Inland Norway University of Applied Sciences

Faculty of Applied Ecology, Agricultural Sciences and Biotechnology

Christopher Johnsen Bronndal

Master thesis

Wolf Dens in Scandinavia at a closer look:

Characteristics and small-scale habitat selection

Master thesis in applied ecology

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Abstract

Wolves (*Canis lupus*) are born in an altricial state and require extensive care in the early stages of life as they are born blind, naked, and unable to hide. In their first weeks they stay around the den, and as such, the wolves' choice of den location is crucial to the survival of the pups. In this study, I collected data from 40 previously active wolf dens within the core breeding area in Norway and Sweden, where the wolves live in a mostly human-altered landscape with a vast road network due to commercial forestry. I investigated the role of the environment as concealment along with how human infrastructure impacts their choice of den sites and provide key characteristics of the different den types. For denning, wolves preferred steep areas and dense forest far from buildings at an intermediate distance from forest roads. Paved roads were never the closest road for any of the dens. Den types varied in structure, from boulders and overhangs, to excavated anthills and toppled tree roots. Most dens were selected in a way that provided shelter and some sort of concealment. Almost half (45%) of the dens were located in between or excavated under boulders, which would be hard to identify as dens for humans, thus providing an additional layer of concealment. In the immediate area surrounding the den, canopy and visibility proved to be the most significant for the wolves' selection of den sites. As they selected dense steep forest for their general denning area, they selected even denser and more concealed den sites. Variation in habitat selection among the different wolf pairs suggests an adaptive selection, and a possible trade-off between tolerating short term human presence and selecting good denning areas.

Keywords: *Canis lupus,* habitat selection, den site selection, concealment, humans

1. Introduction

Parental care amongst animals varies between species and is crucial for the survival of the offspring (Gaillard et al., 1998; Gross, 2005). Whereas some species produce large numbers of offspring but only provide simple forms of parental care, others will go to great lengths to raise them both in terms of nurturing and protection from predators and environment (Gross, 2005; Royle et al., 2012; Sibly & Brown, 2009). All mammalian species provide some form of parental care for their offspring, in the form of warming, feeding and protection (Gross, 2005; Royle et al., 2012; Wolff & Peterson, 1998). While most female mammals care for and protect their young alone, some carnivorous mammals exhibit some form of biparental care (Malcolm, 1985; Woodroffe & Vincent, 1994).

For birds and mammals, the developmental state of which they are born can be referred to as precocial or altricial (Derrickson, 1992). Precocial mammalian species are often able to see, walk, and hide shortly after birth (Fisher et al., 2002; Starck & Ricklefs, 1998), and following their parent while relying on hiding and protection is common among ungulate species across the world (Fisher et al., 2002). While still fully dependent on one or both of their parents, they require less parental care in the first weeks compared to altricial species born in a relatively helpless state (Starck & Ricklefs, 1998). In contrast, many mammalian carnivores (Carnivora) are often born in a somewhat altricial state, naked, unable to either see, run or hide for their first weeks (Derrickson, 1992; Starck & Ricklefs, 1998; Wolff & Peterson, 1998). This leaves them vulnerable to not only infanticide from conspecifics or predation from other species, but also environmental risks such as weather and insects (Norris et al., 2002; Sidorovich et al., 2017; Wolff & Peterson, 1998). To mitigate the dangers and increase the success of survival for the offspring, species may select for specific areas within their home range or territory during this period. (Bowyer et al., 1996, 1999). Many species also select or build structures, such as nests or burrows, to keep the offspring warm and safe (Boggs et al., 1984; Deeming, 2023).

Denning is widespread among several mammalian carnivores, especially canid species when rearing young (Malcolm, 1985; Mech & Boitani, 2003). Larger social canids such as coyotes *(Canis latrans*), dingoes (*Canis lupus dingo*) and wolves (*Canis lupus*) all exhibit forms of territoriality and denning behavior for protecting offspring in addition to resource availability (Gese & Ruff, 1997; Harrington & Mech, 1978; Thomson, 1992). Regardless, dens serve the same purpose. They provide shelter, concealment, and protection for their pups in the early stages of life. Den site selection is often a trade-off between access to food and water, and the risks from competition and predation. For example, African wild dogs were found to spatially avoid lions by selecting den sites away from places commonly traversed by lions such as roads and waterholes (Van der Meer et al., 2013), and brown bears selected more concealed den sites when denning close to human activity, probably due to the perceived risk of humans as predators on bears (Sahlén et al., 2011). These are common local spatio-temporal adaptations by species inhabiting and reproducing within their home range (Nisi et al., 2022).

