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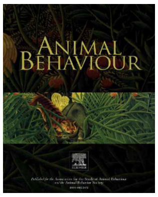

Wolves on ice: habitat use and selection of water bodies by wolves during winter

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Terrestrial mammals are in many ways connected to water bodies, although studies on habitat selection within anthropogenic landscapes often overlook the importance of water. The recolonization of grey wolves, *Canis lupus*, across parts of Europe, together with developments in GPS technology, has offered opportunities to study detailed spatial movements of this large carnivore in human-influenced landscapes. Here, we investigated wolf use, habitat selection and step length in relation to water bodies in the boreal forest during winter. We hypothesized that wolves select for larger water bodies during ice periods and use them as travel corridors for efficient movement, similar to forest roads. We used step selection analyses with data from 71 GPS-collared adult wolves in 44 wolf territories in Scandinavia to investigate habitat selection in relation to water bodies, time of day and season. The study included >50 000 GPS positions taken at 4 h intervals between 2001 and 2023. Wolves selected for lakes and rivers during ice periods, especially at night, with step length increasing when travelling on ice. Deep snow generally impeded wolf step length, but not more on frozen water than in other habitats. These results indicate that wolves utilize frozen water bodies as travel corridors for easier mobility during winter, possibly to reduce human-encounter risk. Our findings emphasize the adaptability of wolves and, more generally, contribute to our understanding of mammalian movement patterns and space use in the boreal zone.

Water bodies connect aquatic and terrestrial trophic systems, increasing productivity, species richness and diversity in surrounding areas (Burgis et al., 2007). Most terrestrial mammals are partly connected to riparian areas, as they offer the primary source of fresh water necessary for hydration, body functions and thermoregulation (Campbell & Norman, 1998; Degen, 1997). Several terrestrial predatory mammals have adapted to utilize water, such as brown bears, *Ursus arctos*, hunting for migrating salmon, *Oncorhynchus keta* (Levi et al., 2020; Mangipane et al., 2020); jaguars, *Panthera onca*, hunting for aquatic prey (Franco et al., 2018); and wolves, *Canis lupus*, ambushing North American beaver, *Castor canadensis*, and fishing (Freund et al., 2023; Gable et al., 2018).

Water bodies are strongly affected by seasonality, especially in the boreal and arctic parts of the northern hemisphere. Large open water (lakes and, to a lesser extent, rivers) during summer can hinder movement and fragment the landscape (Leblond et al., 2016; Newton et al., 2017) while providing resources at the same time. During winter, much of this water freezes to ice and gives way to new terrains (Banfield, 1954). This can facilitate movement, thereby reducing energetic costs. For example, polar bears, *Ursus maritimus* (Pagano et al., 2021), arctic foxes, *Vulpes lagopus* (Pamperin et al., 2008), and caribou, *Rangifer tarandus caribou* (Leblond et al., 2016), use (sea) ice as part of their home range and for migration and dispersal movements. However, if and how the availability of water bodies affects the ecology and space use of terrestrial species in boreal ecosystems, especially in Scandinavia, is an overlooked topic in ecological research.

The grey wolf, *C. lupus*, being one of the key apex predators of boreal ecosystems, has recolonized large parts of northern Europe since its near extirpation (Chapron et al., 2014; Ordiz et al., 2015; Wabakken et al., 2001). It was previously shown that water bodies are used by wolves for foraging and movement in North America (Latham et al., 2011; Mech, 1981), especially along the Pacific Northwest (Roffler et al., 2018). For instance, wolves have been found to make frequent kills near open water (Bojarska et al., 2017; K. E. Kunkel & Pletscher, 2000) and on ice (Kauffman et al., 2007;

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McPhee et al., 2012; Webb, 2010), while ungulate prey seek refuge in water as a survival strategy (Mech et al., 2015). Moreover, frozen water bodies could serve as travel corridors (Kingdon et al., 2025; Kittle et al., 2017; Newton et al., 2017), similar to roads, trails and power lines (Johnson-Bice et al., 2023; Muhly et al., 2019). However, the use of human infrastructure by wolves, in particular main roads, is mostly restricted to night-time and varies with road density, probably to maintain cryptic behaviour towards humans (Bojarska et al., 2020; Zimmermann et al., 2014). Thus, frozen water bodies might be used as travel corridors when human influence is high, as wolves tend to avoid areas of high human density, perceiving them as a risk (Hebblewhite & Merrill, 2008; Ordiz et al., 2015). Conversely, large rivers are situated in valley bottoms, where snow is less deep and prey accumulate during winter (Bunnefeld et al., 2011; Mysterud et al., 2011; Ordiz et al., 2020), but where roads and settlements are also situated.

Snow is known to affect mammals in the boreal zone (Boelman et al., 2019), causing increased energetic costs of travel (Crête & Larivière, 2003) and decreased movement activity (Droghini & Boutin, 2018a, 2018b; Melin et al., 2023). Therefore, wolves might select habitats with lower snow depth during periods of increased snowfall (K. Kunkel & Pletscher, 2001). Snow might be less deep on frozen water, as it repeatedly melts and freezes on top of the ice and forms snow-ice (Jeffries et al., 2005), blows away on larger lakes (Bengtsson, 1986; Burgis et al., 2007) or starts accumulating later than on surrounding land if the water is not yet frozen during the first snowfall. Forest roads, however, are ploughed irregularly (Zimmermann et al., 2014) and only partially, probably causing ploughed sections to have increased human traffic and unploughed sections to have deep snow unfavourable for mobility.

