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Master Thesis

A Wolf's Way of Water:

Wolf space use in relation to waterbodies

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Abstract

Terrestrial mammals are in many ways connected to waterbodies, although studies on habitat selection within anthropogenic landscapes often overlook the importance of water. The recolonization of grey wolves (*Canis lupus lupus*) across parts of Europe, together with technological advancements, has offered opportunities to study spatial patterns of large carnivores in human-influenced landscapes, yet our understanding of wolf interactions with waterbodies remains limited. We hypothesized that wolves utilized frozen water during winter as travel corridors, and kept close proximity to water during hot periods in summer for hydration and thermoregulation.

We used integrated step selection analyses with data from 10 GPS-collared adult individual wolves in 5 territories in Scandinavia to investigate habitat selection in relation to waterbodies, time of day, and seasonal changes. The study included >32,000 GPS positions taken at 4-hour intervals between 2018 and 2022.

In winter, wolves selected for frozen lakes and rivers during ice periods, especially at night. Wolf travel speed increased on ice, suggesting that they likely used frozen waterbodies as travel corridors or for hunting. Moreover, wolves decreased their use of forest roads while simultaneously selecting for frozen water, suggesting a trade-off between human encounter risk and travel efficiency. In summer, wolves kept closer distances to streams and rivers during hot periods, likely for drinking hydrated or seeking cooler environments while active or resting. Lactating wolves showed no increased selection for close proximities to water.

This study shows the adaptive, seasonal utilization of water by wolves in an anthropogenic landscape, highlighting the importance of water in the wolf's life-history. Our findings suggest more intricate interactions with water influence the way wolves use water, such as for hunting or during the denning period.

Keywords: Habitat selection, Integrated step selection analysis, Wolf, *Canis lupus lupus*, Frozen waterbodies, Water proximity, Scandinavia, Roads

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1. Introduction

Despite having fully evolved for life on land, all terrestrial species retain a certain dependence upon water (Ripl, 2003). Waterbodies form crucial landscape elements to make life on land possible, and their availability affects species' life-histories (Western, 1975). Waterbodies can connect aquatic and terrestrial trophic systems, causing high productivity in surrounding areas, which affects species richness and diversity (Burgis, 2007). Some species are fully adapted for a semi-aquatic lifestyle, like otters (Lutrinae) (Harano & Kutsukake, 2024) and beavers (*Castor fiber*) (Müller-Schwarze 2011). However, most terrestrial mammals are connected to waterbodies, as water offers the primary source of freshwater that is necessary for hydration and bodily functions (Degen, 1997; Campbell and Norman, 1998). Additionally, water cools down, which supports thermoregulation in mammals. Several species of predatory mammals have adapted to utilize water, such as brown bears (*Ursus arctos*) hunting for migrating salmon (*Oncorhynchus keta*) (Mangipane et al, 2020; Levi et al, 2020) and jaguars (*Panthera onca*) hunting for aquatic prey and being excellent swimmers (Franco et al, 2018).

In large parts of the northern hemisphere, waterbodies are strongly affected by seasonality. Open water during summer can create barriers and fragment the landscape, but during winter much of this water freezes over and gives way to new terrains (Banfield, 1954). Frozen water facilitates mammalian distribution, 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).

Overall, the availability and necessity of water for terrestrial species is often considered a given, causing it to be an overlooked topic in ecological research. In the case of grey wolves (*Canis lupus lupus*), little is known about their relationship with water. Wolves, being one of the key apex-predators of the boreal ecosystem, have recolonized large parts of northern Europe since their near extirpation (Pletscher et al, 1997; Ordiz et al, 2015; Kaartinen et al, 2015). Wolves now occur in human-dominated landscapes, but tend to avoid areas of high human density, perceiving them as a risk (Malcolm et al, 2020; Hebblewhite & Merrill, 2008; Theuerkauf et al, 2003a; Lesmerises et al, 2012), given that these areas cause increased mortality (Sunde et al, 2021). However, wolves have been shown to use human infrastructure to their advantage, using them to promote their mobility (Kittle et al, 2017; Muhly et al, 2019; Dickie et al, 2016; Nelson et al, 2012). Most of these studies have focused on the interaction with manmade linear features, such as roads, trails, seismic lines, pipelines, and power lines (Johnson-Bice et al, 2023;

Malcolm et al, 2020; Barocas et al, 2018). For example, wolves have been found to utilize forest roads for fast and easy travel, meanwhile maintaining cryptic behavior by using them during the night and avoiding them during daytime (Zimmermann et al, 2014; Bojarska et al, 2020; Theuerkauf et al, 2003a, 2007). Frozen waterbodies could serve a similar purpose, yet our understanding of how wolves utilize frozen water remains limited. A study by Kittle et al (2017) found that wolves used frozen waterbodies, but their findings suggested that ice was only used in the absence of forest roads. However, frozen waterbodies could be used as travel corridors when human influence is high, in order to avoid increased human-encounter risk. Additionally, linear waterbodies such as rivers and streams are most often situated in valleys, where snow is less deep, and might serve as a connection between key areas of a wolf's territory. Usage of frozen waterbodies as main winter routes by North American wolves has been described by Mech (1981) but has not been studied in detail. Furthermore, frozen lakes might facilitate central meeting points with little human disturbance during winter. Depending on their size, frozen lakes might connect key areas of a wolf home range and offer open spaces with increased visibility.

Additionally, several prey species of wolves find suitable foraging habitats in wetlands and close to waterbodies. Moose (*Alces alces*), which is the main prey of wolves in Scandinavia (Sand et al, 2008), have been shown to select for wetland habitats (Melin et al, 2019; Laforge et al, 2016; Olsson et al, 2011su), foraging on riparian vegetation (MacCracken et al, 1993; Bump et al, 2009; Fraser et al, 1980) and vegetation that grows mainly along waterbodies (Shiple et al, 1998). Several prey species have been shown to find refuge in waterbodies when chased by wolves, such as moose (Stotyn et al, 2005), red deer (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), caribou, and elk (*Cervus canadensis*) (Mech, 2015). Wolves have been found to follow seasonal prey migration routes into valleys (Ordiz et al, 2020), and to make frequent kills near open water (Bojarska et al, 2017; Kunkel & Pletscher, 2000) and on ice (Kunkel & Pletscher, 2001; McPhee et al, 2012; Webb, 2009; Kauffman et al, 2007; Voyageurs Wolf Project, 2024). This suggests that both wolves and their prey select areas close to water for hunting and survival strategies.

Besides frozen waterbodies, wolves can make use of open water during ice-free periods. Wolves continuously lose water from their system, through thermoregulation, their metabolic system, excretion of waste, and transportation (Degen, 1997; Campbell & Norman, 1998). They extract water from a variety of sources, including their prey, snow ingestion, and drinking from both small puddles and larger waterbodies (Mech & Boitani, 2003). As temperatures rise, wolves cool down by seeking cooler environments, and use evaporative cooling through panting and increased salivation (Mech & Boitani, 2003). Especially during hot periods in summer, wolves would lower

their activity to reduce energy expenditure and water loss (Careau et al, 2007; Afik & Pinshow, 1993). Wolves are mainly active at night, and rest during daytime (Sunde et al, 2024; Eriksen, 2006; Theuerkauf et al, 2003b; Mech, 1992). Thus, wolves might select to rest close to water during hot summer days. Several studies have shown that wolves select rendezvous- and den sites in proximity to freshwater sources, for example in Canada (Benson et al, 2015), Greece (Iliopoulos et al, 2013), and Alaska (Person & Russell, 2009; Joly et al, 2018). As stated by Mech (1981), den sites may be limited to locations near water for nursing females to drink frequently (Joslin, 1967; Mech & Boitani, 2003). When active during summer nights, wolves might also keep close proximity to freshwater sources, to stay hydrated during their energy-expensive activity peaks.

The primary aim of this study was to investigate wolf habitat use and selection in relation to waterbodies, given that no studies have focused solely on the spatial and temporal use of waterbodies by wolves yet. The first objective of this study was to quantify the use of waterbodies by wolves, and how their usage varied across seasons and time of the day. The second objective was to find out if wolves selected for frozen waterbodies during ice periods. We hypothesized that (H1) wolves would select to be on frozen waterbodies during winter and selected for them as travel corridors, similar to forest roads. We predicted that the selection of frozen waterbodies was stronger during night than during daytime. Subsequently, we predicted higher travel speed of wolves moving on frozen waterbodies compared to when moving on land. Concerning habitat selection during summer, we hypothesized that (H2) wolves would keep closer distances to waterbodies during hot summer days, to stay hydrated and cool to reduce energy expenditure when they are mostly resting. Furthermore, we hypothesized that (H3) generally, wolves would keep closer proximity to waterbodies during nights, for increased prey-encounter while hunting and to maintain hydration during activity-peaks. Lastly, we hypothesized that (H4) lactating females would stay closer to water during the pup rearing period than non-lactating females, and males. Through these objectives, this study aimed to explore the adaptive behaviors of wolves in response to natural water features and seasonal climatic changes in a human-dominated landscape.

2. Methods

2.1. Study area

The study was conducted in the western territories of the wolf breeding range of the Scandinavian population, in the Finnskogen area situated on the border between Norway and Sweden (Figure 1). Figure 1 shows the wolf territories ($n = 5$ territories, 100% MCP) with an area of mean \pm SE: $1,196.76 \pm 186.93 \text{ km}^2$, and the extended study area around these territories of $7,925 \text{ km}^2$. The territories were mainly covered by boreal coniferous forest ($79.96 \pm 1.35 \%$). The second most abundant land cover type was open areas, which mainly included mires, but also mountains and boulder fields ($14.83 \pm 1.72 \%$), followed by lakes ($4.13 \pm 0.65 \%$), cultivated areas ($0.61 \pm 0.16 \%$), rivers ($0.29 \pm 0.10 \%$), and built-up areas (0.02%).

Forests were dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), mixed with deciduous species, such as birch (*Betula pubescens*) and aspen (*Populus tremula*). Birch was also often found in mires and along waterbodies, together with willow (*Salix sp.*), and alder (*Alnus sp.*). There was a mean (\pm SD) length of $1269.14 \pm 247.28 \text{ km}$ of forest roads per wolf territory, with forest road density being $1.03 \pm 0.08 \text{ km/km}^2$ (Appendix 9). Main roads had a mean length of $240.39 \pm 42.09 \text{ km}$ per territory, and main road density was about 5.15 times lower than forest road density ($0.20 \pm 0.01 \text{ km/km}^2$). Building density within territories was 1.78 ± 0.17 per km^2 . The study area had a low human population density, with <1 person per km^2 (Wabakken et al, 2001). The mean length of streams per territory was $1433.03 \pm 258.81 \text{ km}$, and rivers had a mean length of $55.6 \pm 15.4 \text{ km}$ per territory. Stream and river density per territory was $1.24 \pm 0.07 \text{ km/km}^2$. The mean area of lakes per territory was $48.35 \pm 11.23 \text{ km}^2$. The main prey of Scandinavian wolves is moose, representing more than 95% of the food biomass during summer

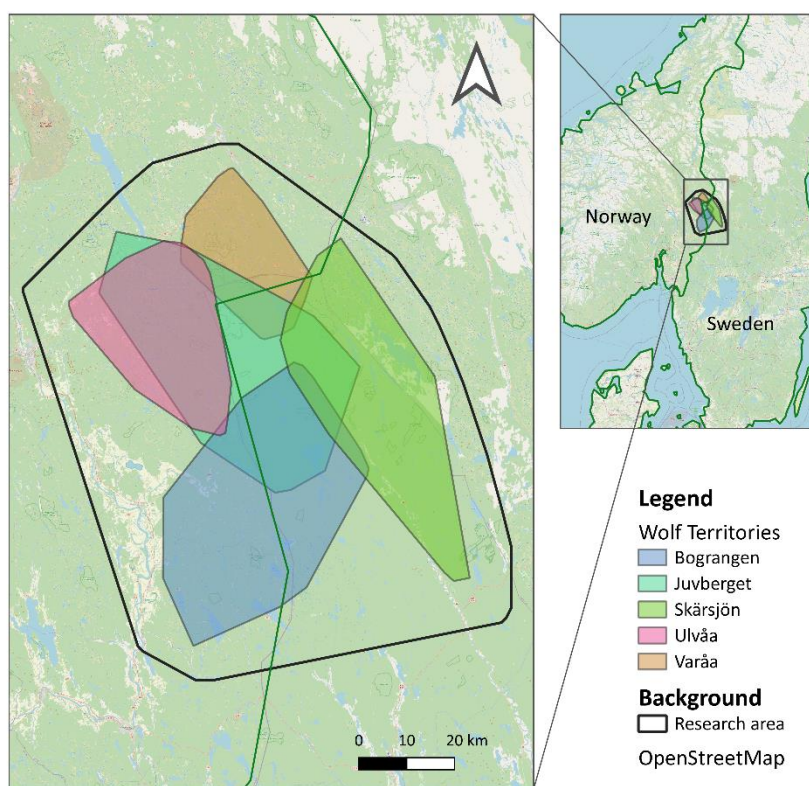


Figure 1

Map of the study area of Finnskogen, on the border between Norway and Sweden. Shown are the 100% MCPs of the 5 wolf territories, and the extended study area.

(Sand et al, 2008). Wolves in the study area also predate on roe deer (*Capreolus capreolus*), and red deer. Smaller prey that is available to them includes Eurasian beaver, badger (*Meles meles*), red fox (*Vulpes vulpes*), mountain hare (*Lepus timidus*), western capercaillie (*Tetrao urogallus*), and black grouse (*Lyrurus tetrix*) (Sand et al, 2008; Di Bernardi et al, 2021).

2.2. Study animals and period

For this study we used GPS data of 10 adult individual wolves from 5 territories obtained between February 2018 and December 2022 (Table 1), provided and collected by the Scandinavian Wolf Research Project (SKANDULV). The wolves were immobilized by helicopter and equipped with GPS neck collars (GPS-Plus or GPS-Lite by Vectronic Aerospace, Germany) (Sand et al, 2005; Kreeger et al, 2023; Arnemo & Evans, 2017). GPS-collar fix-rates were set to 4-hourly intervals, with 1-hourly intervals during predation studies. The dataset consisted of data for 25 individual wolf years, and 16 territory years, where wolves living in the same territory in the same year are considered together (Carricondo-Sanchez et al, 2020). Through information on pack sizes, we could identify the reproductive status of most individuals and packs in most years (Appendix 8). With this information, we identified that three female individuals were lactating during 9 individual years, but only had GPS data during the nursing periods for 6 of those years (Table 1, Appendix 8). Lactation was estimated to occur between May 1st, which is the median date wolves give birth in Scandinavia (Nordli et al, 2023), until 6 weeks after, which is within a female wolf's nursing period (Mech & Boitani, 2003).

Table 1

GPS-collared adult wolves included in the study, with sex, territory, study period, number of years, reproduction and lactation periods, and count of 4-hourly GPS positions.