The wolf and its subspecies are widely distributed across the world and is found in a wide range of habitats, ranging from mountains and deserts to tundra and forests (Mech & Boitani, 2003). Thus, they are a highly adaptable species capable of surviving and reproducing in diverse climatic conditions and environments, feeding on most animals from rodents to moose, and even marine life in coastal areas (Mech & Boitani, 2003; Peterson & Ciucci, 2003; Philips et al., 2003). Wolves have been persecuted across the world for their depredation on livestock and competition for game species, but since the 1970's they have recolonized parts of their former range both naturally and by human reintroductions (Chapron et al., 2014). On the Scandinavian peninsula (i.e. Norway and Sweden), wolves were considered functionally extinct by 1966 until the first confirmed reproduction in 1978 (Wabakken et al., 2001a), and their behavior, dispersal, habitat, and prey selection have since been studied extensively (Carricondo-Sanchez et al., 2018; Karlsson et al., 2007; Nordli et al., 2023; Zimmermann et al., 2015).

Wolves' habitat selection occurs at multiple spatial scales; habitat availability at the landscape scale affects where they establish a home range. At a more regional scale, habitat availability is a determinant of the wolves' area use within their home range, and at a local scale, habitat can direct the wolves' selection of travel routes, bed and denning sites (Johnson, 1980; Zimmermann et al., 2014). After individual dispersal from their natal packs, wolves search for a potential mate, and either together or by themselves, seek out available areas to form a new territory (Mech & Boitani, 2003; Rothman & Mech, 1979). Together, they make up a monogamous territorial breeding pair (Mech & Boitani, 2003), and in Scandinavia, their mating season takes place from late February to early March, with a median birth date 1st of May (Nordli et al., 2023). Wolves as a top predator have few, if any natural predators, especially in Scandinavia except for humans (Ordiz et al., 2013). Still, examples from North America have shown that they are susceptible to infanticide or competition from conspecifics (Smith et al., 2015), and competition in Scandinavia from larger predators such as brown bears when sympatric (Ordiz et al., 2015). Two studies from North America by Ciucci and Mech (1992), and Ballard and Dau (1983), both found dens to be located relatively central within their territory. In terms of intraspecific competition, this could mitigate the risk of encountering neighboring packs closer to a potential overlapping territorial buffer zone (Mech & Boitani, 2003), and reduce human presence. For either reason, the selection of den sites is an important step in protecting the pups, whether it be from disturbance, environment, or competition of any form. Even though the wolves have returned and for many represents wilderness, they today live in a human-altered landscape and select their territory accordingly (Ordiz et al., 2015).

While repeated exposure from human activity and people can lead to wolves being more habituated towards humans (Heilhecker et al., 2007; Thiel et al., 1998a), wild-living wolves in general are thought to have low tolerance of human activity, especially in proximity to dens and pups (Thiel et al., 1998a). Though wolves in Norway and Sweden was found to use gravel roads for travel, particularly during night hours, road use by breeding wolves was lower than proportional to road availability (Zimmermann et al., 2014). This behavioral bias towards using roads during nighttime to avoid human encounters have been documented in Denmark (Sunde et al., 2023), Canada (Hebblewhite & Merrill, 2008) as well as entering villages and cities in Europe during night (Fuller et al., 2003). The results of a study from Scandinavia showed that wolf pairs avoided areas close to humans if human exposure was high in their natal territory (Milleret et al., 2019a), and Finnish and Polish studies found wolves to select breeding areas away from human infrastructure (Kaartinen et al., 2010; Theuerkauf et al., 2003). Generally, the Scandinavian wolves are found to avoid humans, and several studies have shown the anthropogenic effects on wolves' habitat and prey selection (Eriksen et al., 2022; Ordiz et al., 2015). Despite wolves being reported to tolerate human presence where human activity is high, the Scandinavian population is under strict management while also prone to illegal hunting (Liberg et al., 2011; Wabakken et al., 2001a), in a landscape with a vast network of forest roads, and consequently the wolves inhabit a landscape easily accessible by their primary threat – humans.

