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Master's Thesis

Wolf space use in a seasonally changing environment

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Contents

Abstract

In this study, we investigate the space use of a recolonizing predator in Scandinavia in relation to the density of its main prey and other environmental variables. Animal space use is influenced by intrinsic factors, such as age, sex and reproductive phase, presence of other animals (e.g., mates, competitors, predators, prey) and habitats providing food, shelter or disturbance. In heterogeneous landscapes, resources are often not evenly distributed which can influence animal movement and behavior, as well as species interactions. For predators, obtaining food resources is often challenging as prey tend to develop anti-predator strategies and adaptations after predators settle in an environment. In addition, seasonal variation shifts both the spatial and temporal resource availability, which in turn affects the space use of the predator. Here, we study the space use of the Scandinavian wolf (*Canis lupus*) in relation to its main prey, the moose (*Alces Alces*) to gain insight into which parameters lie at the cause. We analyzed GPS locations of nine breeding wolves in five wolf territories and compared their utilization distribution with the seasonally changing distribution of moose fecal pellet groups and other habitat covariates. Contrary to our initial predictions, we found that moose pellet group density was negatively correlated with wolf space use in summer, and that the relationship between pellet group density and wolf space use was weak and its direction unclear during in winter. The space use of wolves reflects multiple behavioral strategies of predator and prey that may explain this pattern. Wolves selected transitional forest stands (young forests) during both summer and winter. Additionally, wolves significantly avoided areas with human infrastructures (buildings and roads) both in summer and winter. In summary, the relationship between wolf space use, prey density and different habitat types differed between seasons, although anthropogenic variables had a negative effect throughout the year. Further research should differentiate between different behavioral states of the wolves, such as resting, breeding, travelling and consuming prey. This would help to understand the importance of seasonal shifts in prey distributions and different habitat types and support the management and conservation of this protected, but conflict-prone species

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I am very thankful for the opportunity to study a wild animal like the wolf, the fact that the recolonization is still possible in a human-dominated world, gives me hope that the collaboration between humans and nature can have a bright future.

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1.   Introduction

One of the central topics of animal ecology is understanding how animals use their surrounding environment over time and space. Animal space use is driven by extrinsic and intrinsic factors. Extrinsic factors are (1) the presence and location of other animals, e.g. mates, prey, predators, competitors (Orjan et al., 2018; Sillero-Zubiri & Macdonald, 1998; Waser, 1985; Wauters & Gurnell, 1999); and (2) the distribution and availability of resources, e.g. food, cover; (Baguette & Van Dyck, 2007; Goltsman, Kruchenkova, Sergeev, Johnson, & Macdonald, 2005; Mangel & Clark, 1986; Schoener, 1971; Waser, 1985). Intrinsic drivers of animal space use are e.g. reproductive status, age, territoriality and site fidelity (Brown, Kotler, & Bouskila, 2001; Kittle et al., 2015; Morales & Ellner, 2002; R. P. Peters & Mech, 1975; Sillero-Zubiri & Macdonald, 1998).

According to optimal foraging theory (OFT), animals seek to obtain food resources at the minimum energetic cost, which in turn maximizes fitness and efficiency (Charnov, 1976). However, for most free roaming animals, resources are not evenly distributed throughout the environment. A heterogeneous landscape can be defined as a dynamic mosaic of various habitat patches that are more or less conveniently spread throughout the environment (Barraquand & Benhamou, 2008). Landscape heterogeneity can influence animal behavior (Turlure et al., 2009; Wiens & Milne, 1989), movement (Fahrig, 2007; Fryxell, Sinclair, & Arcese, 1995; Mangipane et al., 2018), and species interactions (Gorini et al., 2012; Polis, Power, & Huxel, 2004). According to the spatial-resource variability hypothesis (SRVH; (Hiller, Belant, & Beringer, 2015)), animals use larger areas to acquire the necessary resources as landscape heterogeneity increases (Hiller et al., 2015; Johnson, Wiens, Milne, & Crist, 1992; Mangipane et al., 2018). Both OFT and SRVH would require animals to possess perfect knowledge of the heterogeneous distribution of resources within their surroundings; however, this information is often incomplete and constrained by an animal's grain size (Baguette & Van Dyck, 2007; Denny, Stenhouse, & Nielsen, 2018; Pyke, 1984). Nevertheless, grain size is believed to increase with body size (Gaston & Blackburn, 1996; Hiller et al., 2015; S. G. Mech & Zollner, 2002), suggesting that large mammals perceive the landscape at broader scales than just the local habitat patch (Denny et al., 2018).

Space use is a fundamental factor in predator-prey interactions (Fernández, Delibes, Palomares, & Mladenoff, 2003; Gervasi et al., 2013, 2012; Gorini et al., 2012; Kauffman et

al., 2007). When deciding which habitat patches to visit, prey faces a trade-off between patches that maximize food intake and secure protection from predators (Fryxell et al., 1995; Laundré, Hernández, & Altendorf, 2001; Lima, Valone, & Caraco, 1985; Matassa & Trussell, 2011). On the other hand, predators select areas that maximize their chances of encountering and killing prey (Gorini et al., 2012; Kauffman et al., 2007; Walton, Cluff, Paquet, & Ramsay, 2001). The resources needed by prey are often unevenly scattered in natural landscapes, which will result in an uneven distribution of prey (Waser, 1985). Consequently, predators need to adjust their space use in relation to heterogeneous prey density within the landscape; This often leads to predators and prey not using their home ranges uniformly (Chamberlain & Leopold, 2000; Fortin et al., 2005; Kie, Terry Bowyer, Nicholson, Boroski, & Loft, 2002; Matassa & Trussell, 2011; Werner, Mittelbach, Hall, & Gilliam, 1983). The heterogeneity of resources leads to prey seeking patches with more and higher-quality resources (Kie et al., 2002; Nabe-Nielsen, Tougaard, Teilmann, Lucke, & Forchhammer, 2013). As a result, predators will be attracted to those patches where prey is more abundant (Emmons, 1987; Flaxman & Lou, 2009; Kittle et al., 2017). However, other studies have suggested that in order to maximize their hunting success, predators hunt where prey is less abundant but more vulnerable (Flaxman & Lou, 2009; Gerritsen & Strickler, 1977; Grant, Hopcraft, Sinclair, & Packer, 2005; Laundre, Calderas, & Hernandez, 2009; Sih, 1984). Following this logic, prey should then avoid areas where predators are more abundant or spend more time, at the expenses of food resources (Fortin et al., 2005; Heithaus & Dill, 2002; Laundre et al., 2009; Lima & Dill, 1989; Matassa & Trussell, 2011; McNamara & Houston, 1987; Milinski & Heller, 1978; Sih, 1980; Turner, 1997).

I here study the interacting space use of an apex predator and its main prey in Scandinavia. The grey wolf (*Canis lupus*) is currently recolonizing parts of the Scandinavian peninsula (Wabakken, Sand, Liberg, & Bjärvall, 2001). Moose (*Alces alces*) is the main prey of wolves for the majority of the Scandinavian population (Sand et al., 2008; Sand, Zimmermann, Wabakken, Andrèn, & Pedersen, 2005). The wolf is a territorial species, and as such, its space use is typically confined to a stable home range defined as territory. The home range is an important life aspect for a wolf since it will reside in it and defend it against neighboring wolf packs and intruders for the majority of its lifetime Prey availability is also an important determinant of space use within the home range. The time wolves spend in different parts of the home range is determined by their main activities, such as patrolling and marking the

territory border, hunting and feeding on prey, resting in day beds, and breeding and caring for young(Arnemo, Evans, & Eczm, 2017; Ballard, Whitman, & Gardner, 1987; L. D. Mech, 1994, 2000; L. David Mech & Boitani, 2003; Murie, 1944; Roffler & Gregovich, 2018; Sillero-Zubiri & Macdonald, 1998; Theuerkauf, Rouys, & Jedrzejewski, 2003; Walton et al., 2001). These activities vary in time and space. During summer, breeding wolves adjust their home range in order to optimize the care for their offspring, their range is reduced and more concentrated around the denning site (Brooks et al., 2017; Walton et al., 2001). Dens and rendezvous sites are usually far from human disturbance (Llaneza, Sazatornil, José, & López-Bao, 2018; Sazatornil et al., 2016). Because wolves prefer to hunt neonate ungulates in this period (Sand et al 2018), they spend little time at these small carcasses and quickly return to the pups. This results in a star-formed movement pattern from and to the den and rendezvous site. Outside of the denning period, wolves usually concentrate their space use on carcass and resting sites (Cagnacci, Boitani, Powell, & Boyce, 2010; L. D. Mech, 2000; Ruprecht, Ausband, Mitchell, Garton, & Zager, 2012; Theuerkauf et al., 2003). Additionally, due to the climate of the region, heavy snowfall causes the main prey to perform seasonal migration (Bischof et al., 2012) which results in most of the main prey to move outside of the wolf territory. This migration comes at great cost for territorial predators like wolves since the prey densities shift considerably over seasons, rendering some seasons with a scarcer food supply.

Fecal pellet counts of moose were conducted inside the home ranges of GPS-collared wolves to describe the seasonally changing distribution of moose and space use of wolves. For the winter season, I predicted wolf space use to be positively related to moose density and to winter habitats favoured by moose, and negatively related to snow depth. For the summer season, I predicted wolf space use to be independent of moose density and summer habitat favoured by moose, and negatively related to sources of human disturbance (roads and settlements).

2. Methods

2.1 Study area

The study was conducted in five wolf territories between 2017 and 2020 in southeastern Norway (municipalities of Trysil and Elverum) and in southwestern Sweden (Värmland county) (*Figure 1*). Snow covers the ground mostly between December and April with mean snow depths ranging between 1.8cm and 75.7cm over the years. The landscape topography is hilly, with elevation ranging between 148 – 1077 m above sea level. The landscape is primarily dominated by coniferous forests, mainly Scot's pine (*Pinus sylvestris*) and Norwegian spruce (*Picea abies*), although deciduous tree species such as birch (*Betula* spp.), aspen (*Populus tremuloides*) and willow (*Salix* spp.) occur sporadically. The European blueberry (*Vaccinium myrtillus),* the crowberry (*Empetrum nigrum*), and other
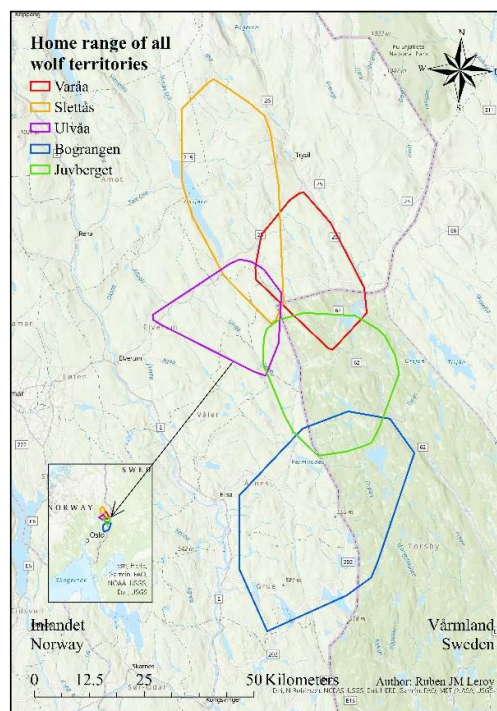

Figure 1: Home range of all observed wolves during the study period. The nine individuals are confined to five separate territories: Slettås (Orange), Varåa (Red), Ulvåa (Purple), Juvberget (Green), and Bograngen (Blue).