Overall, little is known about the importance of water for wolves in Europe, including Scandinavia, and the influence of ice. The primary aim of this study was to investigate wolf habitat use and selection in relation to water bodies during winter. We hypothesized that (H1) wolves would select water bodies depending on whether they facilitate or obstruct their movement. We predicted wolves to select larger ice-covered water bodies (lakes, rivers), using them as travel corridors (similar to roads), but to avoid them during ice-free periods because these may then rather obstruct their movements (while we expected smaller streams to neither facilitate nor hinder movement irrespective of ice cover). Additionally, we hypothesized that (H2) wolves would adjust the use of water bodies depending on the time of day based on their activity patterns and human encounter risk. We predicted that they use frozen water bodies more during night-time when wolves are generally more active and human encounter risk is low, and that during daytime wolves select for ice-covered rivers for travelling rather than roads or lakes (lacking vegetation cover) to reduce human encounter risk. Furthermore, we hypothesized that (H3) movement distances by wolves would vary with water body characteristics and snow depth because of their effects on travel efficiency. Accordingly, we predicted an increased step length by wolves when travelling on ice, because frozen water bodies facilitate linear movement and might have shallower snow depths than surrounding habitats. Finally, we hypothesized that (H4) snow depth would affect wolf use of forest roads depending on whether roads are ploughed. We predicted wolves to reduce forest road use at deeper snow depths when roads are unploughed, due to deeper snow hindering movement efficiency, having instead to select ploughed sections of road with increased human encounter risk (due to concentrated traffic there). Through these hypotheses, this study aimed to explore the adaptive movement behaviour of wolves in response to natural water features and temperature changes during winter.

METHODS

Study Area and Animals

The study was conducted in the core of the wolf breeding range of the Scandinavian population in Norway and Sweden (Fig. 1). We used GPS data of 71 adult, territorial wolves (31 females, 40 males, average pack size of 6; Chapron et al., 2016), collected between February 2001 and November 2023 (see Table S1 in the Supplementary Material) by the Scandinavian Wolf Research Project (SKANDULV). Fix rates were set to a standard of 4-hourly intervals and the position data were collected into the Wireless Remote Animal Monitoring (WRAM) database system for data validation and management (Dettki et al., 2013). Wolf winter territories ($N =$ 44, 100% MCP between 10 October and 1 May) had a mean (± SD) area of 1068 ± 853 km^2 per territory (Fig. 1). The territories were mainly covered by boreal coniferous forest (69 ± 9%), followed by open areas, mainly including bogs, natural grasslands and mountainous areas (20 ± 11%), lakes (6 ± 4%), other forests (3 ± 2%), agricultural areas (2 ± 3%), rivers (0.2 ± 0.2%) and built-up areas (0.4 ± 0.7%; European Environment Agency, 2024b). Forests were dominated by Scots pine, *Pinus sylvestris*, and Norway spruce, *Picea abies*, mixed with deciduous species such as the birch *Betula pubescens*, aspen, *Populus tremula*, willow, *Salix* sp., and alder, *Alnus* sp. There was a mean length (± SD) of 1182 ± 940 km of forest roads (gravel) per wolf territory, with forest road density being 1.14 ± 0.24 km/km^2. Main roads (paved) had a mean length of 265 ± 253 km per territory and main road density was one-quarter of forest road density (0.28 ± 0.16 km/km^2). Building density within territories was 2.14 ± 1.58 buildings per km^2. The territories had a mean human population density of 8.32 persons per km^2 (Earth Science Data System, NASA, 2024). The mean length of shoreline was 2012 ± 1598 km per territory (lakes 605 ± 516 km, rivers 286 ± 342 km, streams 1120 ± 883 km). River density per territory was 0.22 ± 0.14 km/km^2. The mean area covered by lakes per territory was 60 ± 57 km^2. The main prey of Scandinavian wolves is moose, *Alces alces*, representing 73% of the food biomass during winter, with roe deer as secondary prey species (Sand et al., 2016). Smaller prey include Eurasian beaver, *Castor fiber*, badger, *Meles meles*, red fox, *Vulpes vulpes*, mountain hare, *Lepus timidus*, western capercaillie, *Tetrao urogallus*, and black grouse, *Lyrurus tetrix* (Di Bernardi et al., 2021; Sand et al., 2016).

GPS Data Preparation

The original data set consisted of 72 360 winter GPS positions, defined from 10 October (generally earliest ice cover) until 1 May (generally latest ice cover) from 92 wolves. We removed the first 7 days of data after an individual was captured and used data from winters where an individual had ≥14 days of data. Furthermore, as the breeding pair mostly travels together (Carricondo-Sanchez et al., 2020; Nordli et al., 2023), we retained only the individual with the most GPS positions per territory per winter if both adults were collared. We converted individual wolf GPS positions to tracks, using the make_track function from the R package amt (Signer et al., 2019, 2024), for the subsequent step selection analysis (SSA) (Avgar et al., 2016) in R (R Core Team, 2024). We resampled the tracks to 4-hourly positions with a 15 min tolerance and then transformed them into steps (distance moved between 4-hourly GPS positions) using the steps_by_burst function. After resampling, we were left with 50 077 4-hourly actual steps from 71 individuals (44 territories). Each actual step consists of a start and end position, turning angle and step length. Using the random_steps function, we generated 10 random steps for each actual step (Signer et al., 2019; Zimmermann et al., 2014). This