As to be expected from highly adaptable species such as the wolf, previous research has shown that dens come in a variety of different forms, such as ditches, caves, hollow trees, sand banks, dirt mounds, older dens used by other species (Person & Russell, 2009a; Stephenson, 1974), and even generational dens (Mech & Boitani, 2003). While the selection of den sites by wolves has been studied in great detail at multiple scales in North America, less research has been done on a smaller scale in Norway and Sweden. In this study, I will focus primarily on the wolves' choice of habitat when selecting natal den sites in a human altered landscape at two spatial scales: 1) Selection of denning habitat within the territory, hereafter referred to as denning area, and 2) micro-habitat selection within the denning area. Due to the impact and perceived threat of human presence, I hypothesize that:

H1. Wolves select their denning areas away from human infrastructure, and that
H2. Shelter and concealment are the most important factors at a micro-habitat scale.

Based on my first hypothesis, I predict that **P1**: Den site selection is negatively affected by the presence of buildings and roads, as both are indicators of human activity. For my second hypothesis, I predict that **P2**: wolves select for breeding areas in dense forest providing concealment. Separating the selection between denning area and the microhabitat in immediate vicinity of the den, I predict that **P3**: high canopy cover and low visibility have a positive effect on den site location, thus being more important on a micro-habitat scale. Finally, I predict that besides protecting the pups against abiotic factors **P4**: the structure of den type also provides concealment from potential predation.

2. Methods

2.1 Study Area

The study area is located within core parts of the Swedish-Norwegian wolf population's range and breeding area across the border. The study was conducted in Inland County in Norway, and Värmland, Dalarna, Jämtland and Gävleborg County in Sweden (Fig. 1). Boreal coniferous forest dominates the study area, with Scots Pine (*Pinus sylvestris*) and Norwegian spruce (*Picea abies*) as the most common tree species. In addition to wolves, bears, wolverines (*Gulo gulo*), Eurasian lynx (*Lynx lynx*) and golden eagle (*Aquila chrysaetos*) are all present. Moose (*Alces alces*) is the most common wild cervid species and the wolves' main prey, and roe deer (*Capreolus capreolus*) is found in most parts of the study area (Zimmermann et al., 2015). Due to extensive commercial forestry, the area has a vast network of unpaved forest roads four times higher than public paved roads in the region (Zimmermann et al., 2014). For the same reason, substantial portions of the forest on the Swedish side of the study area consists of young trees planted after harvest.

A large number of bogs, smaller rivers and lakes are present throughout the study area. Combined with human alterations and land use, the study area can be characterized by its mosaic landscape. Most of the region is sparsely populated, with a large portion having less than 1 person per km^2 compared to the average human density in Scandinavia of 17 inhabitants per km^2 (Mattisson et al., 2013; Wabakken et al., 2001), and an average house density within the wolf territories at 3 per km^2 (Zimmermann et al., 2014). The northern and central part of the study area is characterized by its hilly topography and its more mountainous border region, whereas the southern part is flatter, interspersed by hills and smaller ridges in the landscape. The region's intercontinental climate is characterized by its cold and dry winters with snow lasting for 3-6 months from November to April (Zimmermann et al., 2015).