Vaccinium subspecies dominate the shrub layer and ground layer together with several mosses and peat vegetation. Intensive logging of Scots pine and Norwegian spruce has resulted in a wide network of gravel roads (0-0.003km²/km²). Typical for the region within the wolf distribution is the low human density, including areas with less than one person per km²(Wabakken et al., 2001). After pellet count, we averaged the pellet density of the study areas to calculate the moose density. In accordance with the defecation rate of moose, the pellet density was divided by 14 and then multiplied by a hundred to scale for hectare. Average moose densities within the wolf territories ranged between 1.7 – 2.1 individuals per ha in summer and 0.4 - 0.6 individuals per ha in winter. Other common prey species of wolves include roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*) and the European hare (*Lepus europaeus)* which were present in the study area.
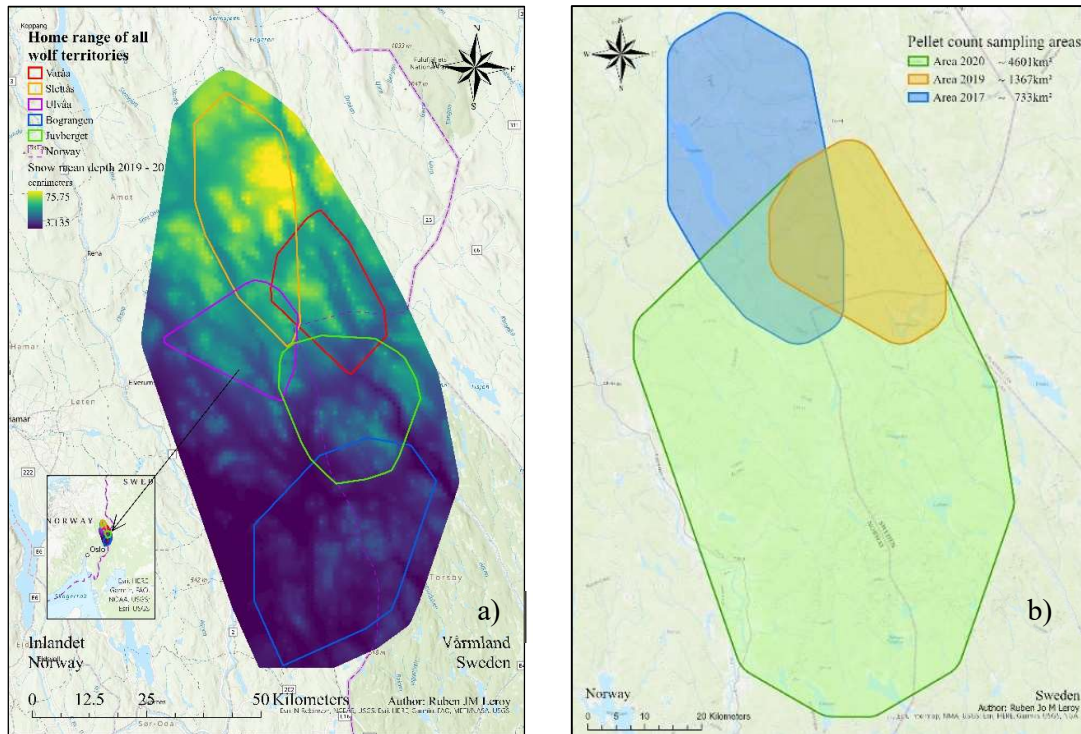
Figure 2: Mean snow depth in the study area in the winter of 2019 – 2020, with delineated wolf territories (a). Sampling areas for the fecal pellet counts of moose(b)

2.2 Wolf GPS positions

Wolves were immobilized using darts during winter months from a helicopter (see (Arnemo et al., 2017), for immobilization details). Within the study area, we captured nine wolves belonging to five packs: Slettås, Juvberget, Varåa, Bograngen and Ulvåa (Figure 2). In the Slettås territory we collared and monitored two individuals during 2017; in the Varåa territory we collared and monitored two individuals in 2019 and 2020; whereas in the Juvberget, Bograngen and Ulvåa territories we collared two and one individuals, respectively, during 2020. All territories had pups during the observation period. The GPS-collars (Vectronic Vertex Lite and Vertex Plus) were programmed to send one position every four hours during the entire study period.

2.3 Pellet counts

We used pellet count surveys to estimate moose density within our study area in 2017, 2019 and 2020. Pellet count surveys were first conducted in 2017 in the Slettås territory (area = 1367km², 605 plots, *Figure 2*B). In 2019, pellet counts were carried out in the Varåa territory (area=733 km², 190 plots). In 2020, pellet counts were conducted in an area covering Varåa, Ulvåa, Juvberget and Bograngen territories (area=4601 km², 1540 plots).

Figure 3: Sampling site with point sampling transects characteristics and arrangement

Pellet counts were conducted two times per year: one in May to represent the winter period (October-May) and one in October to represent the summer period (June-September). Each period took about one and a half months to complete. The study area for the pellet count surveys consisted of a systematic grid with sampling sites which were evenly spread throughout the landscape, at a distance of approximately 3.0 km. If a site was located too close or inside agricultural lands, settlements, on roads) or in water the site was moved to approximately 100 to 150 meters to the nearest area

Figure 4: point sampling transect characteristics and methodology.

that was considered accessible for moose, in either a north or east direction from the original square location. Each sampling site contained five sample plots, see *Figure 3*, ordered in a square formation of 50*50 m where one plot was located at each corner of the square and one at the center of the square (*Figure 4*). We placed a marking stick in the center of each plot and used a rope to indicate the inner $10 \, \text{m}^2$ and the total area of $100 \, \text{m}^2$ (*Figure 4*). We first searched the inner circle clockwise and counterclockwise. We then searched the outer circle by moving back and forth between plot border and center, both in clockwise and counterclockwise direction. We carefully scanned the ground layer and counted all fecal pellet piles from ungulates. To be registered, a moose pile had to contain at least 20 pellets. The majority of the pellets had to be inside the plot in cases where the pile was spread across the plot border. After counting, all piles were removed. Counts were registered into a digital filing system with the use of Kobo Collect V1.27.3.
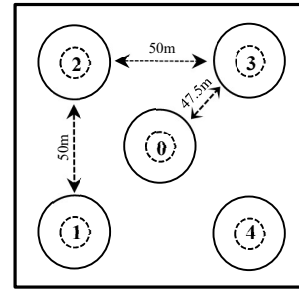
2.4 Additional explanatory variables

We specify the following environmental characteristics in detail due to their importance in the study.

Table 1: Variable description for moose pile density and wolf space use modelling.

Variable name	Abbreviation	Information	Unit	Source
Pellet density	Pellets	Response data – number of piles on the sampling sites over a season. Count	Continuous	Collected observation. Piles per season.
Site identification	Trakt	Unique sampling site identity	Character	Predefined
Winter days	Winterdays	The days between the winter sampling session.	Continuous	Calculated: Sampling day – day of start winter period.
Summer days	summerdays	The days between the summer sampling session.		Calculated: Sampling day – day of start summer period.
Solar radiation	Sol_sum/ Sol_win	Surfaces that are exposed to solar radiation, usually due to the lack of overgrowing vegetation. Expressed in Watt per 625m² area.	Continuous	DEM ArcGIS processing, using the solar radiation geoprocessing functions. (European commision 2009, Copernicus open Acces Hub, European Environment Agency, & Geocenter Denmark, 2014)
Elevation	Elev	Height above sea level, defined in meters. Ranging between 148-1077m.	Continuous	Digital elevation model (European commision 2009 et al., 2014)
Elevation deviation	Elev_dev	Height difference compared to the mean height of the area	Continuous	DEM ArcGIS processing
Ruggedness 25x25m² pixel	Rugged25	The mean difference in elevation between the 625m² patch and its neighbors. The value is measured in meters.	Continuous	DEM ArcGIS processing using ruggedness index function.
Ruggednes 250x250m² pixel	Rugged250	The mean difference in elevation between the 62500m² patch and its neighbors. Expressed in meters.	Continuous	DEM ArcGIS processing using ruggedness index function.
Slope 25x25² pixel size	Slope25	The inclination of the horizontal in degrees over an 625m² area.	Continuous	DEM ArcGIS processing using slope function.
Slope 250x250m² pixel size	Slope250	The inclination of the horizontal in degrees over an 62500m² area.	Continuous	DEM ArcGIS processing using slope function.
Corine land type	CORINE / CORINEF	Corine defined land types	Character	Extracted metadata (Copernicus open acces hub & European Environment Agency, 2018)
Corine determined transitional forest stands	Young forest	Corine define transitional woodlands	Character	Extracted metadata (Copernicus open acces hub & European Environment Agency, 2018)
Corine determined other forest stands	Mature forest	Corine defined forest types:	Character	Extracted metadata (Copernicus open acces hub & European Environment Agency, 2018)
Density of buildings	Build_dens / Builddensity	Building density in continuous proximity.	Continuous	From open access cadaster data in sweden and Norway. (Geodata.no & SSR Kartverket, 2016) & (Lantmäteriet, 2017)
Density of main roads	Dens_mroad / Roaddensity	Density of main roads, usually paved and well used roads. Up to a proximity of 1000m	Continuous	[1:50000] for the Norwegian roads (Kartverket, 2021) & [1:100000] for Swedish roads (Lantmäteriet, 2020)
Distance to main roads	Dmroad	Distance towards the nearest main roads in continuous proximity. Using proximity to raster function.	Continuous	[1:50000] for the Norwegian roads (Kartverket, 2021) & [1:100000] for Swedish roads (Lantmäteriet, 2020)
Density of forest roads	Dens_froad	Density of forest roads, up to 1000meters proximity. Using proximity to raster function.	Continuous	[1:50000] for the Norwegian roads (Kartverket, 2021) & [1:100000] for Swedish roads (Lantmäteriet, 2020)
Distance to forest roads	Dfroad	Distance towards the nearest forest roads in continuous proximity. Using proximity to raster function.	Continuous	[1:50000] for the Norwegian roads (Kartverket, 2021) & [1:100000] for Swedish roads (Lantmäteriet, 2020)
Density of all roads	Dens_roads	Density of roads in continuous proximity, up to 1000 meters	Continuous	[1:50000] for the Norwegian roads (Kartverket, 2021) & [1:100000] for Swedish roads (Lantmäteriet, 2020)