<i>Individual ID</i>	<i>Sex</i>	<i>Territory</i>	<i>Years</i>	<i>Number of individual years</i>	<i>Number of reproductive years</i>	<i>Number of lactating periods*</i>	<i>Number of 4-hourly GPS positions</i>
M17-08	M	Varåa	2018-2021	4	3		5,571
M18-12	M	Juvberget	2018	1	0		1,342
M18-13	F	Juvberget	2018-2022	5	3	3	8,814
M18-17	F	Varåa	2018-2020	3	3	2	3,312
M19-01	F	Bogringen	2019-2020	2	0	0	1,438
M19-02	M	Juvberget	2019-2021	3	3		4,355
M19-04	M	Bogringen	2019-2020	2	0		2,216
M20-02	F	Ulvåa	2020-2021	2	3	1	1,567
M21-02	M	Skärsjön	2021-2022	2	1		2,270
M22-01	M	Ulvåa	2022	1	1		1,621
Sum				25	17	6	32,506

* Lactating periods indicate reproducing females that had GPS-data during the estimated lactation period

2.3. GPS data preparation

The original dataset consisted of 61,274 GPS positions. In order to do integrated Step Selection Analysis (iSSA) (Avgar et al, 2016), the individual wolf GPS positions needed to be converted to tracks. To do this, we utilized the `make_track()` function from `amt` package (Signer et al, 2024, 2019) in RStudio (Posit team, 2024). As the GPS fix-rates varied between collars and during certain periods, and iSSA demands the use of the most detailed regular sampling interval available in the data (Signer et al, 2019), we resampled the tracks to 4-hourly positions with a 15-minute tolerance using `track_resample()`. Afterwards, the tracks were turned into steps using the `steps_by_burst()` function. After resampling, we were left with 32,506 4-hourly actual steps. 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. iSSA using 10 random steps per actual step have been used successfully before (Zimmermann et al, 2014; Whittington et al, 2005; Coulon et al, 2008; Signer et al, 2017), and provide good results due to the relatively large sample size, without causing computational issues (Thurfjell et al, 2014). The `random_steps()` function uses the gamma distribution of the actual step lengths and von Mises distribution of the actual turning angles to generate random steps with random step lengths and turning angles (Signer et al, 2019). This created a dataset of grouped wolf steps, each set including 1 actual step and 10 random steps, and a total of 357,566 steps. Each set of actual and random steps were assigned a unique step ID, which consisted of each individual animal ID number, and a step ID generated by `amt` (Figure 2).

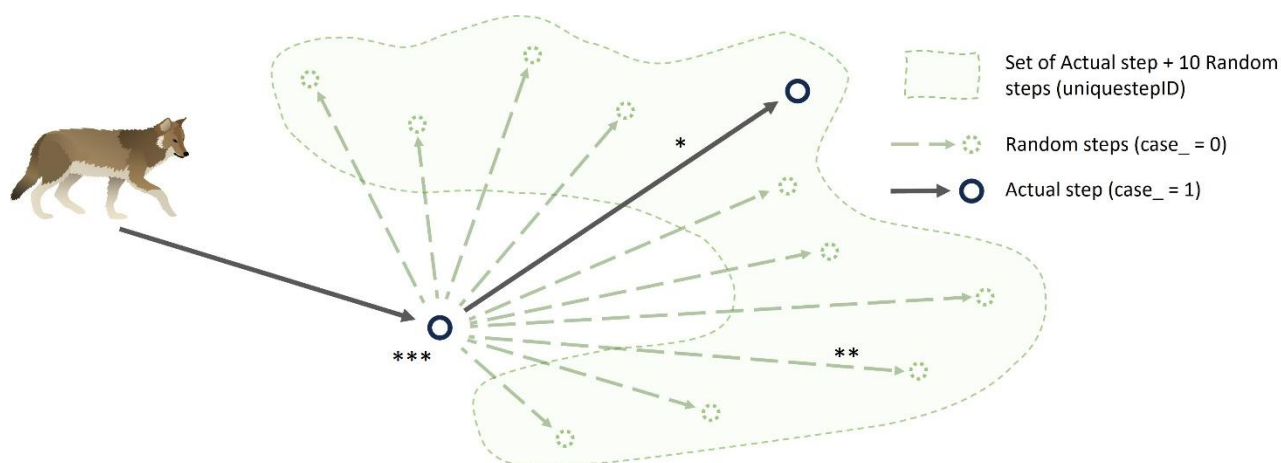


Figure 2

Example of wolf actual and generated random steps: For each actual wolf step we generated 10 random steps, which together formed a set indicated by a `uniquestepID`. * Each actual step goes from the previous GPS position to the next, with a 4-hour time interval. The actual step also contains information of the step length and turning angle. ** The random steps are generated based on the gamma distribution of step length and von Mises turning angle of all actual steps (Signer et al, 2019). *** The start point of each set of steps is the end point of the previous actual step.

2.4. Climate data

To determine ‘ice periods’, we used daily temperature data that was obtained from the *easyclimate* package in RStudio (Cruz-Alonso et al, 2023). We retrieved daily minimum and maximum temperatures in degrees Celsius for the study area (Appendix 9). As there is no public data available on ice presence in the research area, we manually 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 waterbodies are frozen. The ice period would start when maximum temperatures were $< 0^{\circ}\text{C}$ for 7 consecutive days (maximum freezing). The ice period would end if there was a maximum melting temperature $> 0^{\circ}\text{C}$ for 14 days, or a mean melting temperature (averaged from minimum and maximum temperatures) $> 0^{\circ}\text{C}$ for 7 days. The dates of the ice periods were then matched with the according wolf positions by date. This created a binary column that indicated ice presence (1) or no ice presence (0) (Appendix 10).

To define ‘hot periods’, we used hourly minimum and maximum temperatures from the closest weather station in Flisa, retrieved from the Norwegian Centre for Climate Services (Norsk Klimaservicesenter, 2024). The minimum and maximum hourly temperatures were used to calculate an average hourly temperature and were matched with the according wolf positions by hour. A binary column indicated steps when the average temperatures was $> 20^{\circ}\text{C}$ (‘hot period’ = 1) and steps when the average temperature was $< 20^{\circ}\text{C}$ (‘not hot’ = 0) (Appendix 10).

2.5. Landscape and human variables

To obtain variables from landscape features and human variables, we used several vector and raster layers, which were processed in QGIS 3.28.14-Firenze (QGIS, 2024). For all GIS data, we used a projection of EUREF89 UTM zone 33n, which matched with the wolf GPS coordinates. GIS data was retrieved from the Norwegian Water Resources and Energy Directorate (NVE, 2024) and the Norwegian Mapping Authority (Kartverket, 2024) for Norway, and the Swedish Land Survey for Sweden (Lantmäteriet, 2024). We used NVE, N50 and Topografi 50 for all water data, as well as N50 and Topografi 50 for all roads and buildings. The layers were combined, and the values were translated and categorized. We categorized waterbodies as either lakes (“Sjö” in Sweden and “Innsjø” or “Innsjø regulert” in Norway), rivers (“Hovedelv” in Norway and “Vattendrag” in Sweden), or streams (“Elvbekk” in Norway or “Älvbäck” in Sweden). We categorized roads as either forest roads (“Traktorveg” and “Småveg enkel standard” with “private” classification), or main roads (“Landsveg”, “Landsveg liten”, and “Småveg” with “national”, “county”, or

“municipality” classification). Forest roads were considered to be mainly gravel roads, while main roads were considered to be paved. We used line density and kernel density functions in QGIS to generate density maps of forest roads, main roads, and buildings. We used the Tree Cover Density raster from 2018 with a resolution of 10 m (Copernicus, 2018) 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, and from the Markhöydemodell grid 50 for Sweden, both with a resolution of 50 x 50 m. Lastly, we used the DEM to generate a slope layer using the slope function in QGIS.

The end coordinates of all actual and random steps were exported from RStudio and imported into QGIS. We removed all random steps that ended up outside of the study area ($n = 468$). 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 the densities of main roads, forest roads, buildings, tree cover density, elevation, and slope at the end of each step. We proceeded to reimport the dataset into RStudio which we had a total of 357,098 steps, of which 32,506 actual steps and 324,592 random steps (Appendix 1). To create a separate column of general distance to the closest waterbody, we took the closest distance of each step to either lake, river, or stream. To determine whether a step was on water, we took a distance of 10 m as buffer around waterbodies. We chose 10 m to minimize potential steps on shorelines but simultaneously account for GPS error. Previous studies 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). The 10 m buffer created binary variables that indicated whether steps were on lakes, rivers, streams, and on water in general. In addition, we created a similar variable that indicated whether wolf positions were on forest roads and main roads. Lastly, we created variables that indicated whether the end point and/or start point (end point of the previous step) was located on a main road, forest road, lake, river, or stream, which allowed us to analyze the travel speed of wolves when moving to and from waterbodies and roads.

We separated the dataset into summer and winter, to analyze the seasonal interaction with waterbodies separately. For the start and end dates we took the same dates for each year that did not overlap with any of the ice- or hot periods (Appendix 10), using the 10th of October (end of summer, start of winter) and the 10th of April (end of winter, start of summer) as cut-off (Appendix 1). To account for wolf activity patterns, as wolves are mostly active during the night and rest during the day (Theuerkauf et al, 2003b; Mech 1992; Appendix 4), the datasets were split into day (from 08:00 to 19:59) and night (from 20:00 to 07:59; Appendix 1).

2.6. Statistical analyses

The continuous variables were checked for correlation using the Pearson correlation coefficients with the `cor()` function from the *stats* package (R Core Team, 2024). We defined any correlation coefficient > 0.6 or < -0.6 as significant correlation. Correlation occurred between the general water distance and stream distance variables (0.84), the main road distance and main road density (0.62), and between the main road density and building density variables (-0.70). These variables would be used separately during the modelling process.

First, we attempted to explore the spatial patterns of wolves in relation to waterbodies. We compared proportions of positions that ended on waterbodies during summer and winter, day and night, and during ice and hot periods. To visually describe spatial patterns of wolves in relation to waterbodies, we plotted densities of actual and random steps compared to distances to waterbodies. Furthermore, we explored the differences between lactating and non-lactating wolves in summer, and their general distances to waterbodies. As the sample size of lactating wolves was small (3 individuals during 6 individual years) we decided to explore patterns, rather than including lactation in our summer analyses. Additionally, we compared proportions of GPS positions on frozen waterbodies and on roads during day and night, and during ice periods.

To analyze the habitat selection by wolves during winter, we used generalized linear mixed models (GLMM) with a binomial family and logit link using the *lme4* package (Bates et al, 2015). We also explored the use of Cox Proportional-Hazards (*coxph*) models, which are commonly used for step selection analyses, and got similar model results. However, we preferred GLMMs to *coxph* models, as we had a relatively small group of individuals with varying sample sizes and were not interested in drawing inferences for the entire Scandinavian wolf population. GLMMs also allowed for more convenient model selection and interpretation of the results. As response variable we used a binary term of 1 for the actual steps and 0 for the random steps. The models had `OnLake`, `OnRiver`, `OnStream`, and `OnForestRoad` as the main predictor variables, and included interactions with the binary variable for ice presence. Furthermore, we included building density, building distance, main road density, main road distance, forest road density, tree cover density, slope, and elevation as additional predictor variables with already known effects on wolf habitat selection. Main road density was not included in the same models as building density and main road distance due to correlation. We included `TerritoryYear` as a random effect to account for potential correlation in habitat selection between individuals within the same territory and year (Carricondo-Sanchez et al, 2020). Lastly, we added the unique `stepID` as a random effect, to make sure the model compared each actual step to the generated random

steps that belonged to it. We created one set of models for the dataset that contained the steps during daytime, and one set of models for the dataset that contained the steps during nighttime, to account for wolf activity patterns.

To investigate whether wolves utilized rivers to travel faster during winter, we used GLMMs with a Gamma family and log link, using the *glmmTMB* package (Brooks et al, 2017). We used a dataset containing only the actual steps of all wolves during winter, and used step length as response variable, which represented (4-hourly) travel speed. We included the variables that indicated whether the current and/or previous step ended on a lake, river, or stream, as this would allow for analyzing the travel speed when wolves moved to or from waterbodies. In addition, we added the variable that indicated whether the current and/or previous step ended on a forest road, to compare speed between frozen waterbodies and forest roads. We did not include steps on main roads, as the number of actual steps on main roads was low ($n = 21$ for all individuals during winter). Ice period, building density, building distance, main road density, main road distance, forest road density, elevation, slope, and tree cover density were included as fixed effects, and TerritoryYear as random effect. We created two sets of models, one for daytime and one for nighttime.

To analyze the selection of proximity to waterbodies during summer, we used GLMMs with a binomial family and logit link. Here we created two sets of models, with one set having lake distance, river distance, and stream distance, and the other having general water distance as the main predictor variables. All of these were also included as interactions with the binary variable for hot periods. Like with the winter models, building density, building distance, main road density, main road distance, forest road density, forest road distance, tree cover density, slope, and elevation were included as additional predictor variables, and used interchangeably depending on the correlation. TerritoryYear and unqueststepID were included as random effects. These two sets of models were made for both the dataset of steps during the day and night, resulting in four sets of GLMMs.

All continuous variables were scaled separately for each analysis. For model selection in all analyses, we eliminated variables and interactions that led to a reduction in Akaike Information Criterion (AIC) in a stepwise backward procedure (Burnham & Anderson, 2002). The models were compared, and the best model was selected based on AIC (Appendix 12) and the results described.

3. Results

3.1. Descriptive analyses

Wolves had an average ($\pm SE$) 150.3 \pm 49.8 GPS positions that ended on water throughout the year, constituting 3.9 \pm 0.4 % of total positions (3268.3 \pm 724.9 4-hourly positions of 10 individuals, Table 2a). The proportion of positions on water was slightly higher during winter (4.3 \pm 0.3 % of total, Table 2c) than during summer (3.5 \pm 0.6 % of total, Table 2b). During both periods of the year, the largest proportion of positions on water was on streams (1.8 % during winter, 2.6 % during summer). During winter, the percentage of positions on lakes was about 3 times higher than during summer (1.8 % during winter, 0.6 % during summer), and similarly the percentage of positions on rivers was 2.7 times higher than during summer (1.1 % during winter, 0.4 % during summer).

Table 2

Wolf GPS positions on water, and percentages of total positions on the different types of waterbodies, separated for the full year (a), summer (b), and winter (c).

<i>Mean \pm SE</i>	<i>Full year (a)</i>	SEASON	
		<i>Summer (b)</i>	<i>Winter (c)</i>
Number of GPS positions	3268.3 \pm 724.9	1690.5 \pm 355.6	1577.8 \pm 373.4
Number of positions on water	150.3 \pm 49.9	76.6 \pm 32.6	73.7 \pm 19.5
% of positions on water	3.92 \pm 0.35 %	3.54 \pm 0.57 %	4.33 \pm 0.34 %
% of positions on lakes	1.16 \pm 0.10 %	0.58 \pm 0.10 %	1.79 \pm 0.14 %
% of positions on rivers	0.74 \pm 0.17 %	0.42 \pm 0.11 %	1.11 \pm 0.28 %
% of positions on streams	2.24 \pm 0.34 %	2.64 \pm 0.60 %	1.79 \pm 0.16 %

The mean and SE are given for the numbers and percentages for 10 individual wolves.

By analyzing the descriptive plots of distances to waterbodies which compared random to actual steps (Figure 3), we could distinguish the following patterns: higher density of actual steps in close proximity to streams during hot periods in summer (Figure 3a), general avoidance of lakes during summer (Figure 3c), high density of actual steps on lakes during ice periods in winter, but lower than random steps (Figure 3d), and high density of actual steps on rivers during ice periods in winter (Figure 3f).