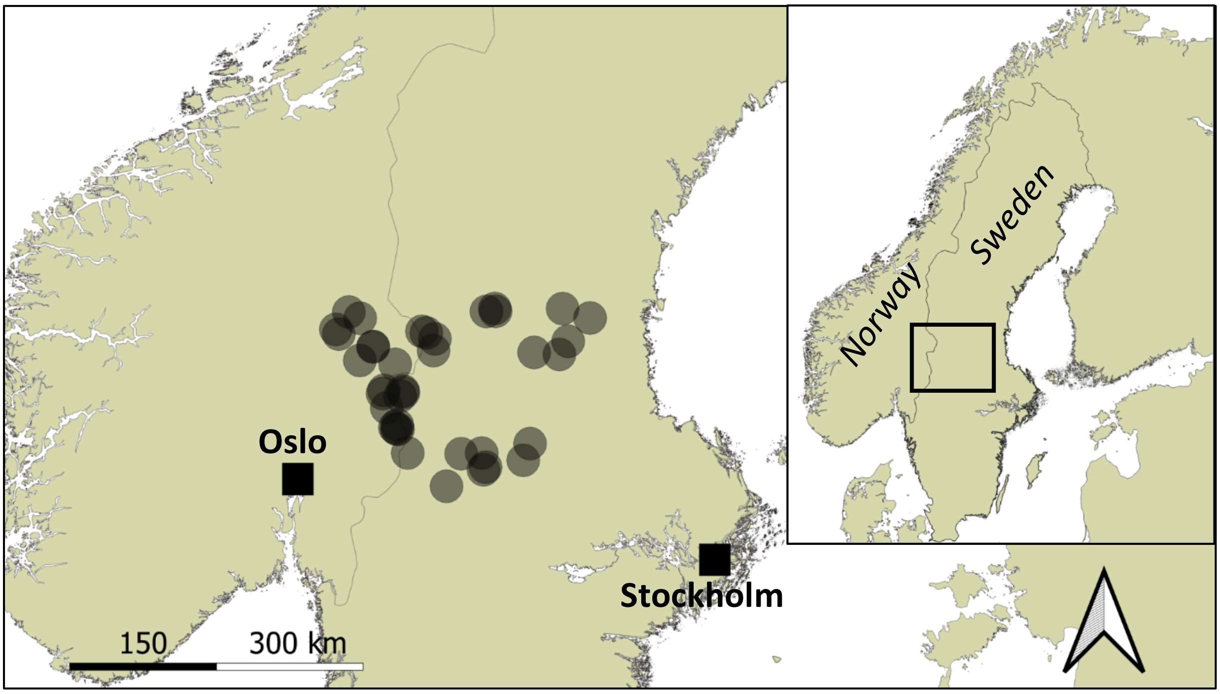

Figure 1. Visited wolf dens (black) within the study area on the Scandinavian Peninsula. 23 dens were in Sweden and 17 in Norway. Dens were active between 2007 and 2023.

2.2 Data Collection

Data collection took place between June 1st – September 9th, 2023, where I visited and collected data from 40 previously active wolf dens in Norway and Sweden (Fig. 1). All dens in Norway (n=17) were in Innlandet county, while the dens in Sweden (n=23) were distributed among the previously mentioned Swedish counties. All dens were confirmed as active during previous den checks by researchers of the Scandinavian Wolf Research Project SKANDULV or managers of the national county administrations. The year in which the dens were active varied, ranging from 2007 to 2023. Arriving at the den site, I placed it in one of the predefined categories: **1**. Boulders/caves, **2.** Under or by tree roots**, 3.** Anthill, **4.** Sand/gravel, **5.** Pitch/sink, **6**. Den used by other species, or **7**. Den not visible.

Canopy cover (%) was then measured 60 cm above ground at the den entrance using the HabitApp application on a Samsung Galaxy Tab 10.1 T M (Samsung Electronics, 2016) tablet, with a minimum of three pictures taken both horizontally and vertically. If the percentage varied more than five percent, more pictures were taken. The application turns the photos into black and white images to calculate the percentage of shade from the black pixels out of the total number of pixels in the image (Spedener et al., 2019). As the different black and white images were different from the original photo based on time of day, lighting, skies and canopy, the cut-off was adjusted for each picture to best represent the original. The mean percentage of the canopy cover from the photos were used in the analysis. Ground cover types recorded was based off the most common types expected to be found in Norway and Sweden and were measured visually for each category (Tab. 1) within a 1.78-meter radius ($10m^2$ area around the den). The forest was categorized based on age (Tab. 1).

Table 1. Variables collected during field work and from digital maps, to describe wolf selection of den sites in Scandinavia.

