, that is, a sharp increase in May that continued throughout June, a decrease in July/August and then a gradual increase toward October. Similarly to our results, a wide range of fine-time-scale movement metrics of adult males (e.g., hourly movement distance, daily activity rate, and speed) also increased during the mating period in other brown bear populations, presumably due to the promiscuous mating of this species (de Gabriel Hernando et al., 2020; Graham & Stenhouse, 2014; Ordiz et al., 2017). The second peak in fall may be related to hyperphagia needs when brown bears consume large amounts of high-calorie food to store fat reserves essential for later hibernation (Swenson et al., 2021, 2023). In our study area, located in a boreal landscape at northernmost European latitudes (Esseen et al., 1997), adult males in the hyperphagic period may have still travelled fast and long daily

Table 2 Values of degrees of freedom (d.f.), AIC_C, ΔAIC_C and Akaike weight (wi) of the best ($\Delta AIC_C < 4$) linear mixed-effects models for each movement parameter considered (see text for details)

Response variable	Competing models	d.f.	AIC_C	ΔAIC_C	wi
Net distance	Anthropogenic areas + Season + Shrubs + Anthropogenic areas * season + Shrubs * season	10	3863.04	0.00	0.51
	Anthropogenic areas + DMR + Season + Shrubs + Anthropogenic areas * season + Shrubs * season	11	3864.52	1.48	0.24
	Anthropogenic areas + DHT + Season + Shrubs + Anthropogenic areas * season + Shrubs * season	11	3865.40	2.36	0.16
	Anthropogenic areas + DHT + DMR + Season + Shrubs + Anthropogenic areas * season + Shrubs * season	12	3866.51	3.47	0.09
	Explanatory variables	β	SE	CI	RIV
	Intercept	7.10	0.19	6.72; 7.48	
	Anthropogenic areas	**−0.43**	**0.08**	**−0.59; −0.26**	**1.00**
	Season (mating)	**0.35**	**0.17**	**0.01; 0.69**	**1.00**
	Shrubs	**−0.36**	**0.09**	**−0.53; −0.18**	**1.00**
	Anthropogenic areas * season (mating)	**0.43**	**0.15**	**0.14; 0.73**	**1.00**
	Shrubs * season (mating)	**0.35**	**0.12**	**0.11; 0.58**	**1.00**
	DMR	**−0.17**	**0.09**	**−0.35; −0.01**	**0.33**
	DHT	0.17	0.10	−0.03; 0.37	0.25
Total distance	Anthropogenic areas + DMR + Season + Anthropogenic areas * season	9	2679.09	0.00	0.42
	Anthropogenic areas + DMR	7	2680.04	0.94	0.26
	Anthropogenic areas + Season + Anthropogenic areas * season	8	2680.14	1.05	0.25
	Anthropogenic areas	6	2682.53	3.44	0.07
	Explanatory variables	β	SE	CI	RIV
	Intercept	8.42	0.13	8.17; 8.67	
	Anthropogenic areas	**−0.21**	**0.06**	**−0.32; −0.10**	**1.00**
	DMR	**−0.15**	**0.05**	**−0.25; −0.04**	**0.68**
	Season (mating)	0.04	0.11	−0.18; 0.25	0.66
	Anthropogenic areas * season (mating)	**0.29**	**0.09**	**0.12; 0.45**	**0.66**
Speed	Anthropogenic areas + DMR + Season + Anthropogenic areas * season	9	2680.08	0.00	0.38
	Anthropogenic areas + DMR	7	2680.79	0.71	0.27
	Anthropogenic areas + Season + Anthropogenic areas * season	8	2681.50	1.42	0.19
	Anthropogenic areas	6	2683.68	3.60	0.06
	Anthropogenic areas + DHT + DMR	8	2683.97	3.89	0.05
	Anthropogenic areas + DHT + DMR + Season + Anthropogenic areas * season	10	2684.07	3.98	0.05
	Explanatory variables	β	SE	CI	RIV
	Intercept	5.26	0.12	5.01; 5.50	
	Anthropogenic areas	**−0.21**	**0.06**	**−0.32; −0.10**	**1.00**
	DMR	**−0.15**	**0.05**	**−0.25; −0.05**	**0.75**
	Season (mating)	0.04	0.11	−0.17; 0.26	0.62
	Anthropogenic areas * season (mating)	**0.28**	**0.09**	**0.11; 0.45**	**0.62**
	DHT	0.09	0.06	−0.03; 0.21	0.11