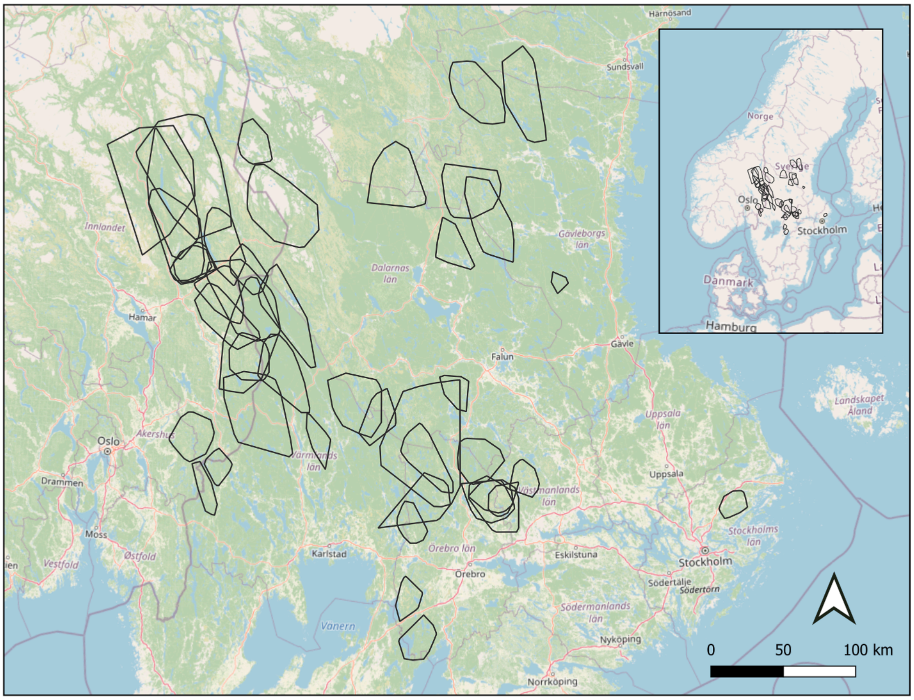

Figure 1. Map of the study area in Scandinavia, showing the 100% minimum convex polygons (MCPs) of the 44 wolf winter territories.

created a data set of grouped wolf steps, each set including one actual step and 10 random steps, and a total of 549 871 steps. Each set of actual and random steps were assigned a step ID.

Climate Data

To determine periods when water bodies were covered by ice (hereafter 'ice periods'), we used daily temperature data that were obtained from the R package nasapower (Sparks et al., 2024), retrieving data from NASA at 0.5 × 0.625 degree resolution (NASA Langley Research Center POWER Project, 2024). We retrieved daily mean temperatures in °C at 2 m above ground for each territory centroid. As there are no public data available on ice cover in the study area, and different water bodies freeze over at different times and conditions, we set ice periods according to a basic set of requirements and standard climate indices (Reig-Gracia et al., 2021). This functions as a proxy and captures most of the period in winter when water bodies are frozen. The ice period would start after daily mean air temperatures were <0 °C for 14 consecutive days (mean freezing). The ice period would end after there was a daily mean temperature >0 °C for 10 consecutive days. The dates of the ice periods were then matched with the according wolf positions by date. This created a binary column that indicated water bodies covered by ice (= 1) or not covered by ice (= 0) for each territory and winter. In addition, we retrieved daily mean snow depth data in cm for each territory and winter from the nasapower package (Sparks et al., 2024).

Landscape and Human Variables

For landscape and anthropogenic variables, we used several vector and raster layers, which were processed in QGIS 3.28.14-Firenze (QGIS Development Team, 2024). GIS vector data for water, roads and buildings were retrieved from the Norwegian Water Resources and Energy Directorate (NVE, 2024) and N50-kartdata from the Norwegian Mapping Authority (Kartverket, 2024) for Norway, and Topografi 50 from the Swedish Land Survey for Sweden (Lantmäteriet, 2024). We categorized water bodies as either lakes, rivers (>5 m wide flowing water) or streams (all smaller flowing water bodies). We categorized roads as either forest roads or main roads. Forest roads consisted of mainly gravel roads, while main roads were paved. We used line density in QGIS to generate density maps of forest roads and main roads. We used the Tree Cover Density raster from 2012 (20 m spatial resolution), 2015 (20 m) and 2018 (10 m; European Environment Agency, 2024a) to account for habitat type, with high densities indicating dense forests and low densities indicating open habitats. We used a digital elevation model (DEM) raster, consisting of data from DTM50 for Norway (Kartverket, 2024) and from the Markhöjdmodell grid 50 for Sweden (Lantmäteriet, 2024), both with a resolution of 50 × 50 m. Lastly, we used the DEM to generate a slope layer using the slope function in QGIS.

We then calculated distances of the closest lake, river, stream, main road, forest road and building at the end of each step. We also extracted elevation, slope and the densities of main roads, forest roads and tree cover at the end of each step. To determine whether a step was on water, we buffered water bodies with 10 m to minimize potential steps on shorelines and simultaneously account for potential GPS error. Previous studies have used varying distances to classify wolf positions on linear features, usually considering distances between 0 and 50 m from the feature depending on the aim of the study (Whittington et al., 2005; Zimmermann et al., 2014). We used the same threshold to define whether wolf positions were on forest roads and main roads. To account for wolf activity patterns, as wolves are mostly active during the night and rest during the day (Mech, 1992; Sand et al., 2005; Sunde et al., 2024; Theuerkauf et al., 2003), the data sets were split into day and night using the suncalc package (Thieurmel & Elmarhraoui, 2022), which we used to calculate times of sunrise and sunset for each territory and date. Positions taken from sunrise until sunset were classified as day and positions from sunset until sunrise were classified as night. For the step selection analyses, we categorized each step based on its end timestamp, whereas for the step length analyses we used the midpoint timestamp between the start and end of the step.

Statistical Analyses

First, we explored the spatial patterns of wolves in relation to water bodies by comparing proportions of positions that ended on water bodies depending on water body type (lake, rivers, streams), day or night and during ice or ice-free periods. We used a set of candidate models (Table 1) to analyse habitat selection, consisting of generalized linear mixed models (GLMMs) with a binomial family and logit link using the glmmTMB package (Brooks et al., 2017). As response variable, we used a binary term of 1 for the actual steps and 0 for the random steps. The full models (Table 1) included being on a water body (on = 1) or not (off = 0; separately for lakes, rivers and streams) as main predictor variables, including interactions with the binary variable for ice period. The binary term for being on forest roads was included in interaction with snow depth. Furthermore, we included distance to closest building, main road density, forest road density, tree cover density, slope and elevation as additional predictor variables, to account for other factors potentially affecting wolf habitat selection. We included the step ID nested within wolf ID to make sure the model compared each actual step to the generated random steps that belonged to it. We analysed the data separately for daytime and night-time to account for wolf activity patterns.