Variable	Variable type	Values (classes)	Source
Canopy cover	Continuous	% cover	Field registration
Ground cover	Compositional	In 10^m2 plot centered at the den: % Sand/gravel, % Heather, % Moss/lichen,% Shrubs, % Rocks, % Grass, % Deadwood	Field registration
Dominant tree species	Categorical	Speuce, Pine, Birch	Field registration
Forest type	Categorical	Mixed age, evenly aged	Field registration
Forest age	Categorical	**1**. Fresh clearcut, ready for planting and regrowth, **2**. Young forest before first thinning (trees up to 10-12 m), **3**. Young forest in thinning stage, **4**. Forest ready for harvest, and **5**. Old-growth forest (forest older than normal harvest size)	Field registration
Visibility	Continuous	Distance (m) walked from den before loosing sight of cylinder	Field registration
Water < 10m	Categorical	Water source within 10 m: Bog, stream, Spring, Pond	Field registration
Elevation	Continuous	m above sea level with 30 cm cell size	Copernicus Elevation Model
Slope	Continuous	Degrees	Digital elevation model
Distance to road	Continuous	Meters from den to closest road	Lantmäteriet and Kartverket
Distance to building	Continuous	Meters from den to closest building	Humanitarian Data Exchange

The most abundant (i.e. dominant) tree species were registered as spruce, pine or birch, along with the forest type (Mixed age or evenly aged). I searched for potential water sources within a 10 m radius from the den site, and if found, they were categorized as either Bog, Spring, Stream or Pond. Lastly, I checked the visibility in each cardinal direction from the den using a red and white cylinder (see Ordiz et al., 2009) placed at the den entrance (Fig. 3). A compass and Garmin GPS were used to as accurately as possible keep the correct direction when measuring. The GPS was used to determine the distance, extending a maximum of 50 meters from the den. The distance was measured up to the first point where I lost sight of the cylinder. For each den, four control points were checked, and the same data collected as the den sites, excluding den type (Fig. 2). During the preliminary testing of the field protocol in June, a distance of 50 meters from the den to control point was determined to be sufficient. This was due to the two first dens both being in hillsides, leading to 50 meters being a far enough distance to see a change in habitat type on a vertical gradient. On a horizontal gradient, the vegetation and forest didn't change until beyond 100 meters. In flatter areas the same distance was also sufficient due to the mosaic landscape within the study area. In addition to the mentioned micro-habitat variables, the distance between dens and closest gravel road, and distance between den and closest building were extracted from QGIS (3.34.3). I noted down the general topography surrounding the denning area (100-meter radius) as either inclined, rugged, or flat. More accurate data on the topography was later extracted from a digital elevation model with 30 m pixel size using ArcGIS Pro 3.0.2 (© Esri Inc. 2022) to be used in the analysis.