For each explanatory variable, coefficient (β), standard error (SE), 95% confidence interval (CI), and the relative importance value (RIV) obtained by averaging the top 4AIC_C of models are reported. Significant explanatory variables (*P*-value <0.05) are shown in bold. Interaction terms between season and a specific environmental variable are indicated with an asterisk.

DMR, distance to main roads; DHT, distance to human trails (see text for all details).

Table 3 Values of coefficients (β), standard errors (SE), and 95% confidence intervals (CI) for the mixed conditional logit models comparing used steps to randomly generated steps; separate models were generated for mating and post-mating season

Variable	Mating season			Post-mating season		
	β	SE	CI	β	SE	CI
TRI	−0.02	0.04	−0.10; 0.06	−0.03	0.04	−0.11; 0.05
Anthropogenic areas	−0.11	0.12	−0.35; 0.12	**0.27**	**0.04**	**0.19; 0.35**
Mixed-deciduous forest	**0.69**	**0.17**	**0.37; 1.01**	**0.57**	**0.16**	**0.26; 0.88**
Coniferous forest	**0.93**	**0.16**	**0.61; 1.26**	**0.71**	**0.10**	**0.52; 0.90**
Open areas	0.22	0.11	−0.004; 0.45	**0.22**	**0.09**	**0.05; 0.39**
Shrubs	**0.30**	**0.10**	**0.10; 0.50**	**0.23**	**0.08**	**0.08; 0.38**
DMR	0.10	0.07	−0.04; 0.25	**0.37**	**0.11**	**0.15; 0.59**
DSR	0.01	0.06	−0.10; 0.12	0.04	0.05	−0.06; 0.13
DHT	0.29	0.21	−0.12; 0.70	**0.55**	**0.27**	**0.01; 1.09**
Step length	**−1.74**	**0.27**	**−2.27; −1.22**	**−1.29**	**0.17**	**−1.63; −0.94**