To investigate whether wolves utilized water bodies for more efficient displacement during winter, using step length of actual steps (defined as distance moved between 4-hourly GPS positions) as response variable, we ran sets of candidate model (Table 1) GLMMs with a gamma family and log link. Here we only used step lengths that were >200 m to exclude steps of resting wolves, and only GPS positions during ice periods. The full model (Table 1) contained the binary variables that indicated whether the current and/or previous step ended on lakes, rivers, streams or forest roads (one or both on water/road = 1, both off water/road = 0) to analyse the displacement when moving to and from these features, including interactions with snow depth. We included steps ending at forest roads as response variable to compare the usage of water bodies with already known travel corridors. We did not include steps on main roads, as the number of actual steps on main roads was low ($N = 156$ for all individuals during ice periods). Building distance, main road density, forest road density, elevation, slope and tree cover density were included as fixed effects and wolf ID as random effect. Again, the data were analysed separately for daytime and night-time.

All continuous variables were scaled and tested for correlation. Distance to main roads was not included in the analyses, as main road distance and main road density (Pearson correlation $r = -0.63$) were highly correlated. For each analysis, we created a set of eight candidate models based on our hypotheses, including a full model and intercept-only model (Table 1). The models were compared using the MuMIn package (Bartoń, 2024) and the best model was selected based on AICc (Table S3 to S6). Estimates of fixed effect variables whose 95% confidence intervals (CI) overlapped zero were considered uninformative (Arnold, 2010; Tables S5 and S6). Selection plots show the relative selection strength (RSS) on a log scale, which was calculated from the relative selection coefficient for 'on' divided by 'off' (Avgar et al., 2017).

Ethical Note

The wolves ($N = 92$) were tracked on snow, immobilized using a CO_2-powered dart gun from a helicopter and equipped with GPS collars (GPS-Simplex or Tellus, TVP Positioning, Lindesberg, Sweden, and GPS-Plus, Vectronic Aerospace, Berlin, Germany, https://www.vectronic-aerospace.com; Sand et al., 2005). Helicopter chase time was always minimized to a few minutes (mean 5.75 min, range 1.0–20.0 min, median 1.0 min) and total anaesthesia duration (from dart injection to reversal) was on average 90.3 min (range 17–160 minutes, median 98.5 min; Ausilio, n.d.). All capture, handling and collaring procedures were conducted by trained personnel according to standardized biomedical protocols (Arnemo & Evans, 2017), complying with international guidelines (ASAB Ethical Committee/ABS Animal Care Committee, 2025). Necessary ethical permits and approval were provided by the Swedish Animal Welfare Agency (no. 5.8.18–18473/2020, C 150/15, 407/12) and the Norwegian Experimental Animal Ethics Committee (FOTS ID 7224, 15370 and 26561). GPS-collar weight

Table 1
Candidate models for habitat selection, including the full model and intercept-only model, for both habitat selection and step length analyses

Model name	Model structure
Habitat selection daytime/night-time models	
Intercept-only model	selection ~ 1 + (1 | Wolf ID / Step ID)
Full model	selection ~ On lake * Ice period + On river * Ice period + On stream * Ice period + On forest road * Snow depth + Building distance + Main road density + Forest road density + Elevation + Slope + Tree cover density + Sex + (1 | Wolf ID / Step ID)
Water model	selection ~ On lake + On river + On stream + (1 | Wolf ID / Step ID)
Water and ice model	selection ~ On lake * Ice period + On river * Ice period + On stream * Ice period + (1 | Wolf ID / Step ID)
Road model	selection ~ On forest road + (1 | Wolf ID / Step ID)
Road and snow model	selection ~ On forest road * Snow depth + (1 | Wolf ID / Step ID)
Human model	selection ~ Building distance + Main road density + Forest road density + (1 | Wolf ID / Step ID)
Landscape model	selection ~ Elevation + Slope + Tree cover density + Snow depth + (1 | Wolf ID / Step ID)
Step length daytime/night-time models	
Intercept-only model	step length ~ 1 + (1 | Wolf ID / Step ID)
Full model	step length ~ To/from lake * Snow depth + To/from river * Snow depth + To/from stream * Snow depth + To/from forest road * Snow depth + Building distance + Main road density + Forest road density + Elevation + Slope + Tree cover density + Sex + (1 | Wolf ID)
Water model	step length + To/from lake + To/from river + To/from stream + (1 | Wolf ID)
Water and ice model	step length ~ To/from lake * Snow depth + To/from river * Snow depth + To/from stream * Snow depth + (1 | Wolf ID)
Road model	step length ~ To/from forest road + (1 | Wolf ID)
Road and snow model	step length ~ To/from forest road * Snow depth + (1 | Wolf ID)
Human model	step length ~ Building distance + Main road density + Forest road density + (1 | Wolf ID)
Landscape model	step length ~ Elevation + Slope + Tree cover density + Snow depth + (1 | Wolf ID)

Given are the model names and model structures. Models for daytime/night-time analyses had the same structure and are therefore described together.

did not exceed 2% of the wolves' body weight and had mechanical drop-off units preprogrammed to release after 900 days (regardless of earlier battery failure). GPS collars functioned on average (± SD) for 148 ± 146 days, with a mean fix success rate of 85 ± 14%. For the period of 1998–2024, there were six cases of capture-related mortality (2.7% of individuals, 1.9% of captures), see Arnemo et al. (2006) and Liberg et al. (2011).