		proximity. Using proximity to raster function.		
Distance to bogs	*Dist_bog*	*Distance to the Corine defined bog edge in meters. Done by creating edge and using proximity to raster function in ArcGIS.*	*Continuous*	*Created from the* (Copernicus open acces hub & European Environment Agency, 2018) *Corine map*
Snow mean density	*Snowmean*	*Mean snow depth over the entire winter period in centimeters*	*Continuous*	*Obtained from NVE(Norwegian Water Resources and Energy Directorate), as in* (Saloranta, 2012)
Predicted moose density	*RSF*	*Outcome of the moose resource selection function map, in density per ha.*	*Continuous*	*Made by the Co-kriging function in ArcGIS with the count data and the best explanatory variables.*
Longitude	*X*	*Coordinate based geolocation for the longitudinal aspect*	*Coordinates*	*Predefined*
Latitude	*Y*	*Coordinate based geolocation for the latitudinal aspect*	*Coordinates*	*Predefined*

2.5   Statistical analysis

2.5.1 Moose density

In order to interpolate moose density across the entire study area from the sampling plots, we first had to identify which variables were most important in explaining variation in moose density. To do this, we modelled the probability of moose presence using both logistic and Poisson regression, based on the pellet count data in two separate models, one for winter and one for summer. The response data used for modelling the moose density map variables existed out of the raw count data from the pellet count. The response variable was either treated as count or binary variable (presence/absence of piles) in Resource Selection Functions [RSF]s models.   To correct for varying lengths of the seasonal accumulation period, defined as "winterdays" or "summerdays", I included the log-transformed period length as an offset in the models Our explanatory variables were extracted from various governmental mapping sites, see *Table 1*. We created a final variable by making a proximity map towards the border of the Corine based bog vegetation which was named "distance to bogs". All pellet count data and spatial environmental data were extracted on plot scale for all the variables included into the moose density modeling, using QGIS (QGIS Association, 2021) and ArcGIS Pro (Esri Inc. 2020).

Each explanatory variable was scaled for modelling and tested for correlation using the "*ggpairs*" function from the "GGally" package in R (Schloerke et al., 2020). We also checked models for collinearity using the "*check_collinearity*" function of the Performance package (Lüdecke, Makowski, Waggoner, & Patil, 2020). Any explanatory variables with correlations higher than 0.7 were removed from further analyses. We used the sampling site identification

as a random factor in order to account for spatial autocorrelation. We used Generalized Linear Models (GLM) and Generalized Linear Mixed models (GLMM) in Poisson and negative binomial distribution to find the best fitting full models.

All statistical modelling and data processing was done in Microsoft Excel(Microsoft Corporation, 2018), R studio(RStudio Team (2020) & RStudio, 2020), QGIS(QGIS Association, 2021) and ArcGIS Pro (Esri Inc., 2020). The range of each density map spanned 5km outside of the minimum convex polygon from the sampling site positions. The significant variables were used for creating three Co-kriging maps per season, one for each observational year. The final results are six moose density prediction maps, with density predictions per 2500m² (*Figure 6*).

Summer density maps

In order to find the model that best explained the presence of moose piles, we used all the explanatory variables that did not show a high correlation with each other in modeling. All the variables were divided into three groups: the natural elements (e.g., solar radiation, slope, latitude and longitude, landcover, forest cover, ruggedness and elevation), human disturbances (distance to main- and forest roads, and density of buildings), and a combination of both. Afterwards the best models of the groups were compared with the best models of the other groups in order to make the best final model. In the final models we only used GLMMs. We used a negative binomial distribution in order to account for overdispersion. The final models were decided via Akaike's weight Information Criterion and were checked for correlation to eliminate any models with high correlations using the "AICcmodavg" (Akaike, 1973; Marc J., 2020) and "Performance" (Lüdecke et al., 2020) packages in RStudio. All the best models were checked for abnormalities in residuals, by means of the KS-test, dispersion-test and outlier-test with the "DHARMa" package in RStudio (Hartig, 2020). The models were checked for zero-inflation with the same package, which found no significant influence. We included the two most significant variables from the best model to create the Co-Kriging prediction maps.

Winter density maps

For explaining the winter density count, we added explanatory variables "snowdays" for days of snow-covered area, maximum depth of snow "snowmax", and "snowmean" for mean snow depth to account for snow effects. The same procedure of model selection as for the summer

models was applied to the winter models. Insignificant variables of the best model were not included into the Co- kriging map due to the limitation of the Kriging function in ArcGIS pro (Esri Inc., 2020).

After model and variable selection, the selected variables were included into the Co-kriging function of ArcGIS pro (Esri Inc., 2020). We combined moose pile count in combination with a maximum of three other variables for the universal kriging prediction function. Since the kriging function does not allow offset variables, we adjusted our response variable in accordance to the kriging function: we first multiplied each pile count by 100 to obtain piles/ha and divided this by the time period between each pellet survey (accumulation period) to obtain average piles/ha/day. We log transformed the moose pile count data and used model optimizers to create the most optimal prediction model. The range of each density map spanned 5km outside of the minimum convex polygon from the sampling site positions. The significant variables were used for creating three Co-kriging maps per season, one for each observational year.

2.5.2 Wolf space use

To assess wolf space use, we built a Kernel Utilization Distribution map from the GPS locations of wolf positions with the "AdehabitatHR" package in RStudio (Calenge, 2006), and imported it into ArcGIS pro (Esri Inc., 2020). The result created 12 Kernel utilization distribution maps. All maps were divided by year and by season for each separate territory. Additionally, we created a Minimum Convex Polygon for each individual to determine the territories of the wolf packs. We divided the territory of the wolves into a 5km² hexagonal grid. Grid cells were excluded from the territory if their coverage included less than 50% of the MCP territory and did not include any positions, or if the grid cells covered less than 75% of the Resource selection function map for the moose densities. We then extracted different variables for each grid cell: road density (forest and main roads combined), moose density, land-cover and elevation. Land-cover was divided into two stages: young and mature forests, since wolves show a preference in space use for semi-open forest stands types, which is associated with increased predation risk of prey species(Kolenosky & Johnston, 1967; Roger P. Peters & Mech, 1975). All hexagons with missing data for any of the variables were omitted. These variables were then used as explanatory variables to model wolf utilization distribution. We first scaled them and checked for multicollinearity before modelling. The data was divided

into two datasets, one for winter and one for summer wolf utilization. The response data consisted of percentages, ranging between 0.01 and 99.9. We inverted the response variable due to its standard inverted form after the KUD extraction. Since the response variable is expressed in percentages, we used a beta regression distribution for modelling with "glmmTMB" in RStudio(Brooks et al., 2017). The year and territory were added as random factors to account for spatial and temporal autocorrelations. Model selection was done in a stepwise backward procedure, leaving out non-significant variables in accordance with AIC. Additionally, the RSF moose density map variable was added to all the models to check for the significance of the variable in all models. Residuals were checked for the best models in the same method as for the RSF models for the moose density.

3. Results

3.1 Moose pellet group density

The dataset included a total of 4704 plot observations, of which 2375 observations during the summer season and 2329 observations in the winter season. Due to different study area sizes in the three years, number of sample plots and sites varied between 190 – 1540, and 38 – 308 respectively. In total, 1399 moose piles were found on the plots (*Table 2*), of those 835 were deposited during winter and 564 during summer. Additionally, 59 piles of red deer were found on the 100 m^2 plots (4% of all piles from the large-bodied ungulates moose and red deer). In the inner 10 m^2 circle of the plots, 70 piles of roe deer were found. Mean pellet group density, corrected for the varying length of the accumulation period, ranged between 0.09 – 0.24 piles/ha/day (*Table 2*). The results were similar for the three summer seasons (0.21 – 0.24 piles/ha/day) but differed more strongly for the three winter studies (0.09, 0.23 and 0.18 piles/ha/day, respectively). Given a defecation rate of 14 piles per day per moose during winter (Rönnegård, Sand, Andrén, Månsson, & Pehrson, 2008), moose densities in winter averaged 0.66, 1.63 and 1.27 moose / km^2 for the three studies in 2016-17, 2018-19 and 2019-20, respectively.

Observation period	Sites	Complete Plots	Area (km2)	Mean accumulation period (days)	Pellet groups of moose	Mean pellet group density (ha^{-1}*day^{-1}) ± 2SE
Winter 2016/17	121	599	1367	233	131	0.09 (±0.03)
Summer 2017	129	645	1367	109	149	0.21 (±0.05)
Winter 2018/19	38	190	733	244	106	0.23 (±0.09)
Summer 2019	38	190	733	108	50	0.24 (±0.12)
Winter 2019/20	308	1540	4601	233	598	0.18 (±0.03)
Summer 2020	308	1540	4601	110	365	0.21 (±0.04)
Total	941	4704	6701	/	1399	/

Table 2: Overview of moose pellet counts conducted for this study, with the number of sampling sites and plots, the monitored area, the accumulation period, the number of moose pellet groups deposited during the sampling period, and the mean pellet group density.

Assuming the same defecation rate during summer, moose densities in summer averaged 1.52 – 1.74 moose / km^2 for the three partly overlapping study areas.