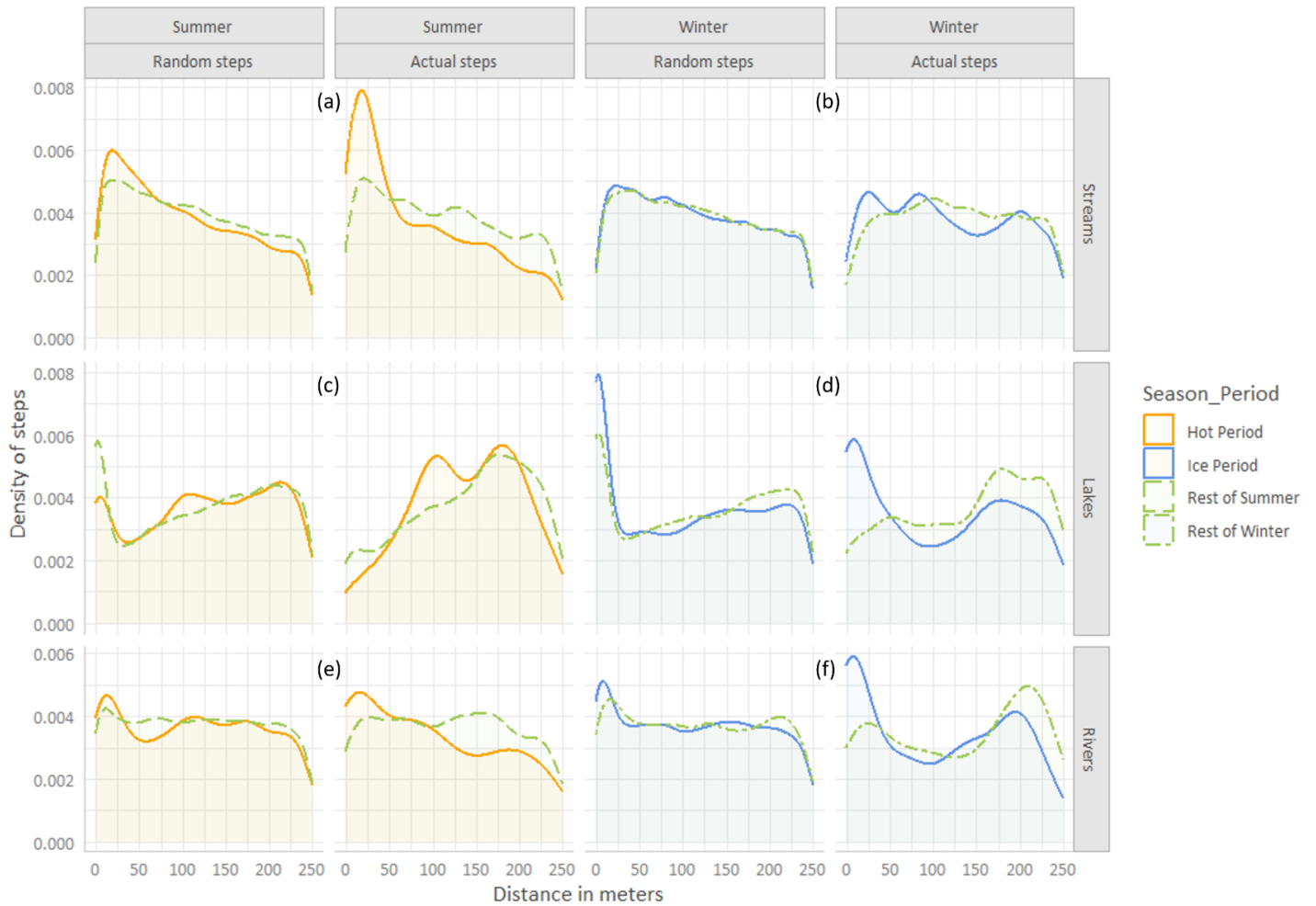


Figure 3

Wolf actual and random step densities during summer (for streams (a), lakes (c), and rivers (e)) and winter (for streams (b), lakes (d), and rivers (f)), during hot and ice periods. Y-axis shows the density of steps, X-axis shows the close distances (0 – 250 m) to waterbodies.

3.2. Winter analyses

Winter use of waterways and roads

During winter, we found that the highest proportion of positions on water was during nights when ice was present ($7.8 \pm 1.2\%$), which was 3.55 times higher compared to nights without ice (2.2%), and 1.86 times higher compared to daytime positions with ice present (4.2%) (Appendix 2). Wolves had 1.45 times more positions on waterbodies during days with ice, than during days without ice (2.9%). Positions on water were mainly on streams during winter days without ice, and on lakes during winter days with ice, and winter nights with and without ice. Positions on rivers had the highest increase during winter nights when ice was present ($2.9 \pm 0.9\%$) and was 9.7 times higher than during nights without ice ($0.3 \pm 0.1\%$; Appendix 2).

During winter days with no ice present, roads and waterbodies were utilized about equally (2.9 % on water, 2.7 % on forest roads; Figure 4, Appendix 2). During winter days with ice, the positions on forest roads decreased to 1.1 %, and positions on water increased to 4.2 % (Figure 4). This means that while the use of waterbodies increased during days with ice (1.45 times), the use of forest roads was 2.5 times lower. During winter nights with no ice, the percentage of positions on forest roads was much higher (6.7 %) than on water (2.2 %), but during ice periods the percentage of positions on forest roads decreased to 4.6 %, and positions on water increased to 7.8 % (Figure 4, Appendix 2). During nights with ice, the use of water increased (3.55 times), and the use of forest roads was 1.5 times lower than during nights without ice.

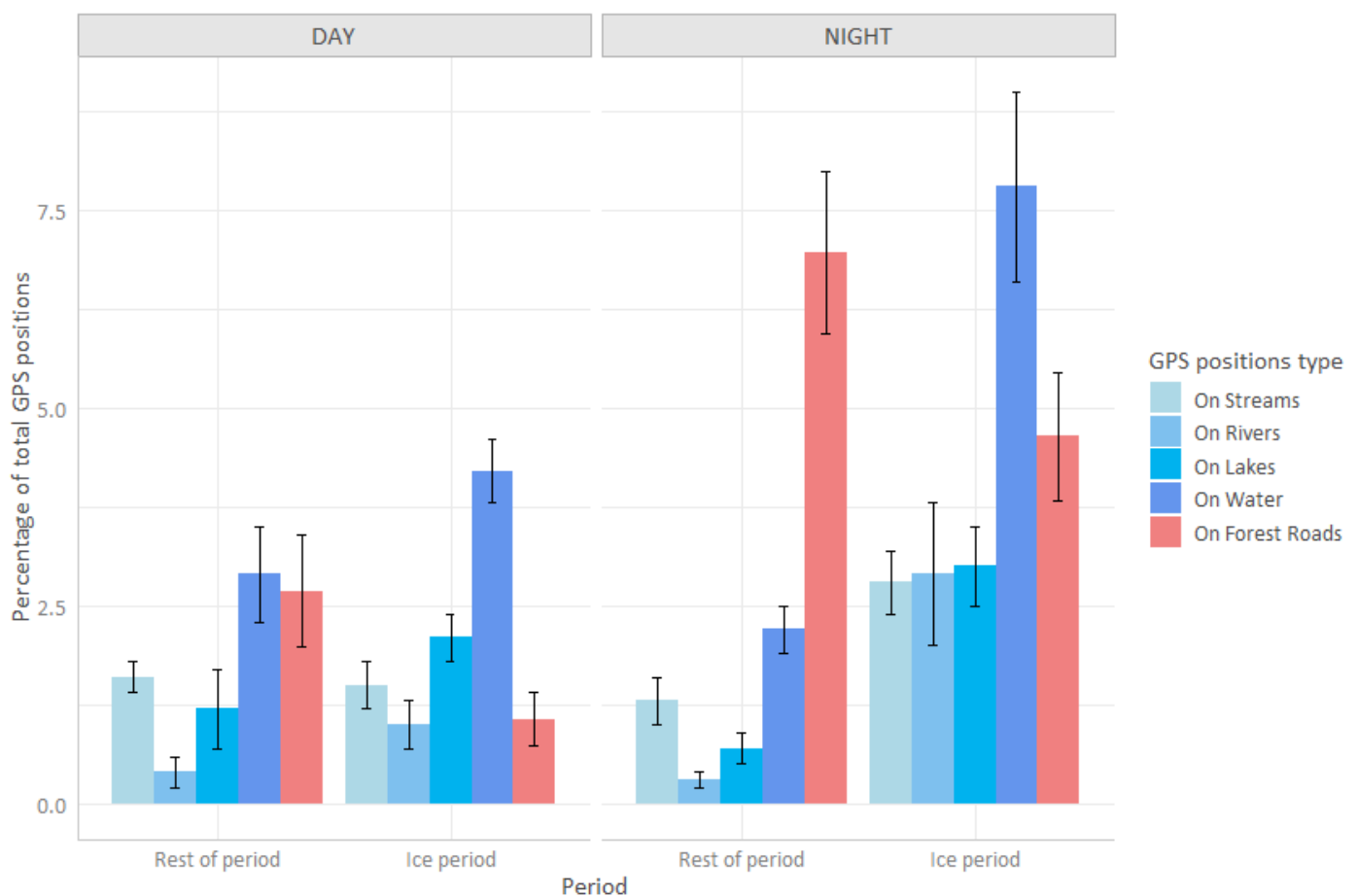


Figure 4

Wolf GPS positions on water (also separated by type, blue bars) and on forest roads (red bars) during winter, divided by day and night, and during ice periods and the rest of winter period. Bars show the mean percentage of the total positions, and SE (Appendix 2).

Winter Step Selection Analysis

For the daytime analysis during winter the most parsimonious model contained OnLake, OnRiver, and OnForestRoad as interactions with ice presence, and OnStream as a fixed effect (Table 3a). The interaction of OnStream and ice presence were not included in the best model. All other fixed effects were retained in the best model. During winter days, wolves avoided lakes and rivers less with ice presence, although selection for rivers was not significant (Figure 5a-b). Forest roads were avoided more strongly during winter days with ice presence (Figure 5c). There was selection for low building density and low forest road density, and selection for high distances from main roads and buildings (Table 3a). Wolves selected for lower elevations, steeper slopes, and higher tree cover densities (Table 3a).

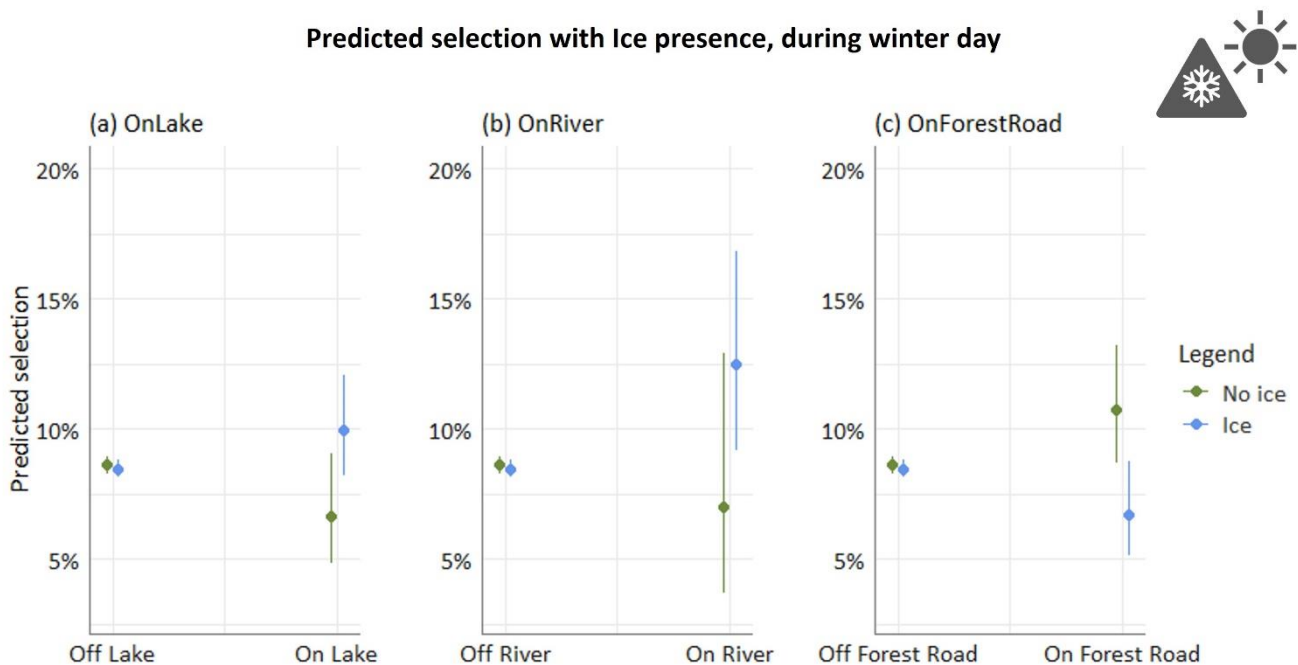


Figure 5

Predicted wolf step selection for lakes (a), rivers (b), and forest roads (c) with ice presence, during winter days.

The best model for the nighttime analysis during winter had OnLake, OnRiver, OnStream, and OnForestRoad as interactions with ice presence retained in the model (Table 3b). Removing forest road density did not significantly improve the model performance. Building distance and main road distance were removed from the final model, as they were uninformative. All other fixed effects were retained in the final model. During winter nights wolves avoided lakes and streams, while selection for rivers was non-significant (Figure 6a-c). However, when ice was

present, wolves selected for lakes and rivers (Figure 6a-b) and avoided streams less strongly (Figure 6c). Wolves selected less strong for forest roads during winter nights with ice presence (Figure 6d). There was strong selection for lower densities of buildings, and selection for higher densities of forest roads was non-significant (Table 3b). Wolves showed strong selection for lower elevations, steeper slopes, and higher densities of tree cover (Table 3b).

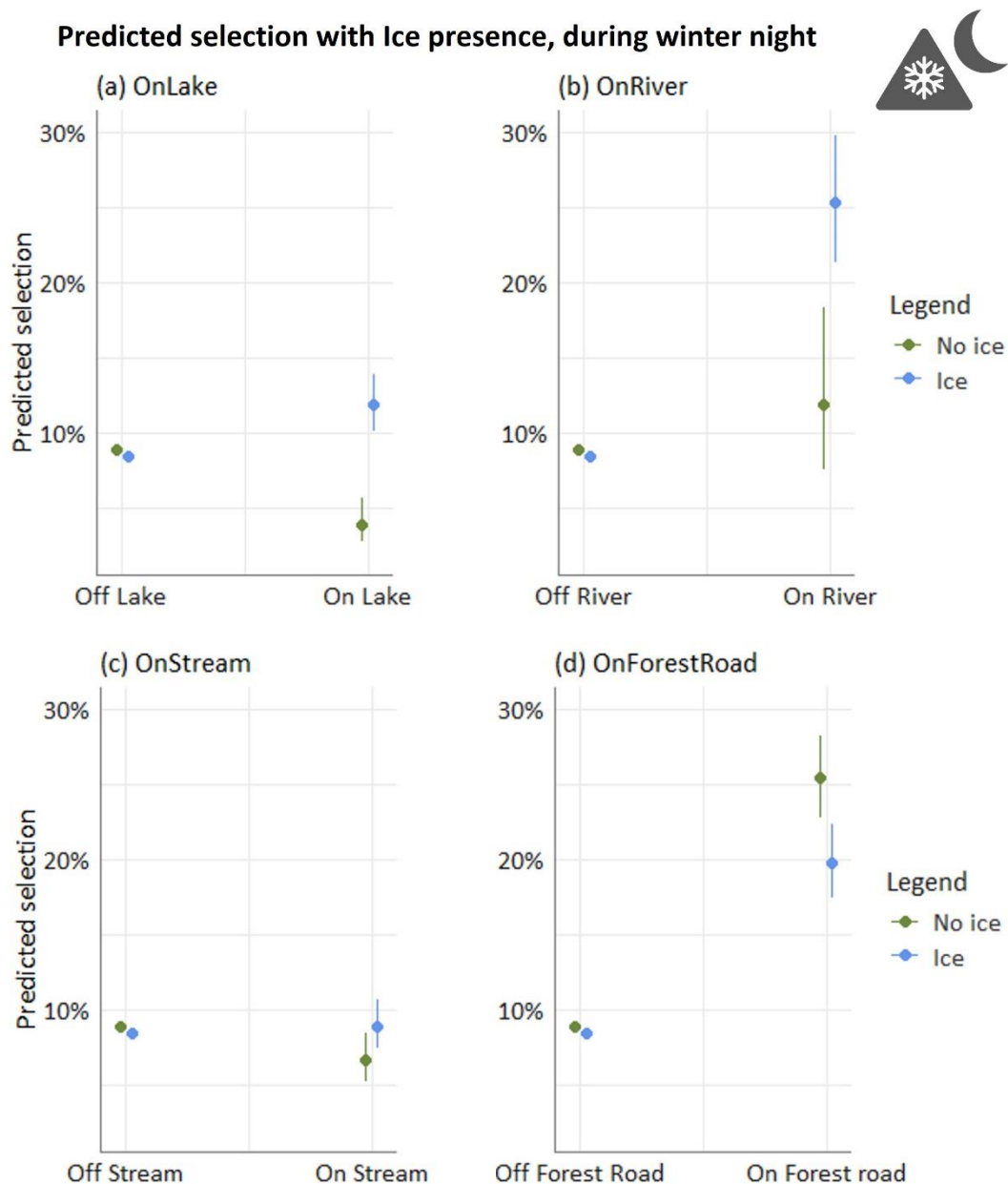


Figure 6

Predicted wolf step selection in percentages for lakes (a), rivers (b), streams (c), and forest roads (d) with ice presence, during winter nights.