RESULTS

Wolf GPS positions that ended on water throughout the winter constituted on average (± SE) 6.9 ± 0.6% of total positions (Table S2, Fig. 2). The proportion of positions on water bodies was 2.2 times higher during ice periods (8.6 ± 0.9%) than during periods without ice (3.9 ± 0.4%). This increased use of water bodies

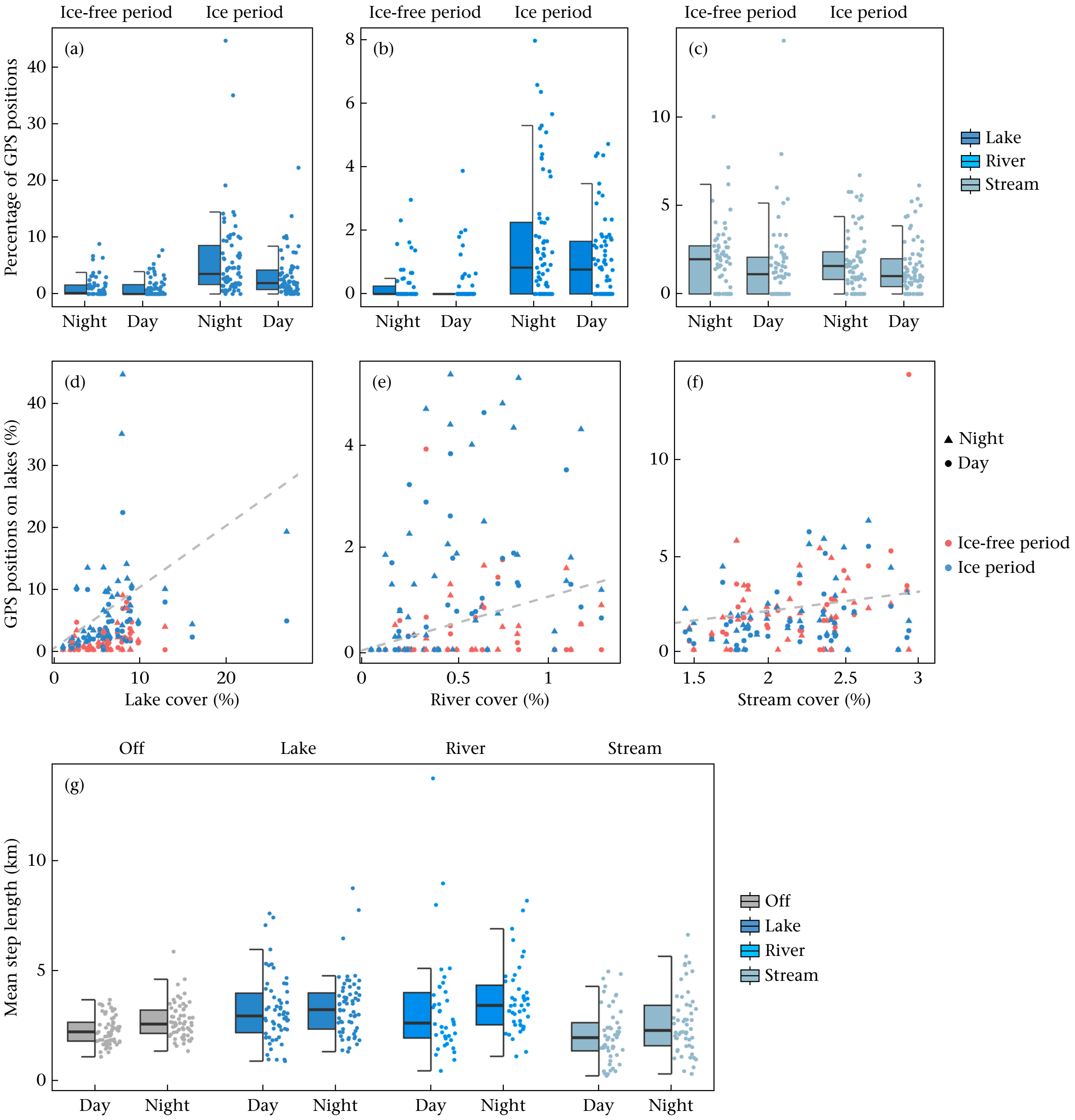

Figure 2. Box plots comparing the percentages of GPS positions of 71 individual wolves on (a) lakes, (b) rivers and (c) streams, comparing ice-free periods (left columns) and ice periods (right columns). The middle row plots show the percentages of GPS positions of wolves on (d) lakes, (e) rivers and (f) streams, compared to the cover (%) of these water bodies per territory. Shapes indicate night (triangles) and day (circles), and colours indicate ice periods (blue) and ice-free periods (red). Dashed line indicates positions in proportion to availability. The bottom plot (g) shows the mean step length (km) for each wolf, divided by lakes, rivers, streams and off all features, and separated by night and day. Plots (a)–(f) are based on the entire data set, while (g) is based only on active steps (step length >200 m) during ice periods. Box plots in plots (a)–(c) and (g) represent the median, interquartile range (IQR) and data spread (whiskers), while the jittered points indicate individual observations, with values beyond the whiskers representing statistical outliers (1.5 x IQR).

during ice periods was related to lakes and rivers, with 3.8 and 4.0 times higher proportions of positions on water during ice versus ice-free periods, respectively (Table S2). Streams were used slightly less in ice periods than in ice-free periods (Table S2).