Numbers in bold represent effects with *P*-value <0.05.
DHT, distance to human trails; DMR, distance to main roads; DSR, distance to secondary roads; TRI, Terrain Ruggedness Index (see text for all details).
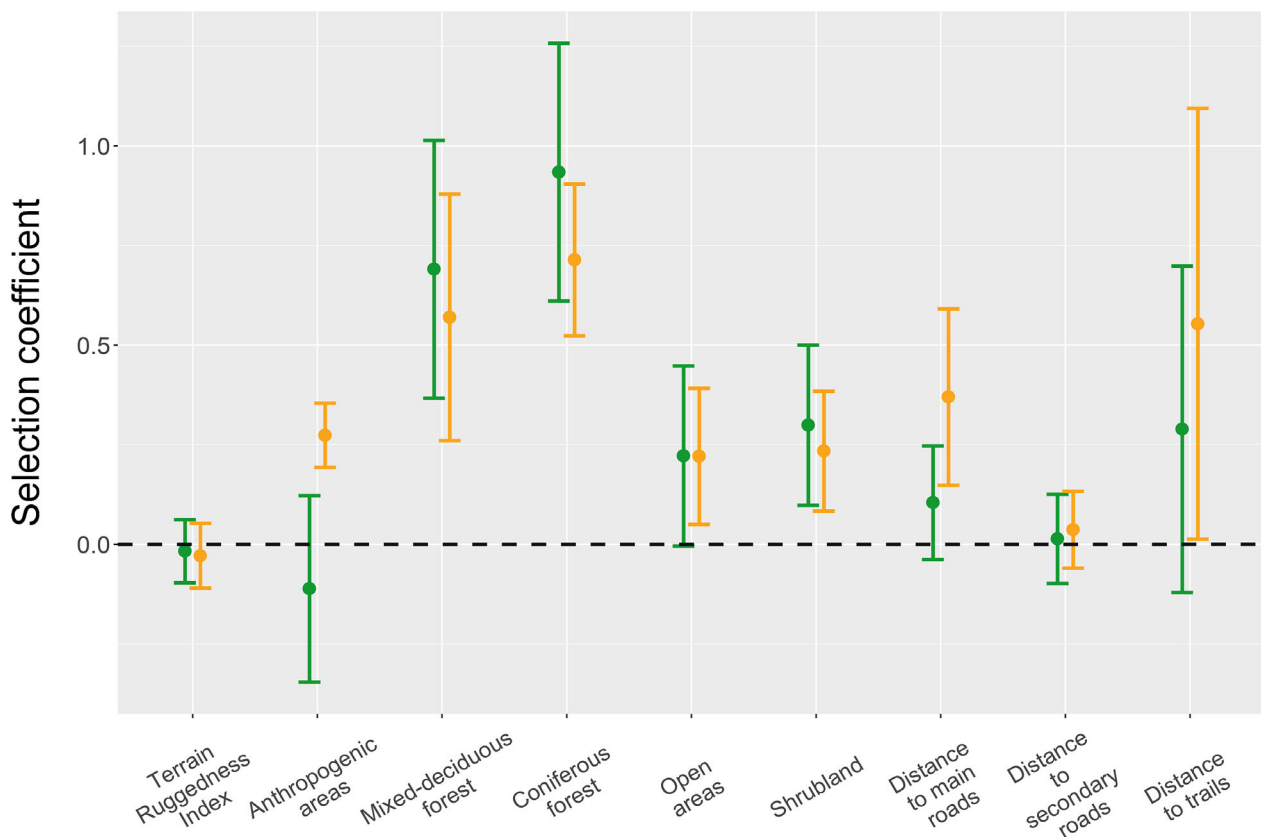

Figure 3 Contrasted selection coefficients (and 95% confidence intervals) as estimated by step-selection functions (see Table 3) for mating and post-mating movements (in green and orange, respectively). Positive coefficients ($\beta > 0$) indicate that resources are used in a larger proportion compared with their availability, negative coefficients ($\beta < 0$) indicate that resources are used in a lesser proportion compared with their availability, and null coefficients (i.e., 95% confidence interval of β includes 0) mean that resources are used in proportion to their availability.

distances in search of food to fatten up before denning (Dahle & Swenson, 2003a; Edwards & Derocher, 2015; Ordiz et al., 2017). Our findings also suggest that at the daily scale, the net distance (i.e., the more directional way of

displacement) may be good proxy to describe both the increased home range size observed during the mating season in brown bears (Dahle & Swenson, 2003a, 2003b; Preatoni et al., 2005) and the roaming behaviour that enabling them to

enhance encounter rates with potential receptive mates (e.g., Fisher & Lara, 1999; Kovach & Powell, 2003).

Throughout the year, males strongly selected coniferous and mixed-deciduous forests, emphasizing their importance across the entire range of brown bears (Swenson et al., 2021, 2023). Forest habitats provide bears with foraging opportunities, canopy cover for thermal comfort and protection against adverse weather and even horizontal cover for hiding and resting during the day (Ciarniello et al., 2014; Cristescu et al., 2013; Ordiz et al., 2011).