Moose winter density

The best winter model to explain the variation in number of piles found per plot, revealed multiple significant explanatory variables. The best negative binomial model (*Table 3*) included solar radiation, mean snow depth, distance to bogs, and the quadratic form of distance to roads as the most significant variables for explaining the variation in pellet group density in the winter (*Figure* 5). According to the model, the moose pellet density increased with increasing distance to bogs, as with increasing amounts of solar radiation. The hump-shaped relationship with the main roads indicates moose pellet density was highest at intermediate distances. In addition, in winter the moose pellet group density was lowest on mixed forest, bogs, and coniferous stands but highest on young forest stands (*Table 6*). However, due to the fact that the Universal kriging function in ArcGIS is only able to include three variables additionally to the response variable, we exclusively included non- quadratic significant variables into the kriging prediction maps. The included variables were the distance to bogs, mean snow depth and solar radiation. The results showed three different moose density maps for the winter density prediction, one for each year sampling was performed.
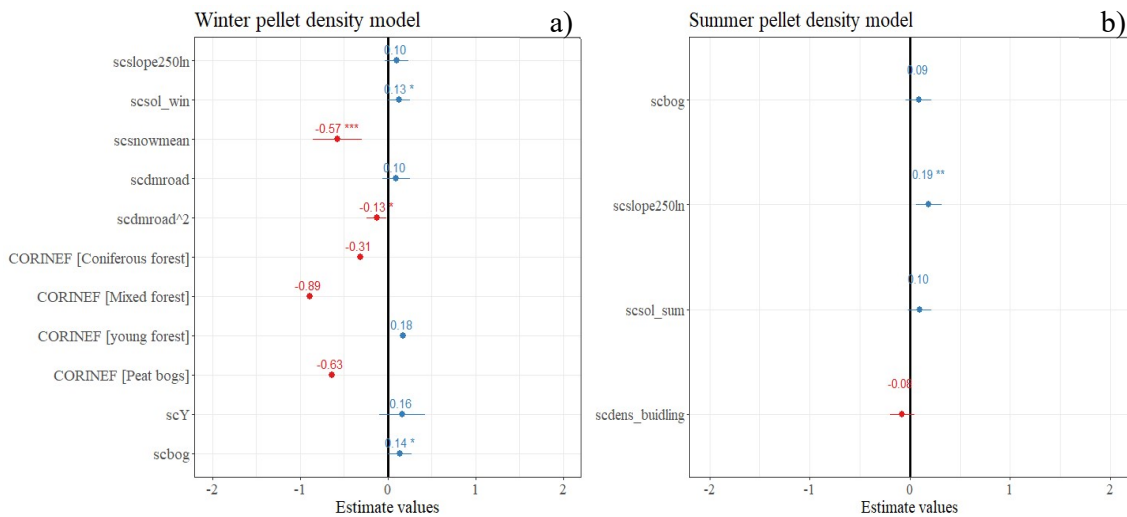

Figure 5: Estimates of the variables included in the top model to predict number of fecal pellet piles of moose for the winter a) and summer b) season. See Table 1 for variable description. "sc" indicates the scaling of variables. Due to the subset category of the CORINE dataset, standard deviation is not present for each factor. See Table 6 & Table 7 for a more detailed description with the SE.

Moose summer density

The best negative binomial model to explain the variation in the number of moose pellet groups per plot contained distance to bog, slope at 250*250 m pixel size, solar radiation, and density of buildings (*Table 3*). The density of moose pellet groups increased with increasing slope, distance to bogs, and increased solar radiation (Figure 5). We selected the predictors with the highest estimates (slope and solar radiation) to include into the density prediction map. The building density and distance to bogs were not included, but since the confidence interval of the slope variable was the only estimate that did not had overlap on zero, the relationship with any other variable is unclear for inclusion into the prediction map.

Table 3: Top models of model selection for moose pellet count. All model variables have been scaled. Sampling site ID is included as random factor and days between sampling sessions was set as an offset variable. All modelling was done with negative binomial regression distribution.

No.	Model selection winter	AIC	AICc	Weight
1	Slope250 + sol_win + snowmean + dmroad + I(dmroad^2) + CORINEF + Y + bog; Ziformula ~ dmroad + I(dmroad^2) + bog	3376.11	0.00	0.57
2	Slope250 + sol_win + snowmean + dmroad + I(dmroad^2) + CORINEF + Y + bog; Ziformula ~ snowmean + dmroad + I(dmroad^2) + CORINEF + Y + bog	3377.45	1.34	0.29
3	Slope250 + sol_win + snowmean + dmroad + I(dmroad^2) + CORINEF + Y + bog; Ziformula ~ snowmean + dmroad + I(dmroad^2) + CORINEF + Y + bog + sol_win	3379.02	2.91	0.13
4	Slope250 + sol_win + snowmean + dmroad + I(dmroad^2) + CORINEF + Y + bog	3386.46	10.35	0.00
5	Slope250 + sol_win + snowmean + dmroad + I(dmroad^2) + CORINEF + Y + bog, Ziformula ~ 1	3388.48	12.38	0.00
6	Slope250 + sol_win + snowmean + dfroad + I(dfroad^2) + elev + dens_building + bog + CORINEF	3388.57	12.46	0.00
7	Slope250 + sol_win + snowmean + dfroad + I(dfroad^2) + elev + dens_building + bog + CORINEF + Y	3389.81	13.70	0.00
8	Slope250 + sol_win + rugged25 + dens_main + snowmean + dfroad + I(dfroad^2) + elev + dens_building + bog + CORINEF + Y + X	3394.76	18.65	0.00
9	Slope250 + sol_win + rugged25 + dens_main + snowmean + dfroad + I(dfroad^2) + elev + dens_building + bog + CORINEF + Y + X + Forestcover	3396.43	20.32	0.00
10	Slope25 + sol_win + dens_building + scdmroad + I(scdmroad^2) + dens_forest + dfroad + snowmean + X + water	3398.67	22.56	0.00

No.	Model selection summer	AIC	AICc	Weight
1	Bog + slope250 + sol_sum + dens_building	2764.89	0.00	0.34
2	Bog + slope250 + sol_sum + elev + dmroad + I(dmroad^2)	2766.04	1.15	0.19
3	Bog + slope250 + sol_sum + dens_building + Y	2766.46	1.57	0.15
4	Bog + slope250 + sol_sum + rugged250 + dens_building	2766.76	1.87	0.13
5	Bog + slope250 + sol_sum + dens_building + (1| Fyear)	2766.90	2.01	0.12
6	Bog + slope250 + sol_sum + rugged250 + dens_building + elev	2769.07	4.18	0.04
7	Bog + slope250 + sol_sum + rugged250 + dens_building + elev + Y + dfroad + I(dfroad^2)	2770.71	5.81	0.02

*Bog: distance to bog edge, sol_win: solar radiation in winter, elev: elevation, dmroad: distance to main road, dfroad: distance to forest road, Y: latitude, X: longitude, snowmean: mean snow depth, CORINEF: landcover type according to Corine (Copernicus open acces hub & European Environment Agency, 2018) **as factor, dens_main: density of main roads, dens_forest: density of forest roads, water: distance to nearest water source , rugged250: roughness on 250-pixel scale, Fyear: year as factor.**

For the interpolation of the moose pellet group density with co-kriging, I selected the two covariates

with the strongest effect, i.e., slope and solar radiation. The outcome of the map (*Figure 6*) showed moose pellet densities were more sporadically distributed over the area, compared to winter. The summer is characterized by a large number of small regions that are favoured or avoided. Compared to winter, pile densities are more evenly spread across the landscape.
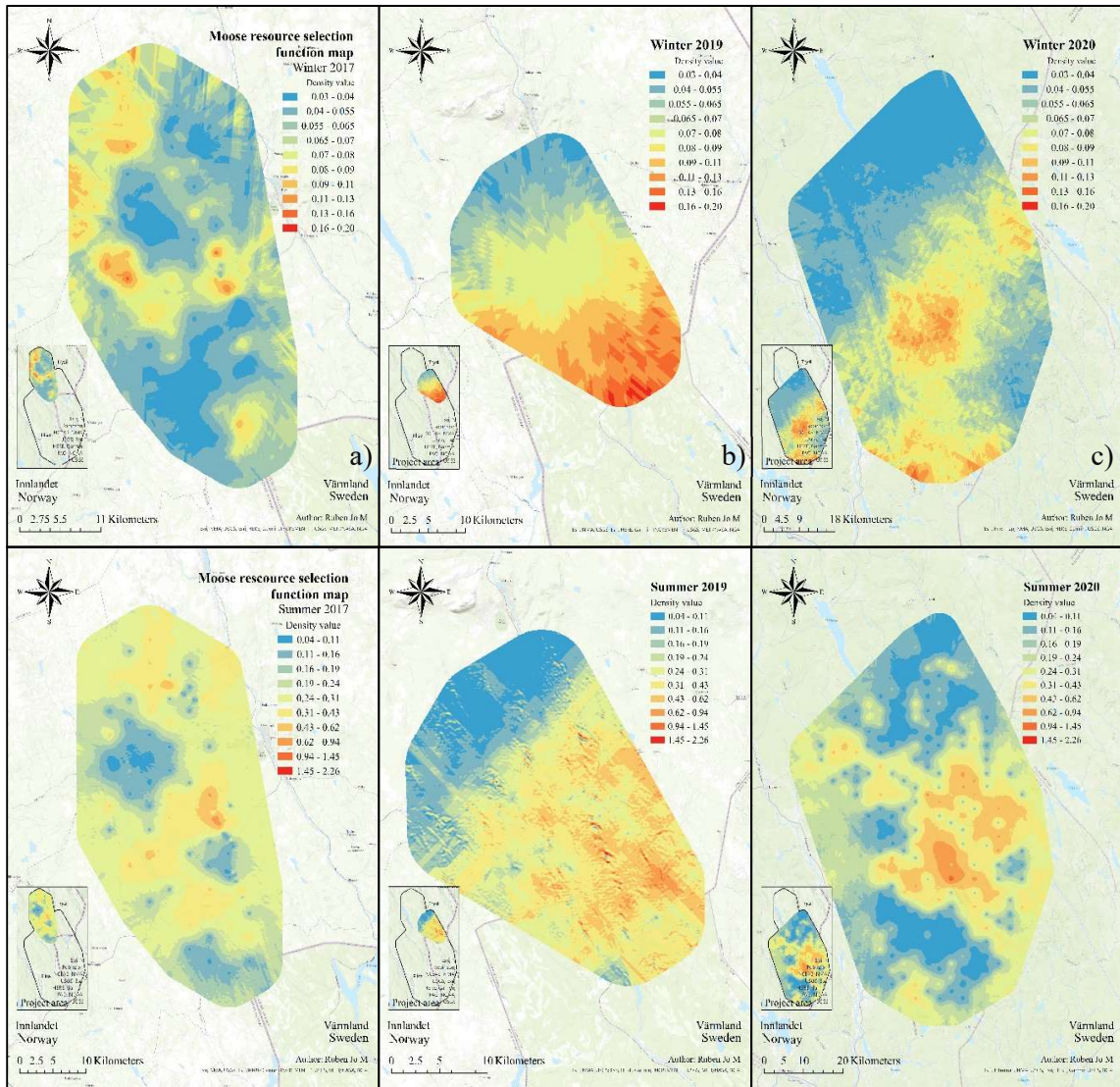

Figure 6: Moose density maps of all study regions, separated by seasons. Slettås region (a - b) sampled in 2017, Varåa region (c - d) sampled in 2019, and the Bogjuvvar region (e - f) sampled in 2020.