Habitat Selection

For both daytime and night-time analyses, the full model was the best performing model (Tables S3 and S5). During ice-free nights, wolves avoided lakes and neither avoided nor selected for being on rivers (Fig. 3a). During nights with ice cover, wolves selected for lakes and rivers (Fig. 3a). The probability of selecting for rivers during ice periods was similar to that of selecting for forest roads (Fig. 3a). Streams were neither selected for nor avoided during nights, regardless of ice cover (Fig. 3a). Wolves selected for greater distances from buildings, lower main road density, lower forest road density, lower elevation, steeper slope and higher tree cover density (Table S5).

During daytime, wolves avoided lakes, but less so during ice periods (Fig. 3b). Wolves selected for rivers in ice periods, but showed no selection for or avoidance of being on rivers during ice-free periods (Fig. 3b). Streams were neither selected for nor

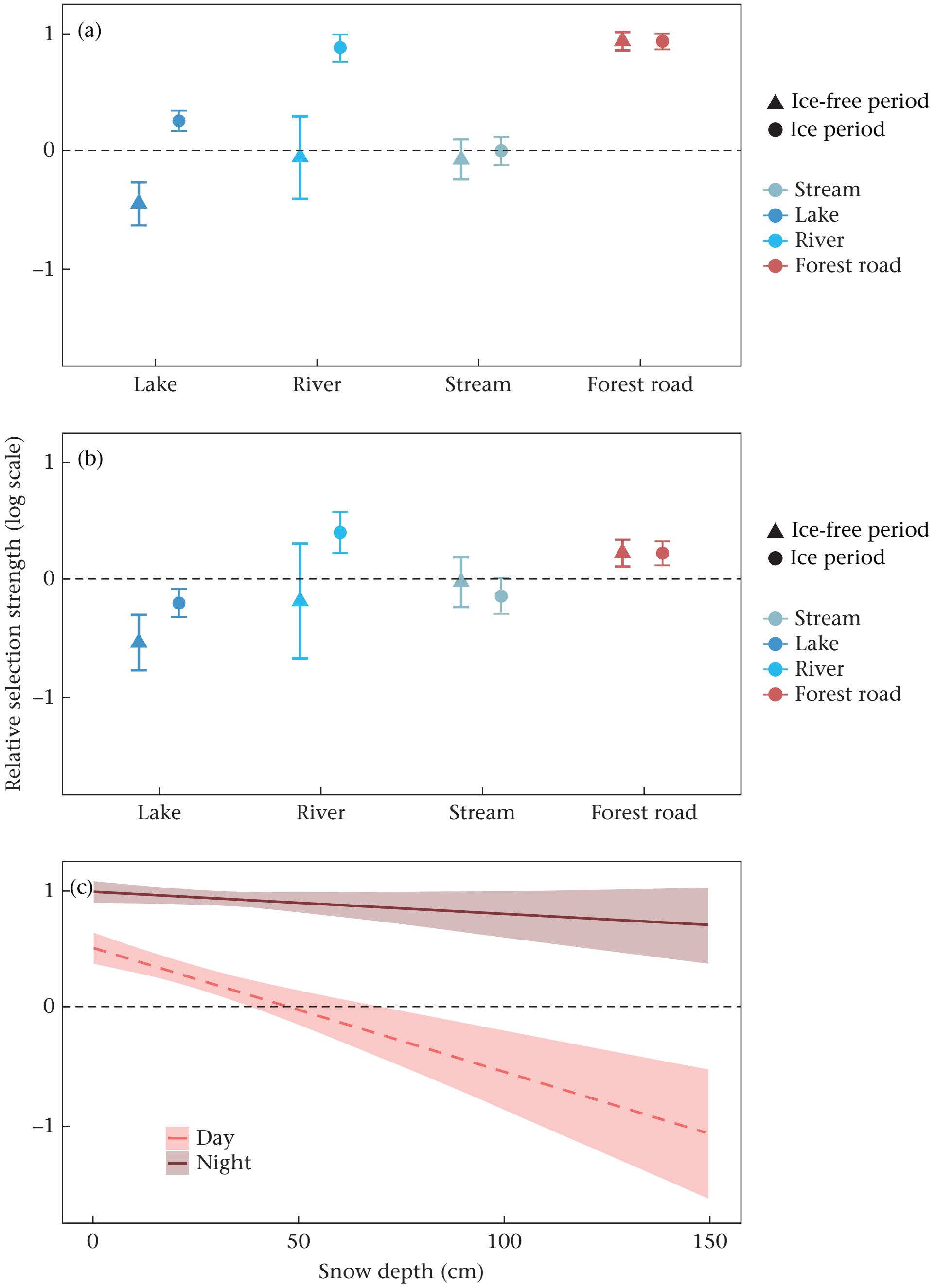

Figure 3. Effect plots of step selection analysis (SSA) generalized linear mixed models (GLMMs), showing the relative selection strength (RSS, log scaled) of streams, lakes, rivers and forest roads during ice periods (circles) and ice-free periods (triangles) during winter (a) nights and (b) days. (c) Bottom plot shows the RSS (log scaled) of forest roads during winter nights (darker solid) and days (lighter dashed) with snow depth. In each plot, positive values indicate relative selection, negative values indicate relative avoidance and 0 indicates no difference to being 'off' features (dashed horizontal line). (a)–(b) Whiskers and (c) shading represent the 95% confidence intervals derived from model prediction bounds.

avoided regardless of ice period (Fig. 3b). Wolves selected for forest roads during night-time irrespective of snow depth whereas increased snow depth resulted in avoidance of forest roads during daytime (Fig. 3c). Similar to night-time, wolves selected for greater distances from buildings, lower main and forest road densities, lower elevation, steeper slope and higher tree cover density during daytime (Table S5).