As residency time within a particular habitat is hypothesized to decrease with longer step lengths (Turchin, 1998), the observed association between a greater proportion of anthropogenic area usage and increased speed/displacements during the mating season may indicate a response by bears to a heightened perception of human-derived risk in these areas (de Gabriel Hernando et al., 2020; Donatelli et al., 2022; Roever et al., 2010; Thorsen et al., 2022). This aligns with findings reported for other brown bear populations, where higher movement rates were observed near roads in spring/early summer (Donatelli et al., 2022; Roever et al., 2010), or where adult males used/ selected disturbed areas near roads and trails during the mating period (Roever et al., 2008; Steyaert et al., 2013; Van de Walle et al., 2019). Male brown bears covered faster and longer daily distances near main roads during the mating season. Since it appears that there was no avoidance of these features, adult males may have used areas closer to linear infrastructures for travelling. This behaviour aligns with previous findings that indicate that roads and trails may serve as efficient travel routes for large carnivores, including brown bears (e.g., de Gabriel Hernando et al., 2020; Dickie et al., 2020; Dickson et al., 2005; Ladle et al., 2019; Roever et al., 2010).

The decreased movement of male bears within anthropogenic areas during the post-mating season fits well with the selection observed for those areas (Turchin, 1998) and was likely influenced by their increased foraging activity during hyperphagia. Since anthropogenic food resources can indeed affect movement patterns in our study area (Penteriani et al., 2021), and our definition of anthropogenic areas also included all agricultural areas (see above), male brown bears may have restricted movements around both natural food-rich patches (e.g., shrublands) and anthropogenic resources to increase foraging success during hyperphagia (De Angelis et al., 2021; Lamamy et al., 2022; McLoughlin et al., 1999). In this regard, seasonal variation in movement and space-use patterns of males seemed to be driven by a shift in limiting resources, from the distribution of receptive females during the mating season to food abundance and its spatial availability in the post-mating season, as reported for other solitary carnivores with a polygamous mating system (e.g., Erlinge & Sandell, 1986; Johnson et al., 2000).

Additionally, the movement and habitat selection patterns observed during the post-mating season may have been influenced, at least partly, by hunting pressure. In fact, hunting has been shown to affect movement behaviour and habitat use in brown bears and other harvested apex predators (e.g., Stillfried et al., 2015; Strampelli et al., 2022). For instance, during the hunting season, Scandinavian bears altered their foraging

patterns, increased movements during night-time hours, and rested during the day in areas with higher concealment far from human settlements (Hertel et al., 2016; Ordiz et al., 2011, 2012). In our study area, the post-mating period largely overlapped with the hunting season, which lasted for about 2 months starting 20 August (Lamamy et al., 2022). Therefore, following the start of the annual hunting season, males may have exhibited increased vigilance behaviour in anthropogenic areas and avoided those closer to roads and trails (i.e., higher perceived human-derived risk), suggesting a potential trade-off between foraging opportunities and risk avoidance (Cristescu et al., 2013).

In conclusion, when comparing male brown bear movements within and outside the mating period, the results obtained lend support to the notion that a close relationship exists between the biological needs of individuals (i.e., mating), their movement behaviour, and their use of space/landscape (Cagnacci et al., 2010a, 2010b; Nathan et al., 2008). During the mating season, males will predominantly be in areas where females are present, thereby largely reflecting areas of female habitat use (Berland et al., 2008; Roever et al., 2008; Steyaert et al., 2013). Conversely, male movements during the post-mating season may primarily mirror their habitat use. Considering the occurrence of human-caused bear mortality in disturbed areas (e.g., Kite et al., 2016; Nielsen et al., 2004), the increased use of anthropogenic areas during the mating season is relevant for the conservation of this species. It may require management interventions where necessary to mitigate conflicts between humans and bears (Roever et al., 2010). The potential trade-off between security and food that became apparent during the post-mating season warrants attention to prevent anthropogenic areas from acting as attractive sinks (Morales-González et al., 2020; Penteriani et al., 2018).

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Author contributions

VP and DF conceived the ideas; DF, VP and MMD designed methodology; IK and SK collected the movement data; DF

analysed the data; DF and VP led the writing of the manuscript. All authors read and approved the final manuscript.

Conflict of interest

The authors declare that they have no conflict of interest.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Details of the environmental variables selected to analyse the structure/characteristics of the landscape where male brown bears moved within Finnish Karelia.

Table S2. Results of the global linear mixed-effects model for the three movement parameters considered, that is, net distance, total distance, and speed.