3.2   Wolf space use

We collected a total of 16953 four-hourly positions from the GPS collars during the entire observation period. The positions encompassed nine collared individuals representing five distinct wolf territories, which were monitored over six territory-years (twelve territory-seasons) because the Varåa territory was monitored in two consecutive years. The territories were covered by 153 to 428 hexagons, used to extract average position density from the kernel utilization distribution, and average resource values.

The total amount resulted in 1500 complete observations (hexagons), 856 for the summer season and 644 for the winter.

Kernel Utilization distribution

 The kernel distribution maps identified centers of activity for all wolf territories and seasons (Figure 7– Figure 10). However, the utilization distributions differed between seasons and wolf territories. In the Bograngen 2020, Slettås 2017 and Varåa 2019 territories, the positions were seemingly more spread out throughout the territory during summer than during winter. The positions still had a peak point at a certain location but also consist of various other highly utilized regions which were not closely located to the main center point. In winter however, the Kernel density shows that the majority of the positions were concentrated in a considerably narrower region, outside which other values were only visible in a low concentration. Specifically, the Slettås territory shows a high contrast between winter and summer, where the space use of summer was far more evenly distributed over the whole territory. In addition, in Varåa 2020 the wolves utilized the norther region of their territory more in summer and the southern region more in winter, while the Slettås territory space use was the exact opposite.
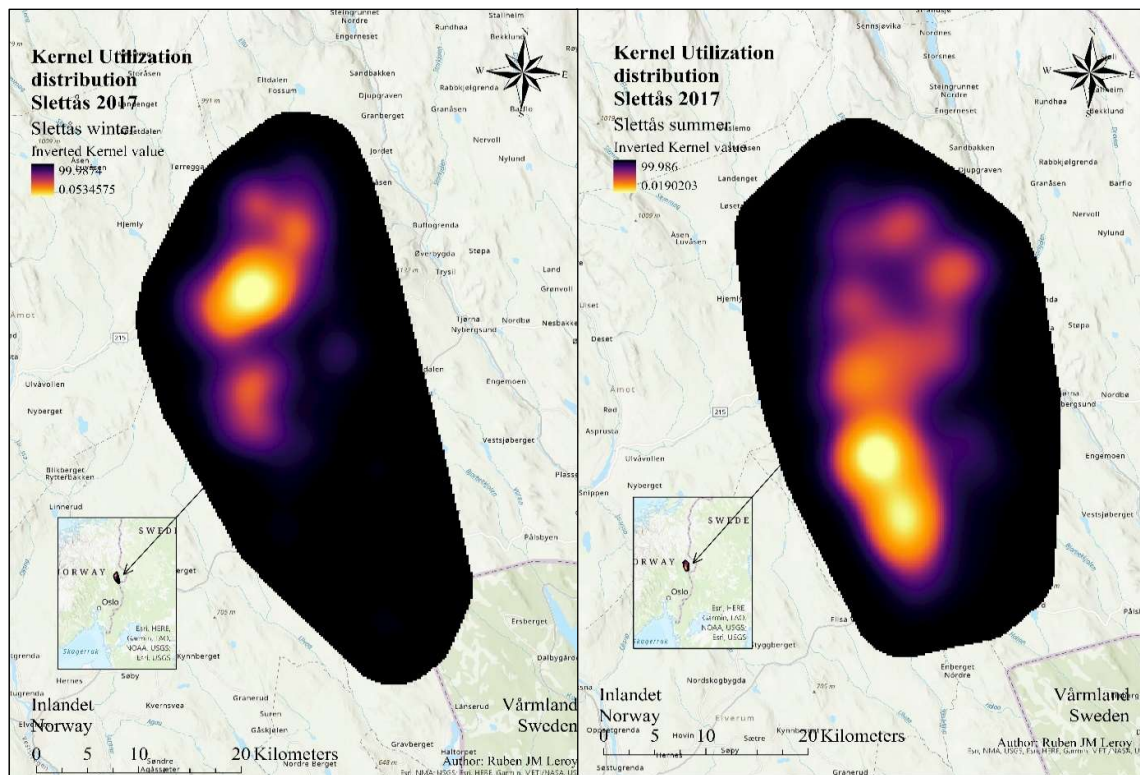
Figure 7: Kernel Utilization distribution of the wolf positions in the Slettås territory of 2017.
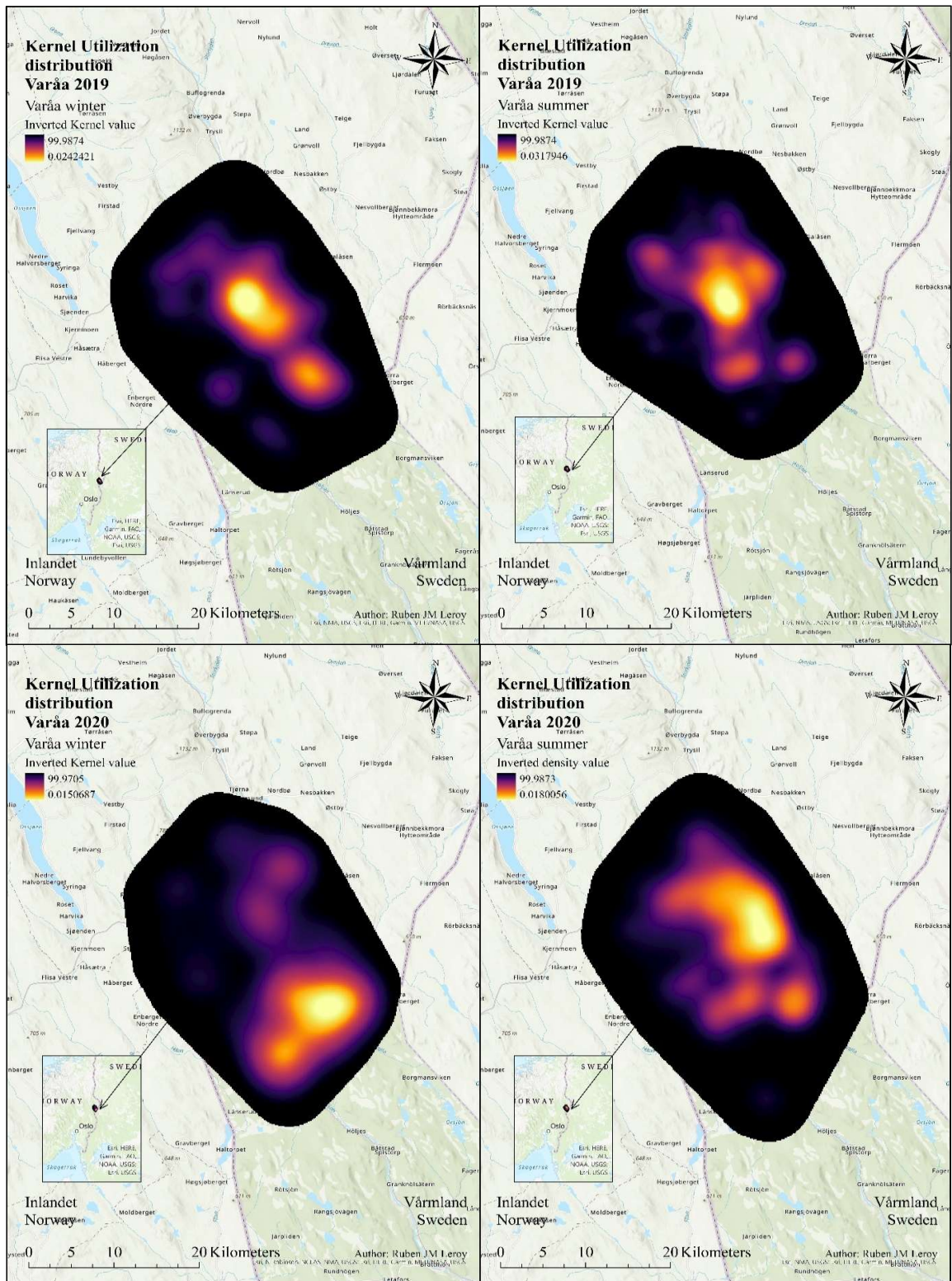
Figure 8: Kernel Utilization Distribution of the wolf positions in the Varåa territory during 2019 and 2020.
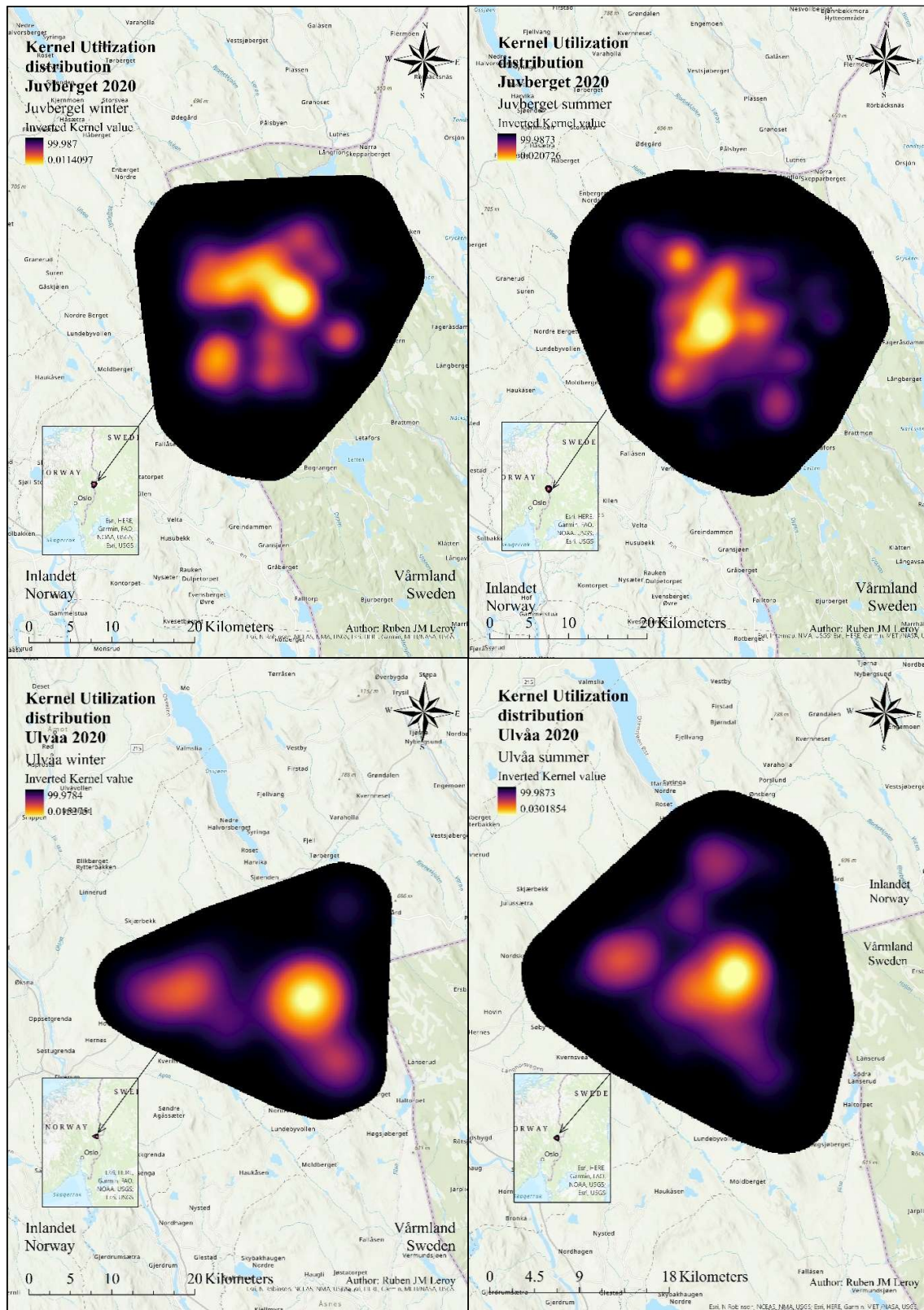
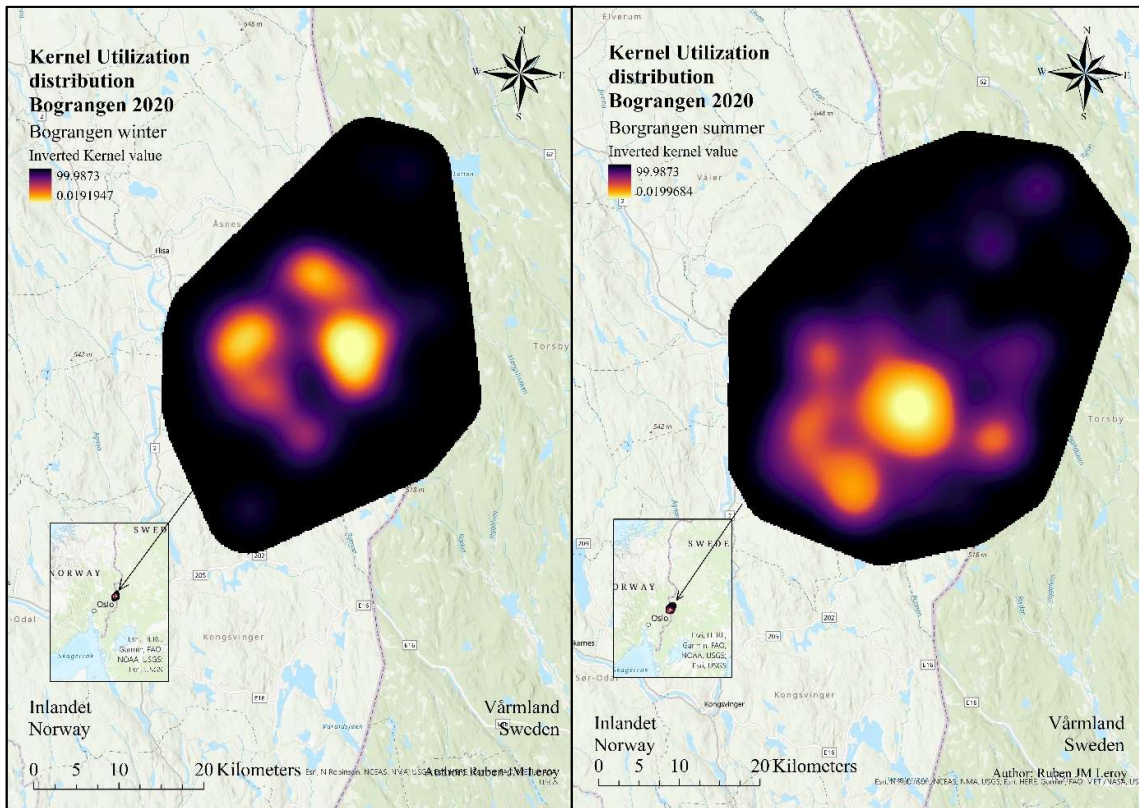*Figure 9: Kernel Utilization Distribution of the wolf positions in the Juvberget and Ulvåa territories during 2020.*