Step Length

The full model was the best performing model from the candidate models (Table S4). During both winter days and nights, wolves moved larger distances when travelling on as compared to off lakes, rivers and forest roads, albeit with smaller distances during days than during nights (Fig. 4a). Step length generally

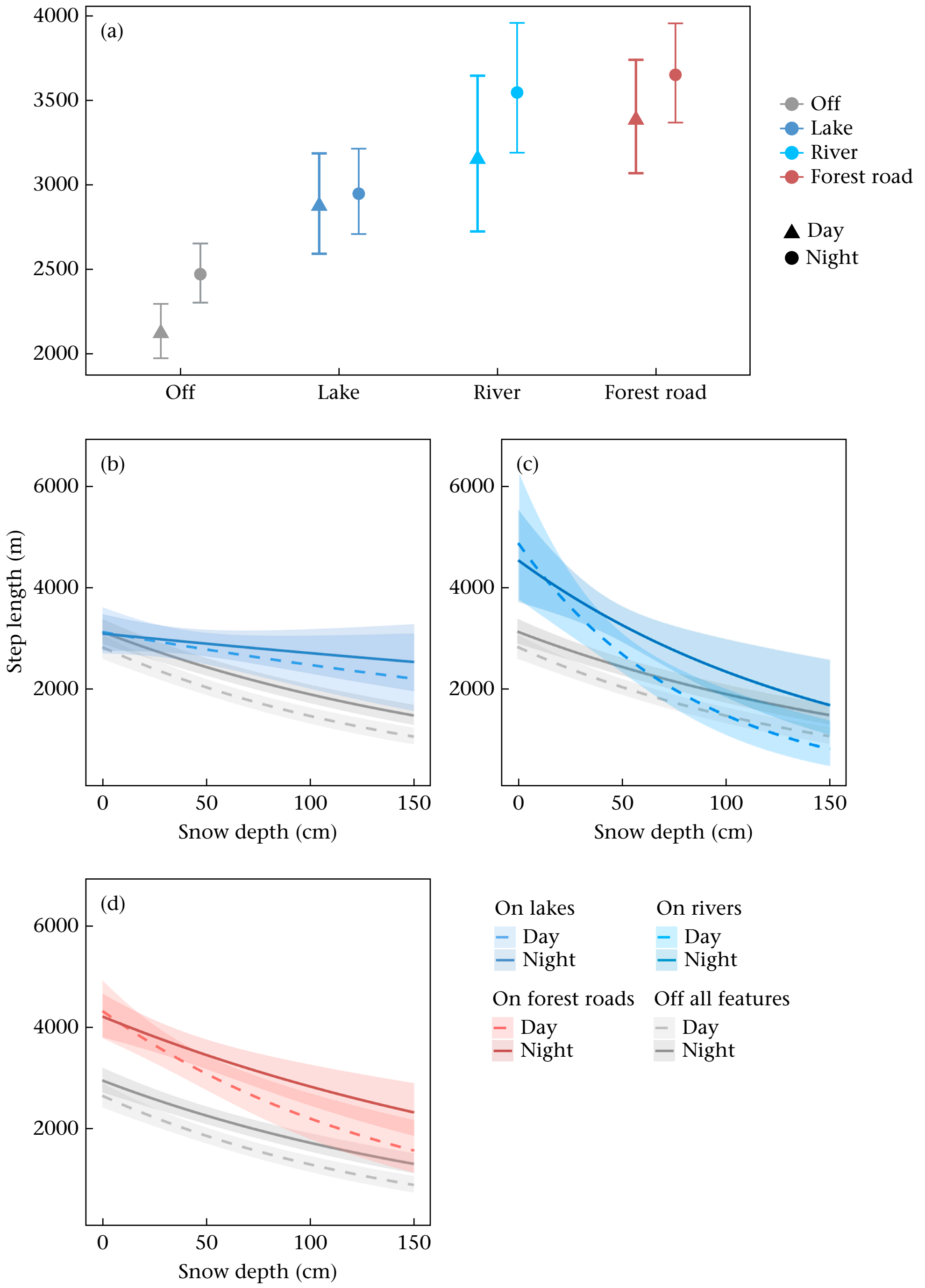

Figure 4. (a) Effect plots of step length analysis from generalized linear mixed models (GLMMs), showing the step length when travelling to/from lakes (dark blue), rivers (light blue), forest roads (red) and all other habitats (grey) during winter days (triangles) and nights (circles). Bottom plots (b–d) show the effect of snow depth on step lengths in interaction with (b) lakes, (c) rivers and (d) forest roads. Lines represent the effect during night-time (solid) and daytime (dashed), and the grey lines refer to step lengths in all other habitats as a baseline. (a) Whiskers and (b)–(d) shading represent the 95% confidence intervals derived from model prediction bounds.

decreased with increasing snow depth, also when travelling on forest roads and rivers, but not when on lakes (Fig. 4b–d). Step length increased closer to buildings, at lower forest road density, higher main road density (during nights only), less slope, lower elevation and lower tree cover density (Table S6).

DISCUSSION

This study explored movement patterns and habitat selection of wolves in relation to water bodies in the boreal zone of Scandinavia. We found that wolves selected for lakes and rivers during ice periods and increased their step length when travelling on frozen lakes and rivers. Below, we discuss how these findings help us to better understand the use of frozen water bodies by terrestrial mammals.

Our results show that wolves avoided lakes during ice-free periods in winter, indicating that larger open water bodies create barrier effects for terrestrial mammals (Leblond et al., 2016; Newton et al., 2017). Conversely, wolves selected for lakes and rivers during ice periods (H1), indicating that wolves are capable of identifying and adapting to this seasonal change. This adaptation is similar to other species' utilization of frozen water. For example, ice cover had a positive influence on caribou movement rates and directionality, with caribou selecting for ice cover when moving across large water bodies (Leblond et al., 2016). There was no selection for or avoidance of streams, with or without ice cover, possibly because streams are too small to have a barrier effect for wolves (Kingdon et al., 2025) or to function as connective linear features for movements during ice periods, and deep snow might completely cover them in the landscape. Wolves selected frozen water bodies mainly during night-time (H2), suggesting that they use them more when they are active, rather than during daytime when activity is lower (Sand et al., 2005; Theuerkauf et al., 2003), similar to the use of forest roads (Carricondo-Sanchez et al., 2020; Zimmermann et al., 2014).