Table 3

Model summaries for the best models of the winter day analysis (a) and winter night analysis (b). Given are the estimates, standard deviation (SD), 95% lower and upper Wald confidence intervals (CI L/U), and P values of each variable retained in the final model.

<i>Explanatory variables</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI L</i>	<i>95% CI U</i>	<i>P</i>
(a) GLMM winter day					
Intercept	-2.362	0.022	-2.404	-2.319	<.001
OnLake (1)	-0.281	0.171	-0.615	0.054	0.010
OnRiver (1)	-0.221	0.347	-0.900	0.459	0.525
OnStream (1)	-0.253	0.094	-0.437	-0.069	0.007
OnForestRoad (1)	0.245	0.121	0.007	0.482	0.043
Ice_periodbinary (1)	-0.021	0.026	-0.072	0.030	0.427
Building Density	-0.226	0.022	-0.269	-0.183	<.001
Building Distance	0.055	0.013	0.029	0.081	<.001
Main Road Distance	0.070	0.014	0.043	0.098	<.001
Forest Road Density	-0.032	0.016	-0.064	0.000	0.047
Elevation	-0.100	0.016	-0.131	-0.068	<.001
Slope	0.270	0.012	0.247	0.293	<.001
Tree Cover Density	0.204	0.015	0.175	0.233	<.001
OnLake (1) * Ice_periodbinary (1)	0.462	0.201	0.068	0.856	0.022
OnRiver (1) * Ice_periodbinary (1)	0.657	0.389	-0.106	1.419	0.091
OnForestRoad (1) * Ice_periodbinary (1)	-0.493	0.190	-0.865	-0.121	0.009
(b) GLMM winter night					
Intercept	-2.333	0.018	-2.368	-2.298	<.001
OnLake (1)	-0.859	0.194	-1.239	-0.478	<.001
OnRiver (1)	0.331	0.259	-0.177	0.839	0.202
OnStream (1)	-0.307	0.131	-0.563	-0.051	0.019
Ice_periodbinary (1)	-0.046	0.025	-0.095	0.003	0.068
Building Density	-0.107	0.015	-0.136	-0.078	<.001
OnForestRoad (1)	1.257	0.075	1.109	1.404	<.001
Forest Road Density	0.022	0.014	-0.006	0.050	0.119
Elevation	-0.059	0.015	-0.087	-0.031	<.001
Slope	0.032	0.013	0.005	0.058	0.018
Tree Cover Density	0.086	0.014	0.060	0.113	<.001
OnLake (1) * Ice_periodbinary (1)	1.232	0.213	0.815	1.650	<.001
OnRiver (1) * Ice_periodbinary (1)	0.967	0.283	0.412	1.521	<.001
OnStream (1) * Ice_periodbinary (1)	0.362	0.167	0.035	0.688	0.030
OnForestRoad (1) * Ice_periodbinary (1)	-0.282	0.110	-0.497	-0.066	0.010

Speed analysis

For travel speed on waterbodies during winter days, our best model contained the variables indicating start and/or end points of steps on rivers, lakes, streams, and forest roads (Table 4a). Elevation, main road density, main road distance, and building distance were not included in the most parsimonious model. During winter days, wolf travel speed was higher for steps moving to and from rivers, lakes, streams, and forest roads (Figure 7a-d) compared to other steps. During ice periods, wolf travel speed was significantly lower (Table 4a). Speed was significantly higher with higher building density and lower forest road density (Table 4a). Steep slopes strongly lowered travel speed, and travel speed was higher with lower tree cover densities (Table 4a).

Predicted step lengths during winter

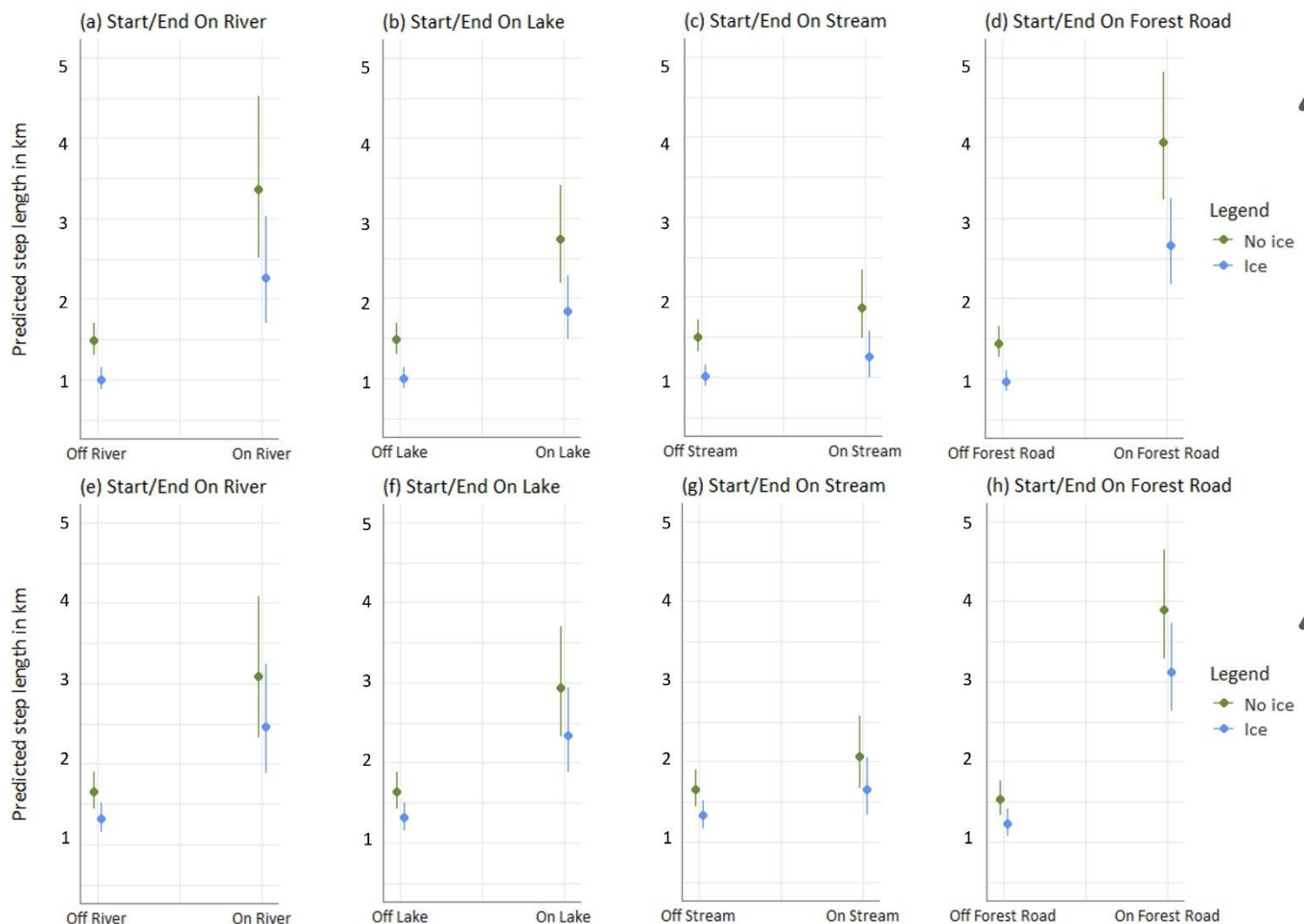


Figure 7

Predicted wolf step lengths (representing 4-hourly travel speed) for start and/or end positions during winter days (on rivers (a), lakes (b), streams (c), and forest roads (d)) and during winter nights (on rivers (e), lakes (f), streams (g), and forest roads (h)).

During winter nights, our best model retained the variables indicating start and/or end point on rivers, lakes, streams, and forest roads (Table 4b). Forest road density and elevation were removed, as they were non-informative. Including building distance did not affect the model performance. Similar to winter days, during winter nights, speed was higher for steps moving to and from rivers, lakes, streams, and forest roads (Figure 7e-h), compared to other steps. Again, travel speed was significantly lower during ice periods (Table 4b). Wolf travel speed increased with higher building densities and lower distances to main roads (Table 4b). Travel speed decreased with steeper slopes and higher tree cover densities (Table 4b).

Table 4

Model summaries for the best models of the speed on waterbodies and forest roads during winter day analysis (a) and winter night analysis (b). Given are the estimates, standard deviation (SD), 95% lower and upper Wald confidence intervals (CI L/U), and P values of each variable retained in the final model.

<i>Explanatory variables</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI L</i>	<i>95% CI U</i>	<i>P</i>
(a) GLMM winter day speed					
Intercept	7.234	0.067	7.102	7.365	<.001
Start / End OnRiver (1)	0.811	0.136	0.544	1.078	<.001
Start / End OnLake (1)	0.611	0.093	0.429	0.793	<.001
Start / End OnStream (1)	0.213	0.098	0.021	0.405	0.030
Start / End On Forest Road (1)	1.004	0.081	0.845	1.163	<.001
Ice_periodbinary (1)	-0.395	0.038	-0.470	-0.321	<.001
Building Density	0.052	0.019	0.014	0.090	0.007
Forest Road Density	-0.042	0.021	-0.083	-0.001	0.046
Slope	-0.037	0.019	-0.074	0.000	0.048
Tree Cover Density	-0.205	0.019	-0.243	-0.167	<.001
(b) GLMM winter night speed					
Intercept	7.295	0.070	7.158	7.431	<.001
Start / End OnRiver (1)	0.624	0.126	0.377	0.871	<.001
Start / End OnLake (1)	0.580	0.097	0.390	0.770	<.001
Start / End OnStream (1)	0.221	0.090	0.044	0.400	0.014
Start / End On Forest Road (1)	0.932	0.061	0.814	1.051	<.001
Ice_periodbinary (1)	-0.222	0.038	-0.295	-0.148	<.001
Building Density	0.089	0.022	0.046	0.131	<.001
Building Distance	-0.325	0.019	-0.071	0.006	0.093
Main Road Distance	-0.042	0.019	-0.079	-0.004	0.029
Slope	-0.213	0.020	-0.252	-0.175	<.001
Tree Cover Density	-0.184	0.020	-0.222	-0.145	<.001

3.3. Summer analyses

Summer use of waterways

During summer, the highest proportion of GPS positions on water were during hot nights (10.16 ± 2.60 %), although individuals had only a mean 41.40 (SE: 9.50) positions during hot summer nights (Appendix 3). During summer days, positions on water were also higher during hot periods (5.43 ± 1.44 %) than the rest of the summer period (2.81 ± 0.49 %; Figure 8, Appendix 3). During both hot periods and the rest of the summer, positions were mainly on streams, but increased during hot periods (Figure 8, Appendix 3).

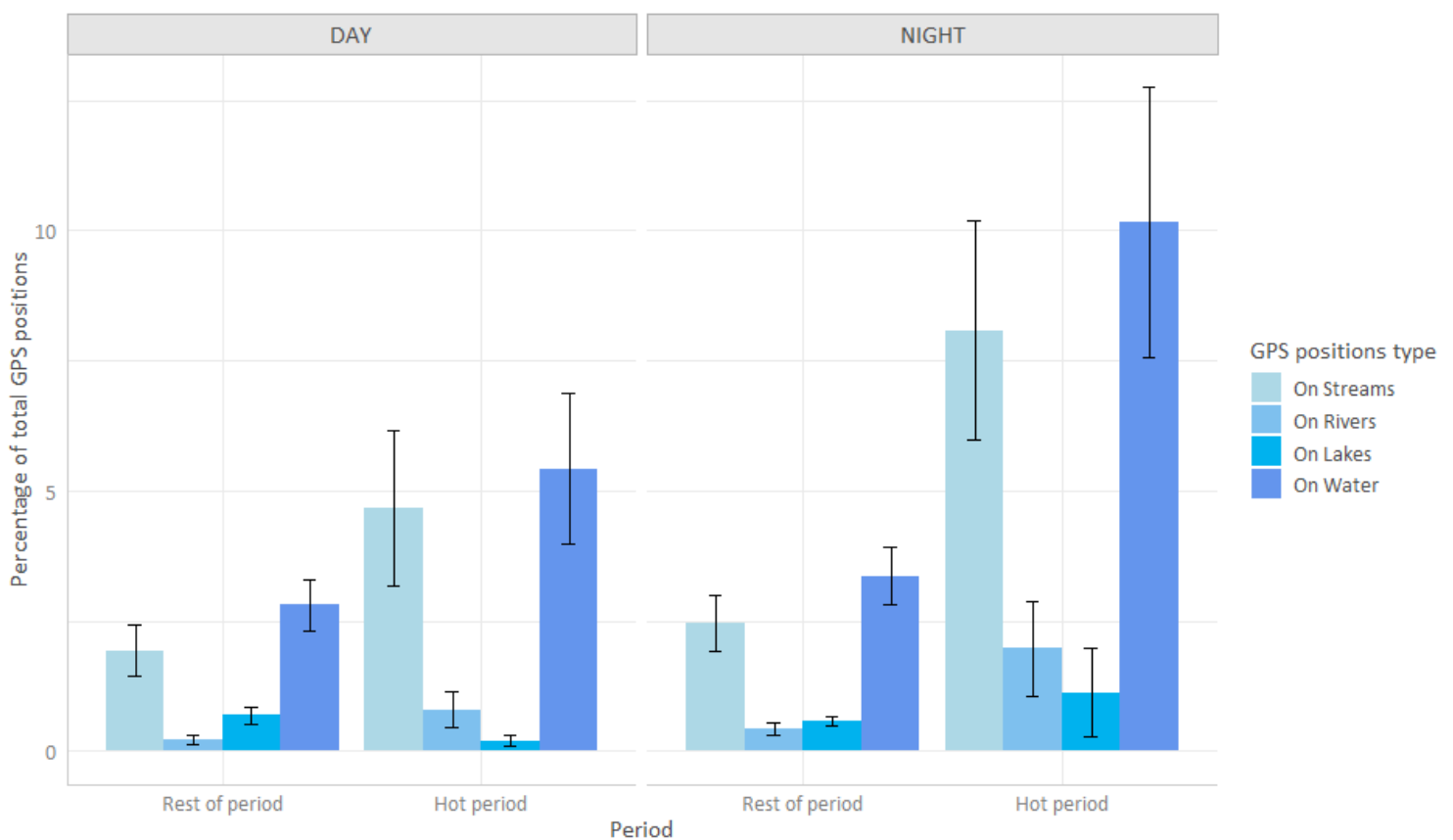


Figure 8

Wolf GPS positions on water (separated by type) during summer, divided by day and night, and during hot periods and the rest of summer period. Bars show the mean percentage of the total positions, and SE (Appendix 3).