Figure 10: Kernel Utilization Distribution of wolf positions from the Bograngen territory in 2020.

Space use in winter

For the winter season, the best random structure was the inclusion of the territory, but not the year of study. The top model to explain wolf space use was the full model, including in descending order of effect size the proportion of young forest stands, the proportion of older forest stands, the elevation, and the densities of buildings, moose and roads (*Table 8*, *Figure 12*). The model selection also shows that inclusion of the moose density substantially improves the models, since the variable is present in the top models. In contrast to the summer season, model selection showed that the random factor of "Territory" proved to be most explanatory for the wolf utilization in the winter models.
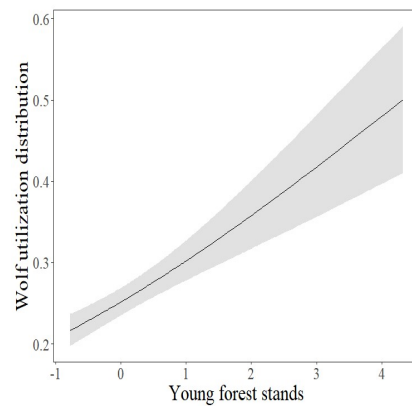
Figure 11: Plot of the estimate with the highest significance of the most explanatory winter model for the wolf utilization distribution.
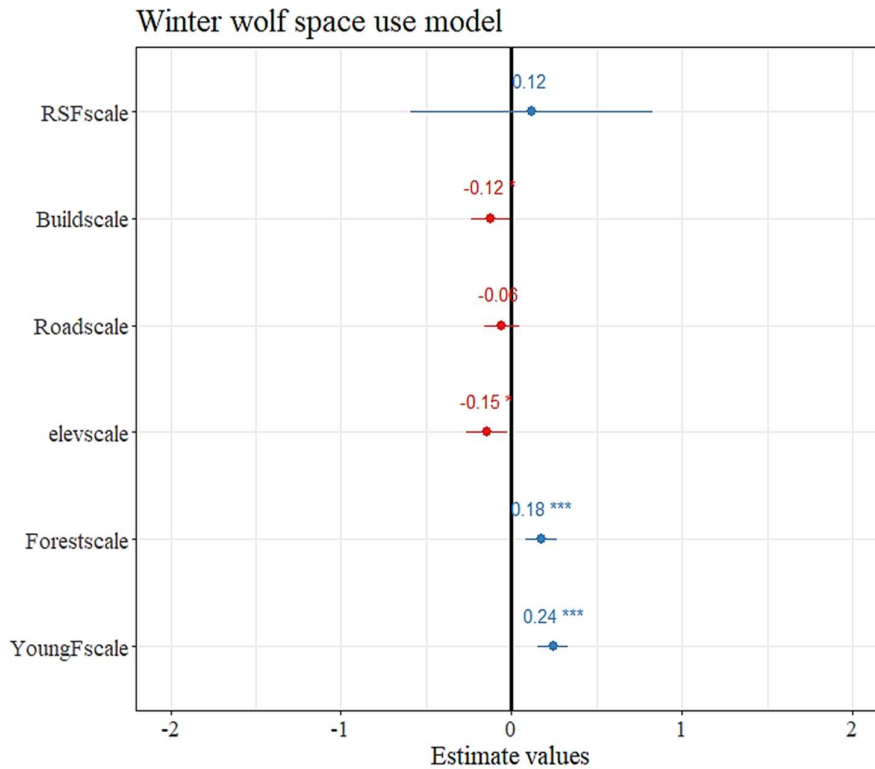
Figure 12: Forest plot estimates with SE of most explanatory model for wolf space use in winter. See Table 1 for variable description and Table 9 for detailed estimate values.

Table 4: Model selection for wolf space use in winter of all wolves throughout the study period. See Table 1 for further explanation of the variables.

No.	Winter model selection	Df	AIC	AICc	Weight
1.	Moosedensity + Builddensity + Roaddensity + Elevation + Young forest + Mature forest	9	-597.58	0.00	0.84
2.	Moosedensity + Builddensity + Roaddensity + Young forest + Mature forest	8	-594.15	3.43	0.15
3.	Moosedensity + Builddensity + Elevation + Young forest	7	-587.38	10.20	0.01
4.	Moosedensity + Builddensity + Young forest	6	-585.58	12.00	0.00
5.	Roaddensity + Builddensity + Young forest	6	-584.83	12.75	0.00
6.	Moosedensity + Young forest	5	-584.72	12.86	0.00
7.	Moosedensity + Builddensity + Roaddensity + Young forest	7	-583.59	13.99	0.00
8.	Moosedensity + Roaddensity + Young forest	6	-582.87	14.71	0.00
9.	Builddensity + Elevation	5	-569.21	28.37	0.00
10.	Moosedensity + Builddensity + Elevation	6	-567.24	30.34	0.00
11.	Builddensity	4	-562.55	35.03	0.00
12.	Moosedensity	4	-561.57	36.02	0.00
13.	Moosedensity + Builddensity	5	-561.43	36.15	0.00
14.	Moosedensity + Builddensity + Roaddensity	6	-561.30	36.28	0.00
15.	Moosedensity + Roaddensity	5	-560.08	37.51	0.00

The wolf space use can be best explained by the model that included all the variables for the winter season. In contradiction to the summer model, the moose density has a positive and insignificant effect on the wolf utilization. Additionally, moose density has a high uncertainty estimation according to the differences in standard error, compared with the other estimates of the model. Building density, road density and elevation revealed to have a negative effect on the utilization for the wolves, although the direction of the relationship between wolf area use and moose or road density is unclear, because the confidence intervals of the estimates include zero. The model estimates show that mature and young forest stands are significantly favored by the wolves. In addition, young forest stands have the most significant effect on the wolf space utilization distribution during the winter season. Compared to the summer model, the winter model shows to have less certainty of the variables but higher beta estimates.