Larger frozen water bodies could form corridors that connect key areas of wolf territories, similar to human-made linear features, such as forest roads (Johnson-Bice et al., 2023; Malcolm et al., 2020; Muhly et al., 2019). Previous research identifying frozen water bodies as travel corridors suggested wolves only used frozen water bodies in areas with low availability or absence of anthropogenic features (Kittle et al., 2017; Newton et al., 2017). In contrast, our results indicate that wolves selected for frozen water bodies while forest roads were widely available (mean density 1.14 km/km^2). Wolves travelled more efficiently on ice compared to when they did not travel on ice, as shown by longer step length when travelling on larger frozen water bodies, both during daytime and night-time (H3). Step lengths were comparable on frozen rivers and forest roads, similar to Musiani et al. (1998).

Additionally, the use of frozen water bodies during night-time by wolves might correlate with high prey density and lower elevations with less snow (Hjeljord, 2001; Mysterud et al., 2011). Frozen rivers, often located in valleys, may serve as travel corridors and foraging areas for prey, thus potentially increasing the likelihood of prey encounters. For example, moose have been shown to partly migrate into valleys during winter (Bunnefeld et al., 2011) and wolves have been found to follow their seasonal migration as a hunting strategy (Ordiz et al., 2020). Although wolves do not necessarily select for hunting near frozen water bodies (McPhee et al., 2012), they have been found to kill prey frequently near or on frozen water (Bojarska et al., 2017; K. E. Kunkel & Pletscher, 2000, 2001; Webb, 2010).

The effect of snow on the selection of forest roads was only found during daytime, thus partially supporting the hypothesis that wolves decrease their use of forest roads with increased snow depths (H4). As forest roads are ploughed irregularly (Zimmermann et al., 2014) or only partially, only ploughed sections of forest roads will facilitate efficient mobility (except at relatively low snow depths). However, during daytime, ploughed roads might also have increased human traffic, causing a trade-off between efficient travel and increased human encounter risk. Additionally, the snow cover will be shallower in forests with high tree cover density when compared to adjacent open areas (including forest roads). Coyotes are known to select habitat on a very fine scale, strongly influenced by snow depth (Crête & Larivière, 2003; Murray & Boutin, 1991), suggesting similar behaviour might occur in wolves. As our snow depth variable was on a coarse spatial and temporal scale, we suggest there may exist a more complex, fine-scale relationship between wolf selection for travel corridors and snow than we could untangle. However, we did find clear effects of snow depth on step lengths, showing that wolf step lengths were indeed impeded by deeper snow (Droghini & Boutin, 2018a), but not more on water bodies and roads than in other habitats. Wolf step lengths remained quite stable when travelling on frozen lakes with increased snow depth in the territory, which could be explained by a different microclimate on lakes as compared to other habitat types (Bengtsson, 1986; Burgis et al., 2007) and the formation of snow-ice causing shallower snow depths on lakes (Jeffries et al., 2005). Wolf step lengths were lower on frozen rivers only during daytime, suggesting that wolves might not use rivers for long-distance travel during daytime.

When interpreting step lengths with regards to linear features, human-made or natural, it is important to approach inferences with care, as these results require nuance and are best understood in combination with other factors of importance for wolves. Linear features lead to more directed movement, thus directly increasing the likelihood of longer distances between steps (Dickie et al., 2017, 2020). Increased step lengths on linear features supports this hypothesis but, combined with the results on habitat selection, our study shows that wolves actively selected for frozen water bodies as travel corridors. The 4-hourly sampling interval of our GPS data were too coarse to analyse space-use patterns of wolves on frozen water bodies in detail. Lastly, our study was limited by our estimation of ice periods, as there were no detailed ice-cover data available. As a consequence, our estimates could not account for differences in water body type, size and depth, altitude, stream flow or water temperature, which might affect ice cover and thickness.

Our findings provide new insights on how wolves use water and contribute to our understanding of mammalian mobility in boreal regions. We show that wolves are highly adaptable concerning their habitat selection, utilizing frozen water bodies for efficient winter travel. To better understand if wolves utilize water bodies for other purposes, such as hunting and/or as meeting points, future studies could investigate finer-scale GPS data that allow for analysing GPS clusters, kill sites and more specific behaviours. For example, relating kill sites and moose densities to water might further explain the use of water bodies as a hunting strategy in both summer and winter. Similarly, further investigation of den sites, rendezvous sites and daybeds could address the importance of water availability during reproduction, pup rearing and resting. Considering the effect of ice, in combination with other variables such as snow and human-made objects, can contribute to our understanding of mammalian seasonal movement patterns and space use in the boreal zone.

Author Contributions

Wessel Veenbrink: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization.

Barbara Zimmermann: Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Håkan Sand:** Writing – review & editing, Methodology, Funding acquisition. **Camilla Wikenros:** Writing – review & editing, Methodology, Funding acquisition. **Petter Wabakken:** Writing – review & editing, Methodology, Funding acquisition. **Martin Mayer:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Data Availability

As the data set used during the analyses contains sensitive content, such as the locations of den sites, all coordinates have been removed. The data set and code are openly available on figshare at https://doi.org/10.6084/m9.figshare.28333220“.

Declaration of Interest

The authors have no conflicts of interest to declare.

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Supplementary Material

Supplementary material associated with this article can be found at https://doi.org/10.1016/j.anbehav.2025.123401.

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