Lactation

Furthermore, we compared the actual steps of lactating and non-lactating wolves in relation to distance to waterbodies during summer (Figure 9). We found that both lactating and non-lactating individuals had high densities of positions in close proximities to waterbodies, but non-lactating individuals had a comparatively higher density of positions close to water than lactating females (Figure 9a). Lactating females did have a peak in density between 500 and 700 m, possibly correlated with the den site (Appendix 6 and 7). Lactating wolves had a slightly higher mean distance from water (319.92 ± 27.20 m) than non-lactating wolves (262.15 ± 12.51 m) (Figure 9b).

Distance to water, Lactating / Not Lactating individuals

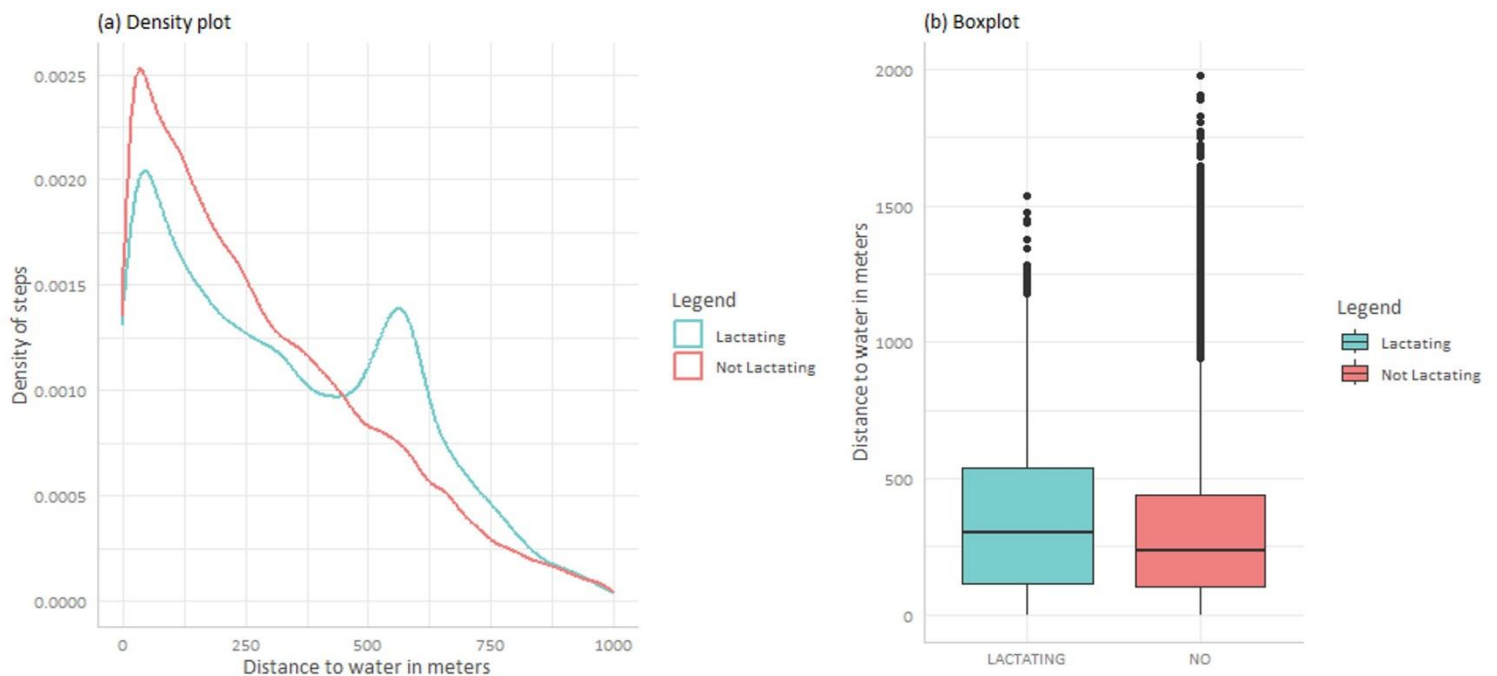


Figure 9

Density plot (a) showing the density of actual steps (Y-axis) of lactating and non-lactating wolves in relation to distance to water distance (m) during summer (X-axis). Boxplot (b) showing the variance in distance to water (m) (Y-axis) between lactating and non-lactating wolves (X-axis).

Summer Step Selection Analysis

For the daytime analysis during summer the best model included distance to lakes, rivers, and streams as interactions with hot periods (Table 5a). Including general distance to water instead of lakes, rivers, and streams, showed similar results, but these models underperformed. Including main road density instead of building density and main road distance also underperformed, therefore those models were not considered. All other fixed effects were retained in the final model. During 'hot' summer days, wolves selected for proximity to streams and rivers and avoided proximity to lakes, but they showed no avoidance or selection for rivers and lakes (but a slight avoidance of proximity to streams) during 'normal' periods (Figure 10a-c, Table 5a). Moreover, wolves selected for lower densities of buildings, and higher distances from buildings, main roads, and forest roads (Table 5a). Furthermore, there was strong selection for lower elevations, steeper slopes, and higher forest cover densities (Table 5a).

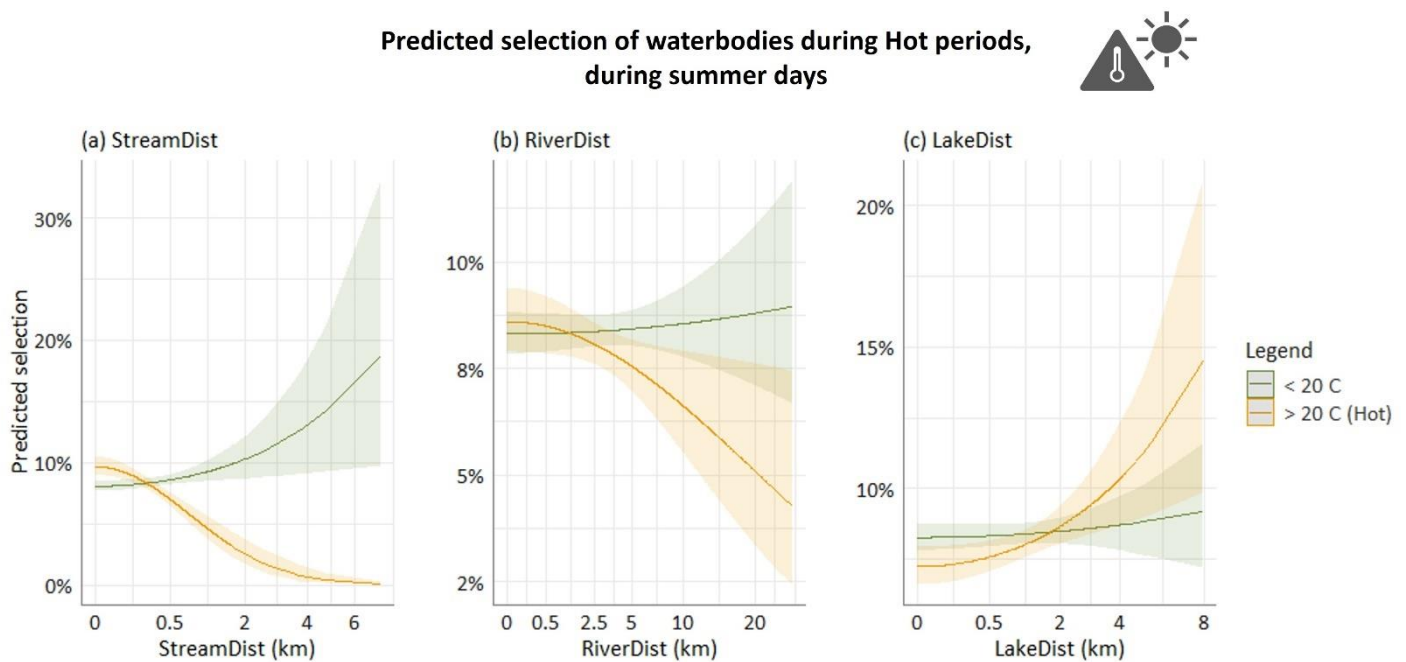


Figure 10

Predicted selection in percentages (Y-axes) for distances in km to streams (a), rivers (b), and lakes (c) (X-axes) for hot periods during summer days. X-axes were square root transformed.

The most parsimonious model for the analysis during summer nights contained distance to streams and lakes as interactions with hot periods (Table 5b), and distance to rivers as a fixed effect. Forest road density, forest road distance, and the interaction between river distance and hot periods were removed. All other fixed effects were retained in the final model. During summer nights, wolves avoided lakes, selected for closer distances to streams, and tended to select for rivers (Table 5b). The selection for closer distances to streams increased significantly during ‘hot’ summer nights (Figure 11). Wolves selected strongly for lower elevations, steeper slopes, lower tree cover densities, and lower densities of buildings (Table 5b).

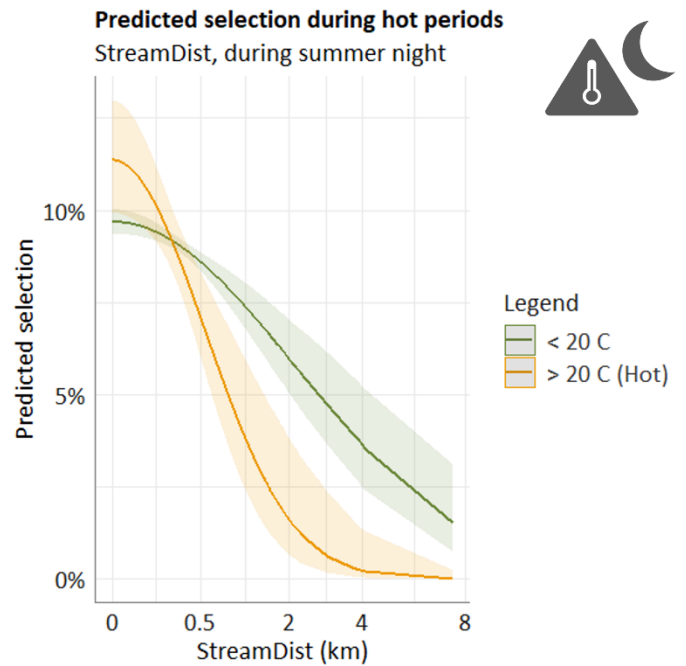


Figure 11

Predicted wolf step selection in percentages (Y-axis) for distances to streams (km) (X-axis) during hot summer nights. X-axis was square root transformed.

Table 5

Model summaries for the best models of the summer day analysis (a) and summer night analysis (b). Given are the estimates, standard deviation (SD), 95% lower and upper Wald confidence intervals (CI L/U), and P values of each variable retained in the final model.

<i>Explanatory variables</i>	<i>Estimate</i>	<i>SE</i>	<i>95% CI L</i>	<i>95% CI U</i>	<i>P</i>
(a) GLMM summer day					
Intercept	-2.392	0.024	-2.439	-2.345	<.001
Lake Distance	0.011	0.014	-0.017	0.038	0.448
River Distance	0.007	0.017	-0.025	0.040	0.657
Stream Distance	0.033	0.014	0.006	0.060	0.016
Hot_periodbinary (1)	-0.057	0.029	-0.114	0.001	0.054
Building Density	-0.209	0.022	-0.252	-0.167	<.001
Building Distance	0.045	0.014	0.017	0.073	0.002
Main Road Distance	0.114	0.014	0.086	0.142	<.001
Forest Road Distance	0.207	0.012	0.184	0.230	<.001
Elevation	-0.145	0.015	-0.175	-0.115	<.001
Slope	0.266	0.011	0.244	0.288	<.001
Tree Cover Density	0.239	0.014	0.211	0.266	<.001
Lake Distance * Hot_periodbinary (1)	0.062	0.028	0.008	0.117	0.024
River Distance * Hot_periodbinary (1)	-0.075	0.031	-0.135	-0.014	0.016
Stream Distance * Hot_periodbinary (1)	-0.208	0.031	-0.269	-0.147	<.001
(b) GLMM summer night					
Intercept	-2.311	0.012	-2.334	-2.288	<.001
Lake Distance	0.045	0.012	0.022	0.068	<.001
River Distance	-0.024	0.012	-0.048	0.0002	0.052
Stream Distance	-0.064	0.013	-0.089	-0.039	<.001
Hot_periodbinary (1)	-0.050	0.056	-0.160	0.060	0.374
Building Density	-0.077	0.014	-0.104	-0.050	<.001
Elevation	-0.030	0.013	-0.056	-0.005	0.018
Slope	0.134	0.012	0.110	0.016	<.001
Tree Cover Density	-0.046	0.012	-0.070	-0.022	<.001
Lake Distance * Hot_periodbinary (1)	-0.082	0.053	-0.187	0.022	0.123
Stream Distance * Hot_periodbinary (1)	-0.188	0.063	-0.312	-0.064	0.003

4. Discussion

This study explored the spatial patterns and habitat selection of wolves in relation to waterbodies in Scandinavia. Using integrated step selection analyses, we found that wolves increased their use of lakes and rivers during ice periods, which is in line with H1. Wolves decreased their use of forest roads when frozen water was available and had increased speed when travelling on ice. Moreover, wolves kept closer proximities to streams and rivers during hot summer days and closer proximity to streams during (hot) summer nights, which partially confirms H2 and H3. Our results did not support H4, as lactating wolves did not stay closer to water. Here we discuss how these findings will help us better understand wolf interactions with water.

Wolves on Frozen Water during Winter

Our results show that wolves avoided lakes and streams during ice-free periods in winter, but there was selection for lakes and rivers during ice periods. We found that with ice cover, wolves no longer avoid these larger bodies of open water and utilize them as an extension or connection of the territory, indicating that wolves are capable of identifying and adapting to this seasonal change. Meanwhile, our results show general avoidance of human presence during both winter days and nights, selecting for lower building densities and higher distances from main roads, which is in line with previous studies (Zimmermann et al, 2014; Malcolm et al, 2020; Hebblewhite & Merrill, 2008). During winter days, there was significant avoidance of forest roads, but during winter nights this avoidance disappeared, similar to earlier findings (Carricondo-Sanchez et al, 2020).

Wolves likely used ice for fast and easy travel during winter, as their travel speed strongly increased when using frozen waterbodies, both during day and nighttime. As wolves are mainly active at night, our findings suggest that they could use ice for travel or hunting purposes. Frozen rivers could form travel corridors that connect key areas of wolf territories, as they use man-made linear features, such as roads, for the same reasons (Johnson-Bice et al, 2023; Malcolm et al, 2020, Muhly et al, 2019; Dickie et al, 2016). Frozen waterbodies have only been identified as travel corridors for wolves in one previous study by Kittle et al (2017), where wolves used frozen waterbodies for increased mobility in the absence of roads. They suggested that when availability of roads was higher, wolves selected less for frozen waterbodies. In contrast, our results suggest that wolves selected for frozen waterbodies while forest roads were widely available (with densities of 1 km/km²). Although the use of roads for travel has mainly been studied in Scandinavian wolves in summer (Zimmermann et al, 2014; Carricondo-Sanchez et al, 2020), our winter analyses showed that steps on forest roads and rivers had similar increased speeds, with

lakes and streams to a lesser extent. This suggests that both forest roads and waterbodies made for faster travel during winter. When comparing proportions of actual steps on forest roads and waterbodies, we found that the use of roads decreased with ice presence (2.5 times decrease during daytime, 1.5 times during nighttime) and the use of water increased (1.4 times increase during daytime, 3.5 times during nighttime). More interestingly, the use of rivers increased 9.7 times during winter nights when ice was present. Although the proportion of use of rivers (2.9 %) was still lower than the use of forest roads (4.64 %) during winter nights with ice, the availability of rivers (55.6 ± 15.4 km per territory) is considerably lower than that of forest roads (1269 ± 247.28 km per territory). This suggests that wolves switch their travel corridors from forest roads to frozen waterbodies once they are covered by ice.