Space use in summer

The best model structure to describe wolf utilization distribution during summer contained year as random factor and moose density, building density, road density, and young forest stands as fixed variables (*Table 5*). Moose density shows high performance in the models, as it is included in all the top models and performs well both in combination with other variables or as single variable for modeling. The negative relation in the summer model shows that wolf utilization was higher in areas

Table 5: Model selection of the wolf space use in summer for all study areas. based on 856 observations. For the summer models "Year" was used as random factor. see Table 1 for variable description and Table 9 for the estimation values of the best model.

No.	Summer model selection	Df	AIC	AICc	Weight
1.	Moosedensity + Builddensity + Roaddensity + Young forest	7	-732.20	0.00	0.40
2.	Moosedensity + Builddensity	5	-731.73	0.47	0.32
3.	Moosedensity + Builddensity + Roaddensity	6	-730.52	1.68	0.17
4.	Moosedensity + Builddensity + Roaddensity + Elevation + Mature forest + Young forest	9	-729.51	2.69	0.10
5.	Moosedensity + Roaddensity + Young forest	6	-723.10	9.10	0.00
6.	Moosedensity + Roaddensity	5	-720.11	12.08	0.00
7.	Moosedensity + Roaddensity + Mature forest	6	-718.56	13.64	0.00
8.	Moosedensity + Roaddensity + Elevation	6	-718.16	14.04	0.00
9.	Moosedensity + Roaddensity + Elevation + Mature forest	7	-716.64	15.56	0.00
10.	Moosedensity	4	-714.33	17.87	0.00
11.	Builddensity	4	-702.85	29.35	0.00
12.	Builddensity + Roaddensity	5	-702.11	30.09	0.00

with low moose density (*Figure 13*). In summer, wolves also spent more time in areas with low building density and a high proportion of young forest stands (*Figure 13*). Road density was also included in the best model, but the confidence interval of the estimate included 0, and therefore the direction of the relationship between wolf utilization distribution and road density is unclear (*Figure 13* or *Table 5*). The logistic regression analysis in *Table 5* shows that the moose density alone is not the best explanatory model. A combination of moose density with building density, road density and young forest stands proofs to form the most explanatory model for the wolf movement behavior. Remarkably, our most explanatory models show that all the explanatory variables from the best summer model are also present in the winter model, but with shifted significance form each variable. The best supported model, as seen in *Table 5*, revealed that the moose density and building density implied a significant negative correlation to the wolf utilization distribution. The model also included a significant positive effect towards young forest stands and an insignificant negative influence towards roads. All variables show a stable prediction as all of them have generally low standard errors. In the model selection of the summer, the second-best model came out on top using REML, and the same model had <2 values differentiation for the AICc, which made them practically similar
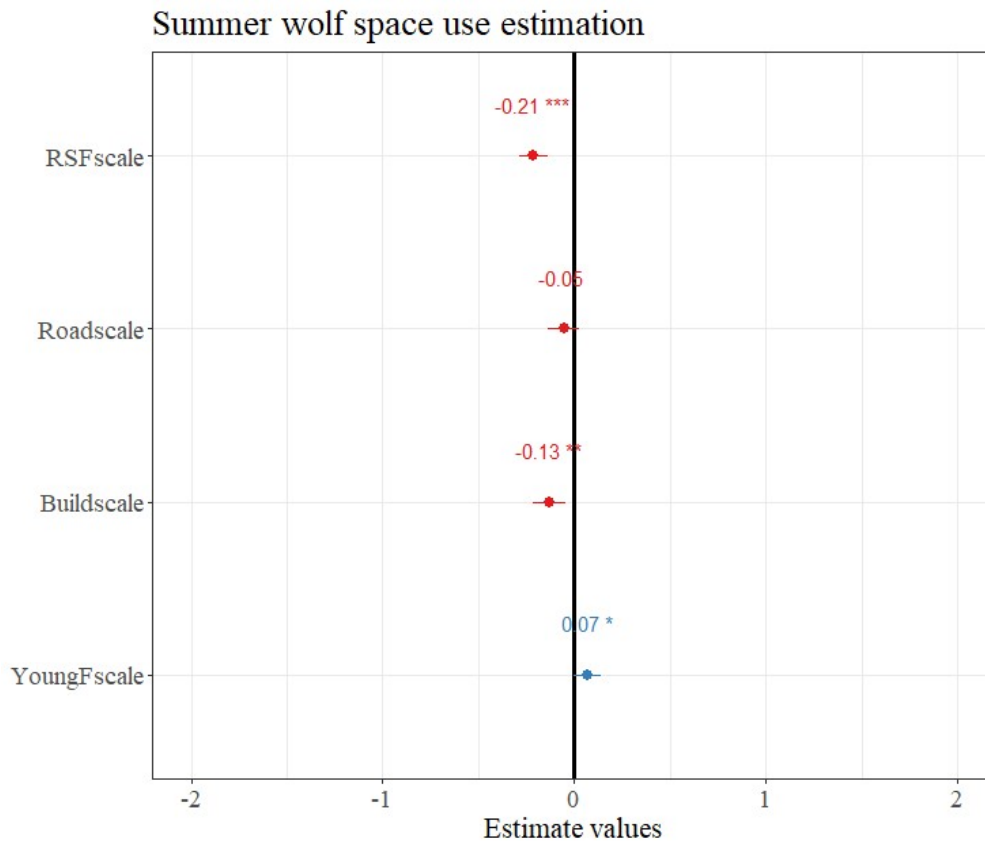
Figure 13: Estimate values of the most explanatory summer model for the wolf space use. See Table 1: Variable description for moose pile density and wolf space use modelling. Table 1 for variable description and Table 9 for full model estimation values.
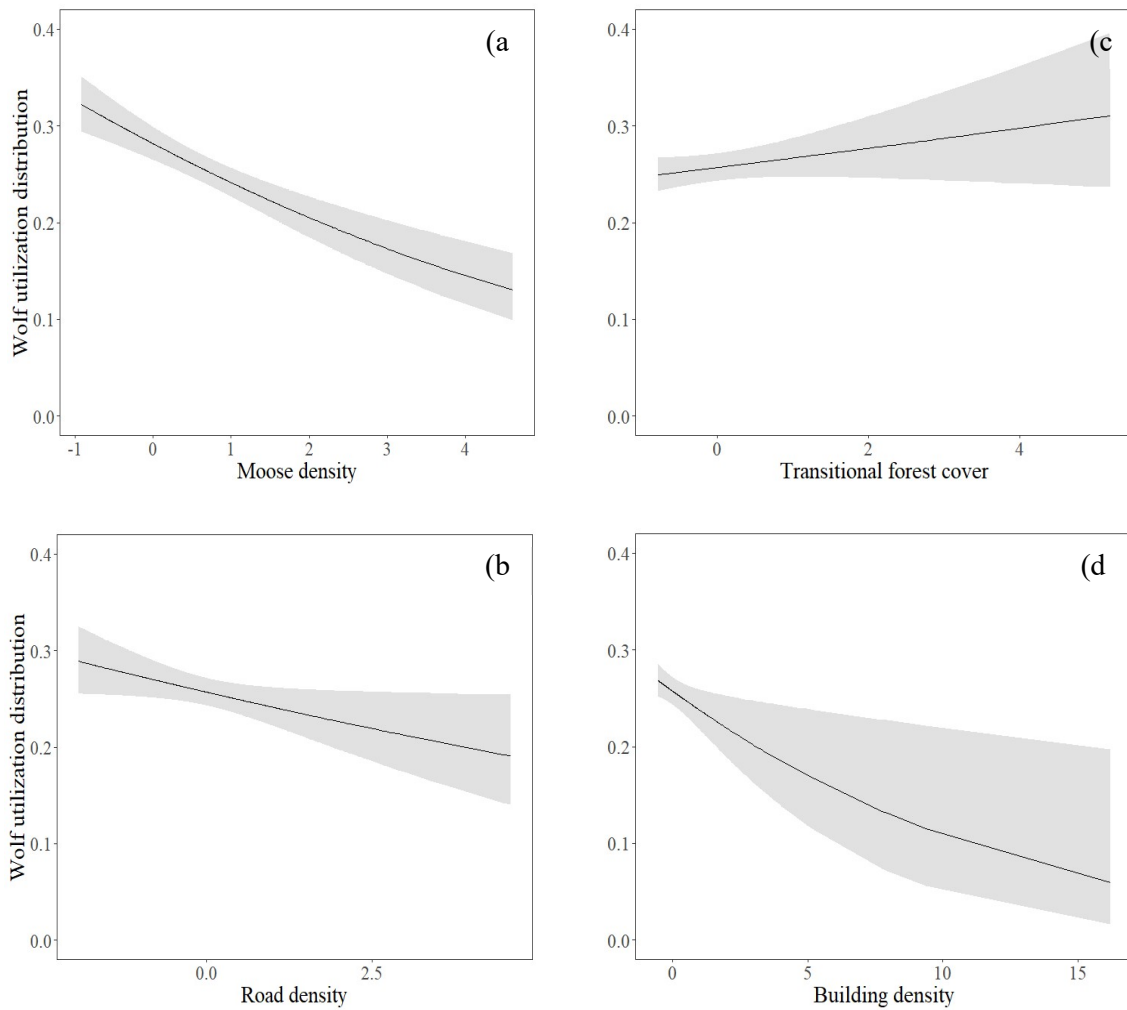
Figure 14: Prediction plots of wolf utilization distribution during summer as a function of moose density (a), road density (b), proportion of young forest stands (c), and building density (d). All variables are scaled for modelling. See Table 1for further variable description and Table 9 for detailed estimate values.

in data explanation(Akaike, 1973). However, due to the fact that the model including young forest performed a better fit than the one without, we selected the model with young forest stands.