One potential explanation for this could be that wolves trade-off fast travel (on roads) with reduced human encounter risk (on rivers). Wolves may be willing to risk human encounters on forest roads during the majority of the year, in return for more efficient mobility, and as frozen water is unavailable. But once rivers freeze over, they offer similar travel efficiency, as well as reduced human encounter risk, thus being a more preferable option for travel corridors during ice periods.

Another possible explanation is that forest roads become less appealing as travel corridors due to high snow depths. The majority of the ice periods in our study area occurred between December and March, which are also months with major snowfall in this part of Scandinavia. During these months, snow accumulates (Schneider, 1996) and, as forest roads in the area are plowed irregularly, snow also accumulates on unplowed roads (Zimmermann et al, 2014). Frozen waterbodies can have similar snow accumulation, but snow depths vary due to different reasons. Firstly, if snowfall already started before waterbodies freeze over, the snow levels will be lower from the start. Secondly, snow can repeatedly melt and freeze again on top of the ice, increasing ice thickness as white ice forms from slush, and the accumulated snow is compressed (Bengtsson, 1986). Lastly, on larger, open waterbodies such as lakes, wind can blow away snow before it settles, preventing the accumulation of snow (Burgis et al, 2007; Bengtsson, 1986). Accumulation of snow and snowfall would also explain why wolf travel speed generally decreased during ice periods (independent of where they travel), which was similar to Droghini & Boutin (2018) in Canada.

Additionally, the use of frozen waterbodies during nighttime by wolves might correlate with high prey density. Frozen waterbodies, often located in valleys, can serve as travel corridors and foraging areas for prey, thus increasing the likelihood of prey encounters. Moose have been

shown to migrate into valleys during winter, and wolves have been found to follow seasonal migration patterns of prey as a hunting strategy (Ordiz et al, 2020). Our analyses further highlight that wolves selected for lower elevations during winter, possibly following the migration of their prey. In addition to potentially higher prey densities, wolves have been found to kill prey frequently near or on frozen water (Bojarska et al, 2017; Kunkel & Pletscher, 2001, 2000). Although McPhee et al (2012) found that wolves did not select to hunt near frozen waterbodies, they did select to kill on frozen water, as was also found by Webb (2009). We did not investigate kill site clusters and their different types, but our findings support further investigation of spatio-temporal clusters in relation to (frozen) water.

Wolves might also use larger frozen lakes as meeting points, or as connective open spaces within their territory. Wolf packs have been observed to gather on frozen waterbodies in Voyageurs National Park, USA (Voyageurs Wolf Project, 2023a, 2023b, 2020), and a pack was observed more often than would be expected on a lake central in their territory in Norway, according to the size of the lake (Lange, 2006). In addition, with the 4-hourly sampling interval of our GPS data, we were unable to analyze usage patterns of wolves on frozen lakes in detail, and access to more detailed GPS data was limited to certain individuals or periods. More fine-scale data would be necessary to properly study the consecutive time wolves spent on ice, and the behaviour of wolves when they are on ice. This would make it possible to study whether wolves use frozen water only for crossing, if they spent consecutive periods on ice, or if they frequently return for shorter periods. In addition, more fine-scale data would make it possible to analyze the linearity of steps, which could reveal their exact travel patterns along linear frozen waterbodies, and detect kill sites.

Wolf Proximity to Water during Summer

Moreover, our study has found that wolves selected for closer proximity to streams and rivers during hot periods in summer, while simultaneously avoiding lakes. These findings partially confirm our hypothesis, as wolves did stay closer to smaller waterbodies. Avoidance of lakes might be explained by their selection for concealment when resting, as wolves have been found to select areas with both higher tree cover densities, as well as steeper terrains during summer days (Llaneza et al, 2016; Bojarska et al, 2021). As lakes are larger, open waterbodies, both the barrier effect and the correlation with low concealment can explain their avoidance. The combination of smaller waterbodies and higher tree cover densities (Ellison et al, 2017) creates cooler conditions for resting wolves during hot summer days (Mech & Boitani, 2003). Furthermore, the proximity to water sources allows resting wolves to drink and cool down in the water without having to travel far distances, enabling them to maintain necessary water intake

and thermoregulate without increasing their energy expenditure during hot periods (Careau et al, 2007).

During summer nights, wolves selected for close proximity to streams, especially during hot periods. One explanation for keeping closer distances to streams during hot summer nights could be to stay hydrated while being active. As wolves have their activity peak during summer nights and mostly spend this time hunting or traveling, they have relatively high energy expenditure (Theuerkauf et al, 2003b, 1992; Appendix 4). Especially during hot nights, it is important for them to maintain their water intake, as high activity and high temperature will induce loss of body-water levels (Mech & Boitani, 2003). Simultaneously, areas around streams might have higher prey densities, as several species of prey have been found to select for water to seek refuge from predators (Mech, 2015), including moose (Stotyn et al, 2005). Additionally, prey species have been found to select areas around waterbodies for foraging, due to easy access and availability of high-quality forage (Laforge et al, 2016; MacCracken et al, 1993; Bump et al, 2009). Moreover, wolf kill-sites were found to be strongly correlated with water (Bojarska et al, 2017), in particular streams (Kauffman et al, 2007). Together with our findings, this suggests that areas close to smaller waterbodies could serve as effective hunting grounds for wolves.

Our results did not support our hypothesis that lactating females would select for closer proximity to water during the nursing period. Lactating females had slightly higher mean distances to waterbodies than males and non-lactating females, which contradicts earlier statements that lactating wolves select for closer proximity to water (Joslin, 1967; Mech & Boitani, 2003). However, these results should be interpreted cautiously as our sample size of lactating females consisted of only 3 individuals during 6 nursing periods. Further studies with a larger sample size could shed light on the importance of water availability during the reproductive period.

Conclusion

In conclusion, our study showed that waterbodies affect wolf habitat selection in Scandinavia, and highlighted that wolves adapted to seasonal changes and utilized waterbodies according to these conditions. Our findings are focused on spatial patterns but give way for a multitude of study possibilities on more specific wolf behaviors related to water. GPS data at a finer scale would make it possible to further investigate usage of frozen waterbodies, in particular on lakes and linear features such as main rivers. This would give way to studying their behavior while on ice, such as repeated travel corridors on ice, or using them for longer distance travel throughout the territory. Relating kill-sites and moose densities to water might further explain the usage of

waterbodies as a hunting strategy in both summer and winter. Lastly, further investigation of rendezvous sites, daybeds, and den sites can potentially show the importance of water in the habitat selection during reproducing and resting phases. Our findings, however, provide preliminary answers to the existing knowledge gap surrounding the way wolves use water, and forms a stepping stone for future research to better understand this interaction.

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Appendix

Appendix 1. Table with each dataset used for analyses

Total number of positions, the number of actual steps, and the number of random steps for each dataset used during the process of this study.

<i>Dataset</i>	<i>Total number of steps</i>	<i>Number of actual steps</i>	<i>Number of random steps</i>	<i>Number of actual steps during ice periods</i>	<i>Number of actual steps during hot periods</i>
Original wolf GPS	61,274	61,274			
4-hourly positions	32,506	32,506			
Grouped with random steps	357,098	32,506	324,592	8,252	2,235
Full winter	173,281	15,778	157,503	8,252	
Winter day	85,993	7,826	78,167	4,114	
Winter night	87,288	7,952	79,336	4,138	
Full summer	185,763	16,905	168,858		2,235
Summer day	92,620	8,428	84,192		1,821
Summer night	93,143	8,477	84,666		414

Appendix 2. GPS positions on water and roads during winter

Table showing the mean and SE number of GPS positions, positions on water and forest roads and percentages of positions on waterbodies and forest roads for $N = 10$ individuals during winter, separated by time of day, and ice periods.

<i>Mean ± SE</i>	WINTER			
	DAY		NIGHT	
	<i>Rest of period</i>	<i>Ice period</i>	<i>Rest of period</i>	<i>Ice period</i>
Number of GPS positions	371.20 ± 98.68	411.40 ± 91.62	381.40 ± 99.48	413.8 ± 90.95
Number of positions on water	10.20 ± 2.90	18.80 ± 4.74	10.80 ± 3.74	33.90 ± 9.28
% of positions on water	2.90 ± 0.60 %	4.20 ± 0.40 %	2.20 ± 0.30 %	7.80 ± 1.20 %
% of positions on lakes	1.20 ± 0.50 %	2.10 ± 0.30 %	0.70 ± 0.20 %	3.00 ± 0.50 %
% of positions on rivers	0.40 ± 0.20 %	1.00 ± 0.30 %	0.30 ± 0.10 %	2.90 ± 0.90 %
% of positions on streams	1.60 ± 0.20 %	1.50 ± 0.30 %	1.30 ± 0.30 %	2.80 ± 0.40 %
Number of positions on forest roads	7.90 ± 1.63	5.10 ± 1.76	25.30 ± 8.29	20.10 ± 6.94
% of positions on forest roads	2.69 ± 0.71 %	1.07 ± 0.33 %	6.96 ± 1.03 %	4.64 ± 0.81 %

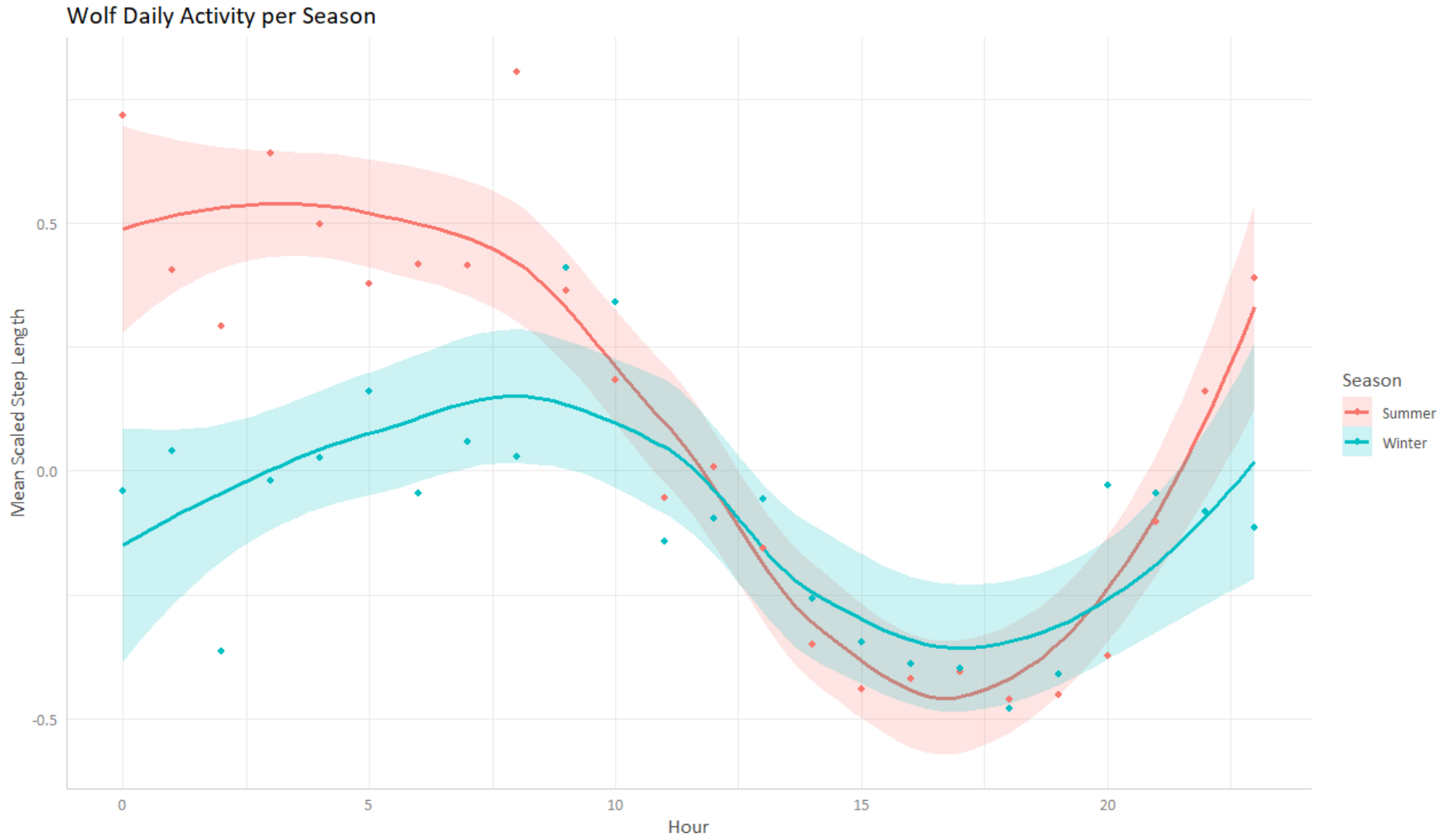
Appendix 3. GPS positions on water during summer

Table showing the mean and *SE* number of GPS positions, positions on water and percentages of positions on waterbodies for *N* = 10 individuals during summer, separated by time of day, and hot periods.

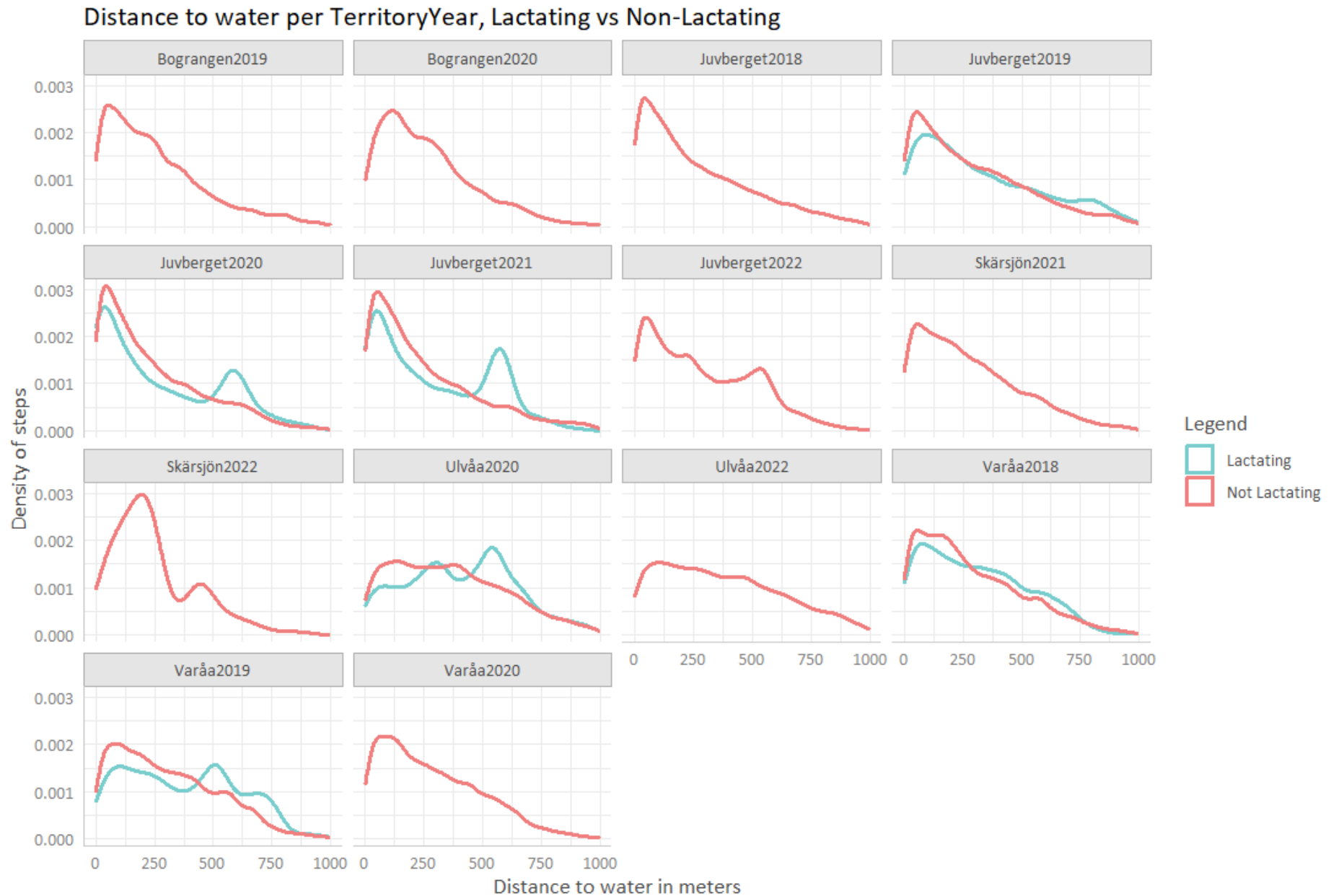
<i>Mean ± SE</i>	SUMMER			
	DAY		NIGHT	
	<i>Rest of period</i>	<i>Hot period</i>	<i>Rest of period</i>	<i>Hot period *</i>
Total number of GPS positions	660.70 ± 139.68	182.10 ± 39.32	806.30 ± 169.84	41.40 ± 9.50
Number of positions on water	21.80 ± 9.00	14.60 ± 7.49	35.30 ± 14.19	4.90 ± 2.21
% of positions on water	2.81 ± 0.49 %	5.43 ± 1.44 %	3.36 ± 0.55 %	10.16 ± 2.60 %
% of positions on lakes	0.69 ± 0.16 %	0.20 ± 0.11 %	0.58 ± 0.10 %	1.13 ± 0.85 %
% of positions on rivers	0.23 ± 0.09 %	0.80 ± 0.34 %	0.43 ± 0.12 %	1.98 ± 0.91 %
% of positions on streams	1.93 ± 0.49 %	4.67 ± 1.49 %	2.46 ± 0.54 %	8.08 ± 2.10 %

* Number of positions during hot nights was comparatively low.

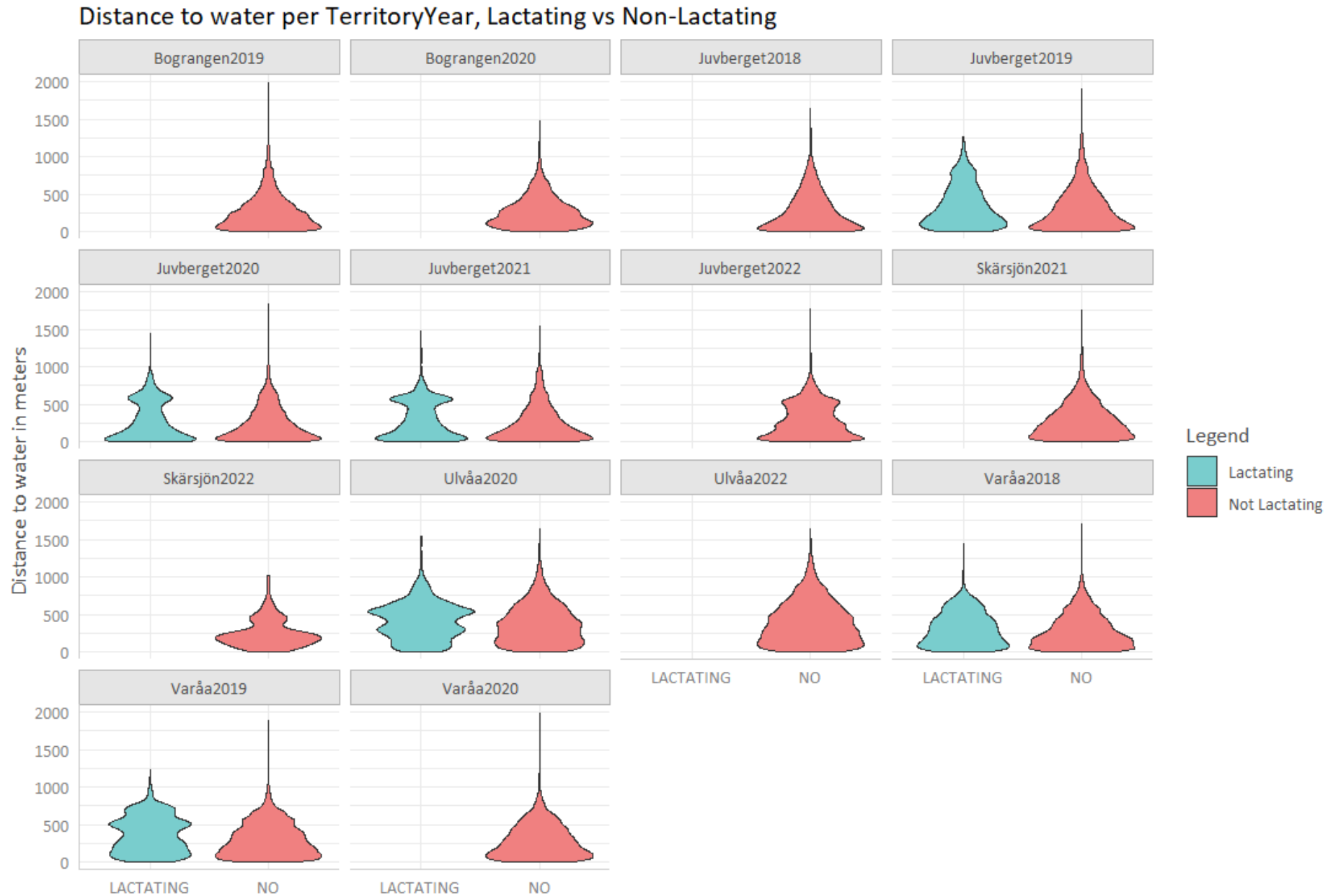
Appendix 4. Daily Activity Patterns during Summer and Winter



Appendix 5. Distances to Water per TerritoryYear, Lactating vs Non-Lactating



Appendix 6. Violin plots of Distances to Water per TerritoryYear, Lactating vs Non-Lactating



Appendix 7. Tables for Reproducing, Lactating, Pack Sizes and Data availability

REPRODUCING/LACTATING

<i>Individual ID</i>	<i>Sex</i>	<i>Territory</i>	2017	2018	2019	2020	2021	2022
M17-08	M	Varåa	NO	YES	YES	YES	UNKNOWN	
M18-12	M	Juvberget	YES	NO				
M18-13	F	Juvberget	YES	NO	LACTATING*	LACTATING*	LACTATING*	UNKNOWN
M18-17	F	Varåa	NO	LACTATING*	LACTATING*	LACTATING		
M19-01	F	Bograngen	NO	NO	NO	NO		
M19-02	M	Juvberget		NO	YES	YES	YES	
M19-04	M	Bograngen	NO	NO	NO	NO		
M20-02	F	Ulvåa		NO	LACTATING	LACTATING*	LACTATING	UNKNOWN
M21-02	M	Skärsjön				YES	UNKNOWN	DIED APRIL 22
M22-01	M	Ulvåa					YES	UNKNOWN

Lactating* indicates there was GPS data available during the nursing period

PACK SIZES

<i>Individual ID</i>	<i>Sex</i>	<i>Territory</i>	2017	2018	2019	2020	2021	2022
M17-08	M	Varåa	2	2	6	10	9	
M18-12	M	Juvberget	7	4				
M18-13	F	Juvberget		4	2	3.5	3.5	7
M18-17	F	Varåa	2	2	6	10	9	
M19-01	F	Bograngen		2	2	2		
M19-02	M	Juvberget			2	3.5	3.5	7
M19-04	M	Bograngen		2	2	2		
M20-02	F	Ulvåa			2	9	11	7
M21-02	M	Skärsjön				2	5	1
M22-01	M	Ulvåa			2	9	11	7

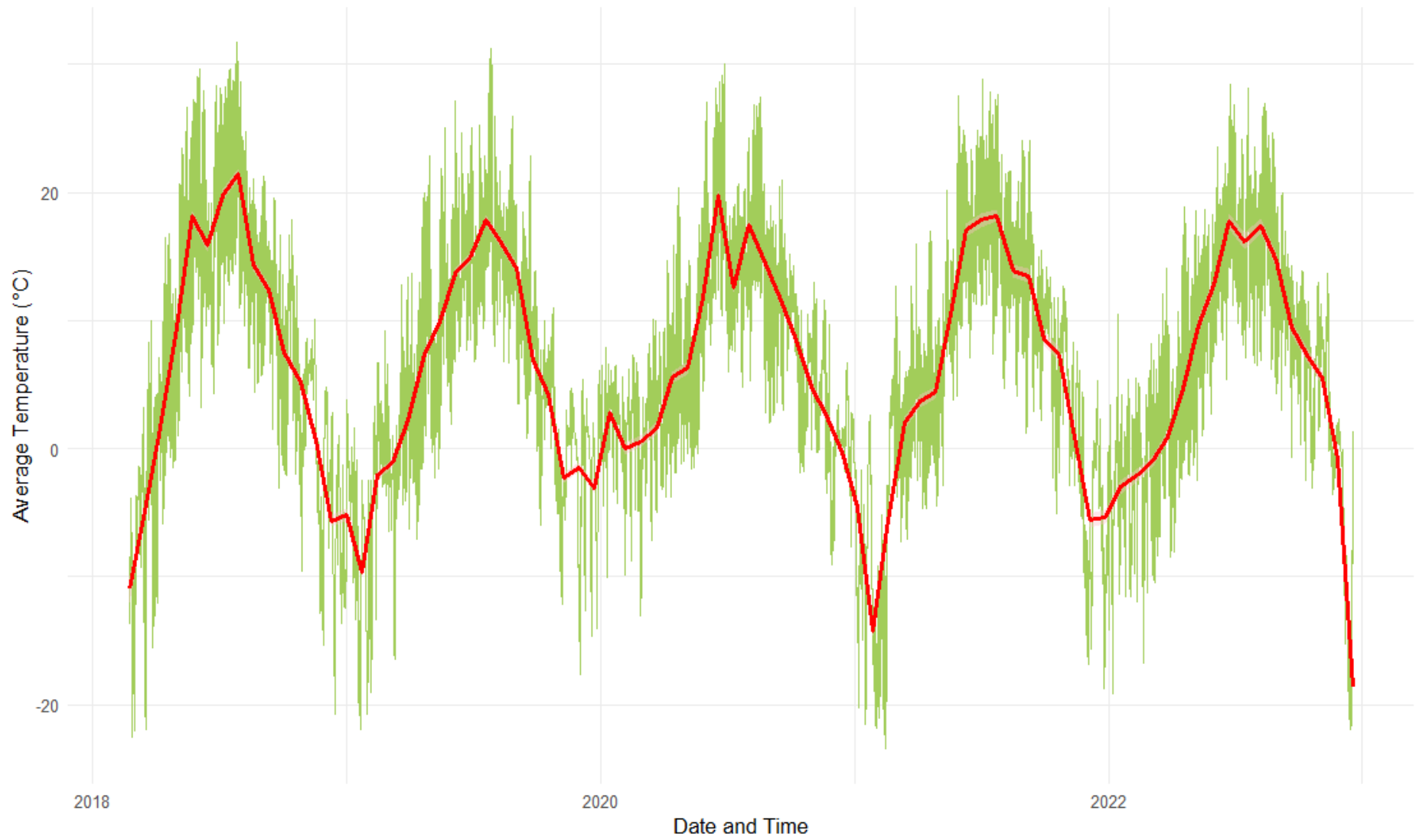
DATA PER YEAR

<i>Individual ID</i>	<i>Sex</i>	<i>Territory</i>	2017	2018	2019	2020	2021	2022
M17-08	M	Varåa		2018	2019	2020	2021	
M18-12	M	Juvberget		2018				
M18-13	F	Juvberget		2018	2019	2020	2021	2022
M18-17	F	Varåa		2018	2019	2020		
M19-01	F	Bograngen			2019	2020		
M19-02	M	Juvberget			2019	2020	2021	
M19-04	M	Bograngen			2019	2020		
M20-02	F	Ulvåa				2020	2021	
M21-02	M	Skärsjön					2021	2022
M22-01	M	Ulvåa						2022

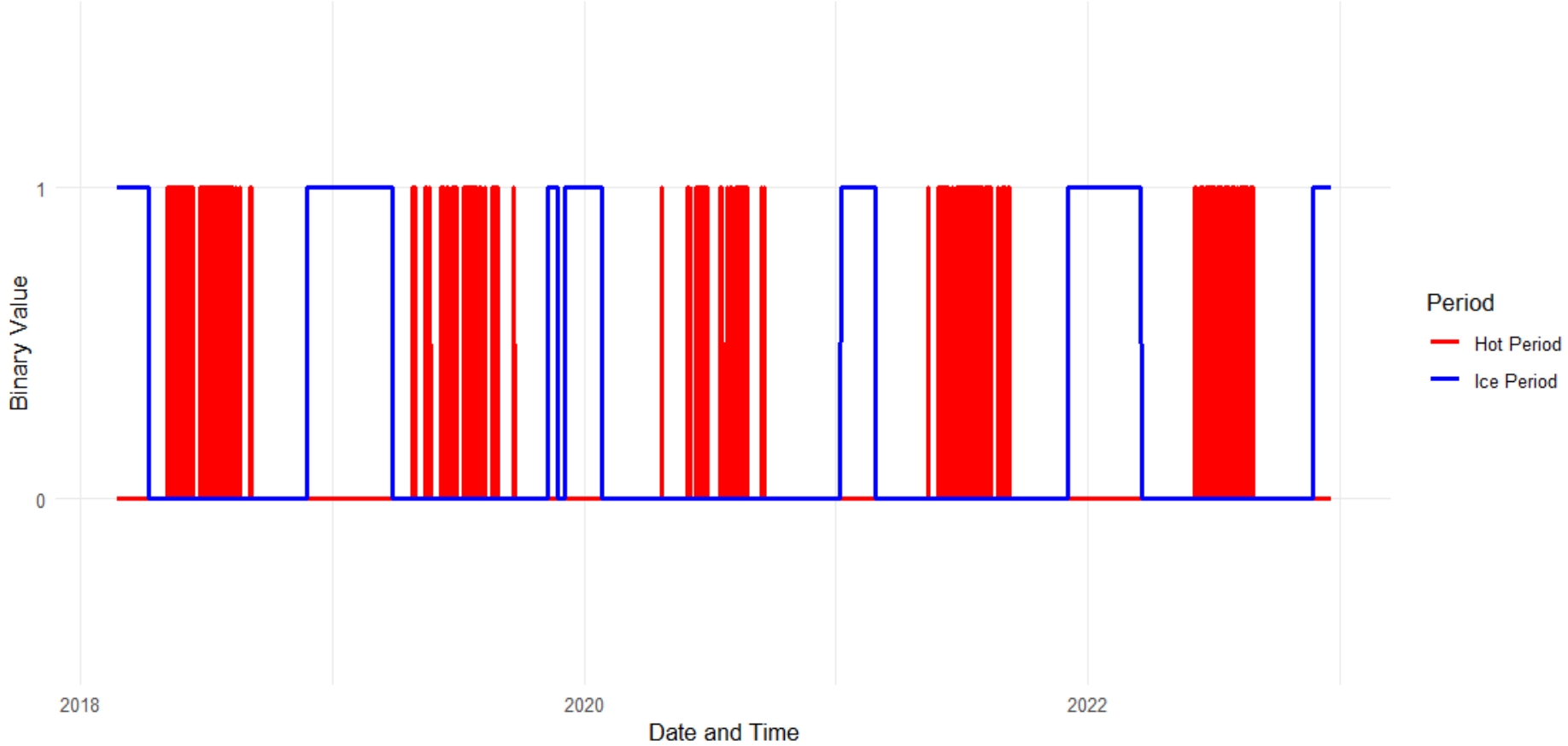
Appendix 8. Table with Water, Roads, and Buildings per Territory