4. Discussion

4.1 Moose density

In winter, the pile density of moose piles was highest in areas with little snow, high solar radiation, far from peat bogs, and at intermediate distance to main roads. In summer the pile density was also positively correlated with solar radiation and was higher in inclined compared to flat areas. Solar radiation affects local snow conditions in winter, with a shorter period of snow cover, less snow, and more compressed snow in areas of high solar radiation. Snow directly affects animal mobility (Dussault et al., 2005; Street et al., 2015) During snow cover in winter, snow depth and consistency determines how much browse is available to moose (McRoberts, Mech, & Peterson, 1995). In early summer, areas with high solar radiation are the first to green up and produce energy-rich shoots and leaves. Ungulates often follow the plant green-up from more southern exposed, lower elevations to more northern-exposed higher elevations to consequently make use of the most energy-rich plant shoots (Bischof et al., 2012; Merkle et al., 2016). I therefore expected solar radiation to be of minor importance in summer. Moose also had a preference for more inclined area than flat area. Inclined areas may contain drier and more diverse habitat types than flat areas which are mostly peat bogs in this study area. The preference for the inclined habitat might refer to the availability to vegetation that does not contain bogs, since bogs are rarely able to form inclined habitat. The model estimation and prediction could include deviation due to the fact that we are implementing a spatial distribution of moose densities based on pellet density rather than knowing the actual prey density of the region. Pellet density can result in bias in predictions if the space use of the moose is not related to the defecation rate of the animal. However, (Månsson, Andrén, & Sand, 2011) found that winter distribution of fecal pellet groups correlated well with the habitat selection of GPS-collared moose.

4.2 Wolf space use

Contrary to expected, wolf space use was not correlated with moose pellet group density in winter: although moose density was included in the top models to explain wolf space use, the direction of the relationship (positive or negative) was unclear. Even more surprising, the space use of the wolves in summer was negatively correlated to moose pellet group density.

I see three interconnected ways to explain this discrepancy from my original hypothesis: 1) Landscape of fear for moose; 2) Wolf behavior other than prey acquisition; and 3) Prey saturation.

As for explanation 1), the observed negative relationship between wolf space use and moose pellet group density may be a response of the moose to wolf presence rather than vice versa. In high-risk areas, prey animals can become more vigilant and respond in reduced time allocated to foraging (Fortin et al., 2005; Laundré et al., 2001). With increased predation pressure in areas of high wolf use moose may avoid to spend time in areas they perceive as high-risk during summer, and instead select to forage in areas of lower predation risk (Fortin et al., 2005; Laundre et al., 2009; Lima & Dill, 1989).However, in Scandinavia, moose have been considered naïve to the recently recovered wolf population (Berger, Swenson, & Inga-Lill, 2001; Kan Sand, Wikenros, Wabakken, & Liberg, 2005), and there so far there is little evidence for a behavioral response of moose to wolf presence.

A second explanation for the observed negative relationship between wolf space use and moose pellet group density is linked to the different behavioral states of the wolves. The wolf is a highly mobile species, and can therefore select the optimal habitat for its different behavioral states. While bedding or caring for young, wolves prefer concealed habitat and areas far from human disturbance (Llaneza et al., 2018; Sazatornil et al., 2016). Only while hunting and consuming prey, they might spend time in areas of higher moose densities. Wolves prefer to prey on moose calves both in summer and winter (Sand et al., 2008; Zimmermann, Sand, Wabakken, Liberg, & Andreassen, 2015). In summer, moose neonates are still small and can be consumed within a short time by an adult wolf pair and their growing pups, as seen by high summer kill rates. In the calving season, wolves kill about one calf per day, and towards autumn, the interval between killed moose increases to three days (Sand et al., 2008). Prey handling at the place where the prey was killed is therefore short but increases throughout the autumn and is longest during winter. However, also in winter, wolves spend most of the daytime in daybeds (Zimmermann, Wabakken, Sand, Pedersen, & Liberg, 2007). To explain wolf space use in relation to prey distribution in more detail, one would therefore have to differentiate between the behavioral states of the wolves, such as single travelling positions and clusters of non-travelling position, and divide them into day and night, which in this study was not performed. The outcome of the results at the observational scale might miss important information that changes the relationship between wolves and their main prey.

The third explanation for the observed negative relationship between wolf space use and moose pellet group density is a combination of explanation two and the overall prey density in the area. Scandinavia has one of the highest moose densities worldwide (Jensen et al., 2020; Lavsund, Nyrgén, & Solberg, 2003), and even the lowest moose densities found in parts of my study area may still be sufficient for wolves to successfully hunt and acquire prey.

Although I did not find a direct positive relationship between wolf space use and moose pellet group density, I found other explanatory variables of wolf space use that may indirectly relate to moose presence. In winter wolves selected for both transitional forest stands and mixed other forest stands over any other vegetation type. Due to the canopy cover of the forest, snow accumulation might be lower and form less thick snow crusts, wolves might be able to take advantage of this condition to hunt on prey when the snow crust is strong enough to support their movement trough forest while movement of moose gets hindered(Ball, Nordengren, & Wallin, 2001; Huggard, 1993). During summer, transitional forest stands are more preferred over any other vegetation type. This preference can indicate a hunting behavior that is focused on the use of habitat favored by the main prey of the wolf, possibly to increase the chances of encountering and killing them (Gervasi et al., 2013; Kauffman et al., 2007; Kittle et al., 2015). In both seasons wolves avoided human infrastructure, buildings more than roads(see *Table 8* and *Table 9*), which coincides with previous findings (Karlsson, Brøseth, Sand, André, & Jens Karlsson, 2007; Zimmermann, Nelson, Wabakken, Sand, & Liberg, 2014). This avoidance behavior of wolves could be beneficial for prey that can use these locations as possible refuge or additional browsing habitat due to the low predation risk.

In conclusion, I found that wolves adapt their space use towards environmental conditions, which is visible in a shift of space use over seasons. Furthermore, even though moose density might impose an influence on the space use of wolves throughout both summer and winter, the relation between the predator and its main prey shifts considerably over seasons. In summer, moose density was negatively related to wolf space use, which contradicts my hypothesis. The possible reason for this relation is a multitude overlapping factors between denning of wolves, landscape of fear, and short-term prey handling. While winter contrasts the relation between moose density and wolf space use, the insignificance shows that the space use is not influenced by moose. However, I found wolf space use is influenced by transitional forest stands, which indicate preference for habitat favored by the main prey. Finally, I found

that the space use of wolves is disturbed by anthropogenic influences, which causes the avoidance towards human infrastructure across seasons.

Future adjustments

Since the wolf space use models included the moose density model as a variable, the results of our wolf space use models have a base amount of unexplained variation and uncertainty included in their structure. Because our models use a grid system for quantifying the spatial parameters of the wolf territory, our models include a form of spatial autocorrelation that could cause bias in the results. The pack size influences in space utilization of the individual wolves, as packs can show shifts with more inhabitants. Space use is equally influenced when neighboring packs are present, which is present in form of at least one overlap with a neighbor in all of the packs in the study.

Since the GPS collars monitored every 4 hours, all the data allows only general statements to be made, on a course scale. Due to this limitation, information which separates long-term activities (e.g., resting, denning, territorial protection) from short-term activities, cannot be determined, giving a bias towards activities that consume more time (e.g., resting), compared to relative shorter time activities (e.g., hunting with fast success). In addition, since the GPS data has not been devided on specific times (e.g., night and day), further information is missing to form specific behavior. New wolves entered the research area, in addition to already existing territories that overlap each other. This can cause the wolves to use their space in relation to territory protection and maintenance(R. P. Peters & Mech, 1975; Schlägel, Merrill, & Lewis, 2017), which cloud have caused inaccuracies in our results and should be included in further research.

Finally, Seasonal estimation in prey density has a long temporal range, which only makes us infer that the densities were more or less present during the wolves' visitation to the high-density regions. Due to the large temporal scale, we cannot say much about how long local densities remained at the same spot or if the high-density spots are just more explained by frequent visits from different animals at different times instead of multiple at the same time.

5. Appendix

5.1 Moose pellet density model estimates

Table 6: Model estimates of the final model for explaining the moose pile count densities in winter of all study areas. Model is based on 2329 counts. "Winterdays" was used as offset, and site identification as random factor.

Winter model moose pellet density	Beta	SE	Z value	P value
Intercept	-6.57703	0.96642	-6.806	1.01e -11
Slope 250 Pixel	0.10171	0.07078	1.437	0.1507
Solar radiation	0.12724	0.06404	1.987	0.0469
Snow mean depth	-0.57495	0.14394	-3.994	6.49e-05
Distance to main roads	0.09521	0.08143	1.169	0.2423
Distance to main roads quadratic	-0.12663	0.05723	-2.212	0.0269
Coniferous forest	-0.30917	0.96862	-0.319	0.7496
Mixed forest	-0.88732	1.11911	-0.793	0.4278
Young forest	0.17646	0.97781	0.180	0.8568
Peat bogs	-0.63332	0.98045	-0.646	0.5183
Latitude	0.16429	0.13393	1.227	0.2200
Distance to bogs	0.13792	0.07024	1.964	0.0496

Table 7: Model estimates of the most explanatory summer model for the moose pile density in all of the study areas. "Summerdays" was use as offset, and site identification as random factor. The models are based on 2375 counts of response data.

Summer model moose pellet density	Beta	SE	Z value	P value
Intercept	-6.37514	0.070	-90.84	< 2e-16
Distance to bogs	0.08747	0.066	1.32	0.188
Slope 250 pixel	0.18770	0.066	2.85	0.004
Solar radiation	0.09597	0.060	1.60	0.109
Density of buildings	-0.07855	0.062	-1.27	0.205

5.2 Wolf space use model estimates

Table 8: Estimates of the best wolf space use model in winter. See Table 1 for variable description. All variables were scaled and included "Territory" as random factor.

Estimates winter model	Beta	SE	Z value	P value
Intercept	-0.91989	0.324	-2.838	0.005
Moose density	0.11743	0.362	0.324	0.746
Building density	-0.12215	0.058	-2.086	0.037
Road density	-0.05648	0.052	-1.094	0.274
Elevation	-0.14534	0.062	-2.338	0.019
Mature forest stands	0.17859	0.047	3.798	<0.001
Young forest stands	0.24410	0.044	5.536	3.10e-08

Table 9: Estimates of the best wolf space use model in summer. See Table 1 for variable description. All variables were scaled and optimized with REML. Year was included as random factor for all the summer models.

Estimates summer model 1.	Beta	SE	Z value	P value
Intercept	-0.84833	0.151	-5.626	1.84e -08
Moose density	-0.22772	0.038	-5.985	2.28e -09
Road density	-0.05680	0.041	-1.303	0.16942
Building density	-0.13189	0.043	-3.046	0.00246
Young forest stands	0.07392	0.0362	1.971	0.04156

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7. Figure list

8.　Table list