<i>Territory</i>	<i>area km²</i>	<i>lake area km²</i>	<i>stream length km</i>	<i>river length km</i>	<i>main road length km</i>	<i>forest road length km</i>	<i>buildings per km²</i>
Varåa	582.33	23.34	682.94	103.60	114.079	473.302	1.27
Juvberget	1666.21	52.34	2109.78	72.98	262.836	1665.682	1.40
Bograngen	1578.06	80.13	1840.01	23.37	360.769	2068.834	1.93
Ulvåa	852.37	16.13	808.10	9.55	150.906	969.758	2.13
Skärsjön	1304.81	69.81	1724.32	68.67	313.345	1168.144	2.18
<i>Mean ± SD</i>	1196.76 ± 186.93	48.35 ± 11.23	1433.03 ± 258.81	55.63 ± 15.41	240.39 ± 42.09	1269.14 ± 247.28	1.78 ± 0.17

Appendix 9. Temperature throughout the Study Period



Appendix 10. Ice Periods and Hot periods



Appendix 11. Model selection tables

Model selection table Winter Day			Models ranked by AICc(x), Random terms (all models): 1 TerritoryYear, 1 uniquestepID GLMM with family binomial (logit)										
	<i>(Int)</i>	<i>Ice period</i>	<i>OnForestRoad</i>	<i>OnLake</i>	<i>OnRiver</i>	<i>OnStream</i>	<i>BuildingDens</i>	<i>BuildingDist</i>	<i>DEM</i>	<i>FRDens</i>	<i>MRDist</i>	<i>Slope</i>	<i>TCD</i>
2	-2.362	+	+	+	+	+	-0.226	0.055	-0.100	-0.032	0.070	0.270	0.204
3	-2.363	+	+	+	+	+	-0.226	0.055	-0.099	-0.032	0.070	0.270	0.204
4	-2.362	+	+	+		+	-0.226	0.054	-0.100	-0.032	0.071	0.270	0.203
1	-2.362	+	+	+	+	+	-0.226	0.055	-0.099	-0.032	0.070	0.270	0.204
6	-2.347	+	+	+	+	+		0.099	-0.105	-0.071		0.269	0.203
7	-2.349	+	+	+	+	+		0.099	-0.104	-0.071		0.269	0.203
5	-2.348	+	+	+	+	+		0.099	-0.105	-0.071		0.269	0.203
8	-2.348	+	+	+		+		0.098	-0.105	-0.071		0.268	0.203

	<i>Ice_prd:OnFR</i>	<i>Ice_prd:OnL</i>	<i>Ice_prd:OnR</i>	<i>Ice_prd:OnS</i>	<i>MRDens</i>	<i>df</i>	<i>logLik</i>	<i>AICc</i>	<i>delta</i>	<i>weight</i>
2	+	+	+			18	-25546.29	51128.6	0	0.425
3	+	+				17	-25547.89	51129.8	1.20	0.233
4	+	+				16	-25549.19	51130.4	1.81	0.172
1	+	+	+	+		19	-25546.20	51130.4	1.83	0.170
6	+	+	+		-0.2	17	-25582.01	51198	69.45	0
7	+	+			-0.2	16	-25583.69	51199.4	70.80	0
5	+	+	+	+	-0.2	18	-25581.92	51199.8	71.26	0
8	+	+			-0.2	15	-25584.94	51199.9	71.31	0

Model selection table Winter Night			Models ranked by AICc(x), Random terms (all models): 1 TerritoryYear, 1 uniquestepID GLMM with family binomial (logit)										
	<i>(Int)</i>	<i>Ice period</i>	<i>OnForestRoad</i>	<i>OnLake</i>	<i>OnRiver</i>	<i>OnStream</i>	<i>BuildingDens</i>	<i>BuildingDist</i>	<i>DEM</i>	<i>FRDens</i>	<i>MRDist</i>	<i>scl(Slp)</i>	<i>scl(TCD)</i>
3	-2.333	+	+	+	+	+	-0.107		-0.059	0.022		0.032	0.086
4	-2.333	+	+	+	+	+	-0.100		-0.069			0.036	0.086
2	-2.333	+	+	+	+	+	-0.103	0.010	-0.059	0.022		0.032	0.087
1	-2.334	+	+	+	+	+	-0.105	0.010	-0.056	0.022	-0.007	0.031	0.086
6	-2.329	+	+	+	+	+		0.036	-0.063			0.032	0.087
5	-2.329	+	+	+	+	+		0.036	-0.064	-0.001		0.032	0.087

	<i>Ice_prd:OFR</i>	<i>Ice_prd:OnL</i>	<i>Ice_prd:OnR</i>	<i>Ice_prd:OnS</i>	<i>MRDens</i>	<i>df</i>	<i>logLik</i>	<i>AICc</i>	<i>delta</i>	<i>weight</i>
3	+	+	+	+		17	-26334.080	52702.200	0.000	0.411
4	+	+	+	+		16	-26335.370	52702.800	0.590	0.306
2	+	+	+	+		18	-26333.800	52703.600	1.450	0.199
1	+	+	+	+		19	-26333.660	52705.300	3.180	0.084
6	+	+	+	+	-0.042	17	-26351.190	52736.400	34.230	0.000
5	+	+	+	+	-0.042	18	-26351.190	52738.400	36.220	0.000

Model selection table Speed Winter Day				Models ranked by AICc(x), Random terms (all models): 1 TerritoryYear GLMMs with family Gamma (log)						
	<i>cnd((Int))</i>	<i>dsp((Int))</i>	<i>Ice period</i>	<i>BuildingDens</i>	<i>BuildingDist</i>	<i>DEM</i>	<i>FRDens</i>	<i>MRDist</i>	<i>Slope</i>	<i>TCD</i>
4	7.234	+	+	0.052			-0.042		-0.037	-0.205
3	7.234	+	+	0.047			-0.045	-0.016	-0.037	-0.204
2	7.231	+	+	0.047		0.020	-0.040	-0.022	-0.043	-0.206
7	7.233	+	+				-0.032		-0.035	-0.204
8	7.234	+	+						-0.040	-0.204
6	7.234	+	+		-0.019		-0.035		-0.036	-0.205
1	7.232	+	+	0.044	-0.008	0.020	-0.041	-0.022	-0.043	-0.206
9	7.236	+	+						-0.040	-0.204
5	7.231	+	+		-0.019	0.020	-0.030		-0.042	-0.207

	<i>S/E FR</i>	<i>S/E Lake</i>	<i>S/E River</i>	<i>S/E Stream</i>	<i>MRDens</i>	<i>df</i>	<i>logLik</i>	<i>AICc</i>	<i>delta</i>	<i>weight</i>
4	+	+	+	+		12	-60784.94	121593.9	0.00	0.394
3	+	+	+	+		13	-60784.62	121595.3	1.37	0.198
2	+	+	+	+		14	-60784.26	121596.6	2.65	0.105
7	+	+	+	+	0.03898	12	-60786.5	121597	3.13	0.082
8	+	+	+	+	0.03062	11	-60787.75	121597.5	3.62	0.065
6	+	+	+	+	0.03757	13	-60786.01	121598.1	4.15	0.050
1	+	+	+	+		15	-60784.18	121598.4	4.50	0.042
9	+	+	+	+		10	-60789.27	121598.6	4.65	0.039
5	+	+	+	+	0.04242	14	-60785.63	121599.3	5.39	0.027

Model selection table Speed Winter Night				Models ranked by AICc(x), Random terms (all models): 1 TerritoryYear GLMMs with family Gamma (log)						
	<i>cnd((Int))</i>	<i>dsp((Int))</i>	<i>Ice period</i>	<i>BuildingDens</i>	<i>BuildingDist</i>	<i>DEM</i>	<i>FRDens</i>	<i>MRDist</i>	<i>Slope</i>	<i>TCD</i>
3	7.294	+	+	0.089	-0.033			-0.042	-0.213	-0.184
4	7.293	+	+	0.102				-0.040	-0.213	-0.183
2	7.295	+	+	0.092	-0.033		-0.013	-0.044	-0.212	-0.184
7	7.290	+	+		-0.056				-0.207	-0.185
1	7.297	+	+	0.092	-0.033	-0.007	-0.015	-0.042	-0.210	-0.184
6	7.289	+	+		-0.055		0.007		-0.208	-0.185
5	7.289	+	+		-0.055	0.000	0.007		-0.208	-0.185

	<i>S/E FR</i>	<i>S/E Lake</i>	<i>S/E River</i>	<i>S/E Stream</i>	<i>MRDens</i>	<i>df</i>	<i>logLik</i>	<i>AICc</i>	<i>delta</i>	<i>weight</i>
3	+	+	+	+		13	-63160.80	126347.6	0.00	0.344
4	+	+	+	+		12	-63162.20	126348.4	0.79	0.232
2	+	+	+	+		14	-63160.64	126349.3	1.69	0.148
7	+	+	+	+	0.101	12	-63162.67	126349.4	1.73	0.144
1	+	+	+	+		15	-63160.59	126351.2	3.60	0.057
6	+	+	+	+	0.099	13	-63162.62	126351.3	3.65	0.055
5	+	+	+	+	0.099	14	-63162.62	126353.3	5.65	0.020

Model selection table Summer Night			Models ranked by AICc(x), Random terms (all models): 1 TerritoryYear, 1 uniquestepID GLMM with family binomial (logit)										
	<i>(Int)</i>	<i>BuildingDens</i>	<i>BuildingDist</i>	<i>DEM</i>	<i>FRDens</i>	<i>FRDist</i>	<i>Hot period</i>	<i>LakeDist</i>	<i>MRDist</i>	<i>RiverDist</i>	<i>Slope</i>	<i>StreamDist</i>	<i>TCD</i>
6	-2.311	-0.077		-0.030			+	0.045		-0.024	0.134	-0.064	-0.046
7	-2.311	-0.077		-0.030			+	0.041		-0.024	0.134	-0.064	-0.046
5	-2.311	-0.072	0.011	-0.029			+	0.043		-0.026	0.134	-0.064	-0.045
4	-2.311	-0.068	0.011	-0.031			+	0.044	0.010	-0.027	0.134	-0.064	-0.045
3	-2.311	-0.068	0.011	-0.031			+	0.043	0.010	-0.026	0.134	-0.064	-0.045
2	-2.311	-0.069	0.010	-0.032		0.005	+	0.044	0.010	-0.026	0.135	-0.064	-0.045
1	-2.311	-0.068	0.010	-0.033	-0.003	0.004	+	0.044	0.009	-0.026	0.135	-0.064	-0.045
11	-2.310		0.027	-0.031			+	0.047		-0.024	0.133	-0.066	-0.044
12	-2.309		0.027	-0.031			+	0.043		-0.025	0.133	-0.067	-0.044
10	-2.310		0.025	-0.036	-0.013		+	0.049		-0.025	0.135	-0.065	-0.044
9	-2.310		0.025	-0.036	-0.013		+	0.049		-0.024	0.134	-0.065	-0.044
8	-2.310		0.025	-0.036	-0.013	0.001	+	0.049		-0.024	0.135	-0.065	-0.044
17	-2.309	-0.077		-0.045			+				0.129		-0.034
16	-2.309	-0.071	0.014	-0.044			+				0.130		-0.034
15	-2.309	-0.069	0.014	-0.045			+		0.004		0.131		-0.034
14	-2.309	-0.069	0.014	-0.045		0.000	+		0.004		0.131		-0.034
13	-2.309	-0.069	0.014	-0.045	0.000	0.001	+		0.004		0.131		-0.034
20	-2.308		0.032	-0.042			+				0.129		-0.032
19	-2.308		0.031	-0.046	-0.009		+				0.130		-0.032
18	-2.308		0.031	-0.046	-0.010	-0.003	+				0.130		-0.033

	<i>Hot_prd:LkD</i>	<i>Hot_prd:RvD</i>	<i>Hot_prd:StD</i>	<i>MRDens</i>	<i>WaterDist</i>	<i>Hot_prd:WtD</i>	<i>df</i>	<i>logLik</i>	<i>AICc</i>	<i>delta</i>	<i>weight</i>
6	+		+				13	-28299	56624	0	0.37
7			+				12	-28300	56624	0.42	0.3
5	+		+				14	-28298	56625	1.34	0.19
4	+		+				15	-28298	56626	2.77	0.09
3	+	+	+				16	-28298	56628	4.61	0.04
2	+	+	+				17	-28298	56630	6.47	0.01
1	+	+	+				18	-28297	56631	7.37	0.01
11	+		+	-0.04			14	-28305	56639	14.94	0
12			+	-0.04			13	-28307	56639	15.4	0
10	+		+	-0.04			15	-28305	56640	16.01	0
9	+	+	+	-0.04			16	-28305	56642	17.87	0
8	+	+	+	-0.04			17	-28305	56644	19.86	0
17					-0.017	+	10	-28322	56664	40.11	0
16					-0.018	+	11	-28321	56665	40.93	0
15					-0.018	+	12	-28321	56667	42.83	0
14					-0.018	+	13	-28321	56669	44.83	0
13					-0.018	+	14	-28321	56669	45.74	0
20				-0.03	-0.02	+	11	-28330	56682	57.89	0
19				-0.03	-0.018	+	12	-28330	56683	59.39	0
18				-0.03	-0.018	+	13	-28329	56685	61.34	0

Model selection table Summer Day													
Models ranked by AICc(x), Random terms (all models): 1 TerritoryYear, 1 uniquestepID GLMM with family binomial (logit)													
	<i>(Int)</i>	<i>BldngDn</i>	<i>BldngDs</i>	<i>DEM</i>	<i>FRDn</i>	<i>FRDs</i>	<i>Hot_prd</i>	<i>LkD</i>	<i>MRDs</i>	<i>RvD</i>	<i>Slp</i>	<i>StD</i>	<i>TCD</i>
2	-2.392	-0.209	0.045	-0.145		0.207	+	0.011	0.114	0.007	0.266	0.033	0.239
1	-2.393	-0.211	0.045	-0.144	0.006	0.208	+	0.010	0.115	0.008	0.266	0.032	0.239
6	-2.395	-0.209	0.048	-0.152		0.205	+		0.112		0.259		0.244
5	-2.395	-0.211	0.049	-0.151	0.006	0.207	+		0.113		0.259		0.244
4	-2.386		0.070	-0.154		0.208	+	0.032		0.028	0.262	0.030	0.237
3	-2.385		0.068	-0.158	-0.020	0.203	+	0.035		0.026	0.263	0.032	0.237
8	-2.389		0.080	-0.150		0.203	+				0.252		0.246
7	-2.388		0.078	-0.155	-0.017	0.199	+				0.253		0.246

	<i>Hot_prd:LkD</i>	<i>Hot_prd:RvD</i>	<i>Hot_prd:StD</i>	<i>MRDn</i>	<i>WtD</i>	<i>Hot_prd:WtD</i>	<i>df</i>	<i>logLik</i>	<i>AICc</i>	<i>delta</i>	<i>weight</i>
2	+	+	+				17	-27333	54700.1	0	0.589
1	+	+	+				18	-27332.9	54701.8	1.71	0.250
6					0.061	+	13	-27338.7	54703.4	3.31	0.112
5					0.060	+	14	-27338.5	54705	4.97	0.049
4	+	+	+	-0.219			16	-27357.4	54746.7	46.65	0
3	+	+	+	-0.216			17	-27356.5	54747.1	47.02	0
8				-0.208	0.060	+	12	-27368.8	54761.6	61.53	0
7				-0.204	0.062	+	13	-27368.1	54762.3	62.19	0