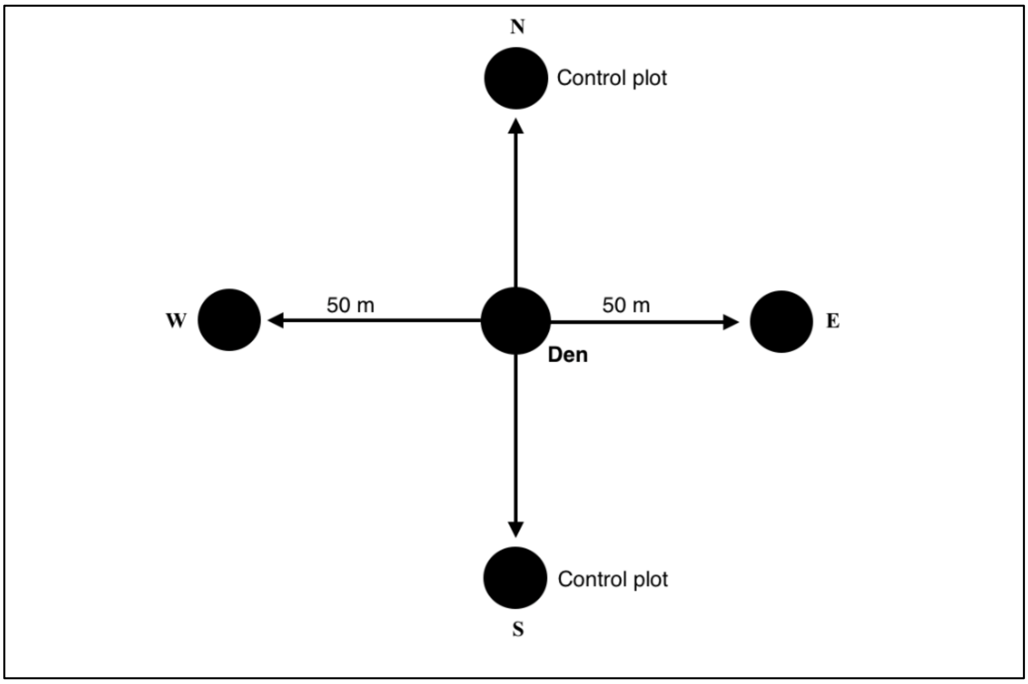

Figure 2. Data sampling method for microhabitat. The den located in the center with each control plot 50 meters away in each cardinal direction.

Figure 3. Cylinder placement at the den entrance (red circle) used to measure visibility.

2.3 Analysis

2.3.1 Selection of denning area withing territory

The distance to the nearest roads and buildings were measured using QGIS (3.43.3). Given the average Scandinavian wolf territory size of approximately 1000 km^2, (Mattisson et al., 2013), 1000 random points were generated within a buffer with a 17 km^2 radius (907 km^2) for each den. I then extracted distance to nearest road and building for each den and random points using QGIS. Paved roads were excluded from the analysis, as they were never the closest road. The analysis includes all gravel roads present on the map within these buffers; thus, I did not distinguish between overgrown, unused roads and frequently used roads. Similarly, all buildings, including unused and rundown cabins or barracks potentially on the map were included in the analysis. It is worth noting that some of the roads might have been made during forestry operations between the first den check and my data collection.

I used logistic regression in a Generalized Linear Mixed Model GLMM framework to examine habitat selection. The binary response variable was den site (1) versus random points (0), and the explanatory variables were distance to road, distance to buildings, elevation, slope, and tree density. DenID was included as random factor to account for non-independence of observations within packs. Although the random factor did not significantly alter the model estimates, I kept it to appropriately model the structure of the data (case-control design, 1 den versus 1000 random points per wolf denning year). Random points generated on lakes were removed prior to the analysis as it didn't represent suitable denning habitat. The tree density used in the analysis was extracted from Copernicus and is representative of the condition of the forest in 2018. I used backward selection and chose the most parsimonious model. While included in the analysis, observations with values greater than the 99th percentile (quantile) were considered outliers and excluded from the prediction plots. I used AIC model selection and chose the most parsimonious model.

2.3.2 Micro-habitat analysis

For the analysis of micro-habitat, I removed five of the total 40 dens prior to modeling: Two due to missing field data (Julussa2014, and Aaamack2008), one due to it being a secondary den (Julussa2015), and two due to forestry operations in the area after the initial den check (Galven2009, and Tandsjön2012). These cases of clearcutting altered the area in such a way that no representative forest and vegetation were left during the data collection. For Julussa2014 and Julussa2015, I checked their secondary den in addition to the primary dens. To avoid multiple dens from the same pair influencing the results of the analysis, Julussa2014's primary den (missing data), and Julussa2015's secondary den was removed prior to the analysis.

I used logistic regression in a GLMM framework to contrast the habitat at the den (1) to the habitat at the four control points (0). This binary variable was entered as response variable. Again, I entered den-ID as random factor to account for the case-control design of the study. Due to my sample size (n=35) and the low degrees of freedom, I tested multiple models with combinations of three explanatory variables. Models including topographical variables were tested separately from models with environmental variables, before testing combined models with both types, with and without canopy and visibility (Tab. 2, Supplementary Table S1).

I used AICc model selection to correct for the small sample size, and explanatory variables in the models were checked for multicollinearity using VIF from the 'car' package. The variables showed no sign of multicollinearity (VIF < 1.7). Lastly, I did not include the ground cover variables in the final analysis, as I deemed them to be more representative of how it would look after the den was active, rather than before they chose the location. I followed the protocol outlined by Zuur et al (2010) for exploration of data and validation of my models. Generalized Linear Mixed Models used in the analysis were fitted with the 'glmmTMB' package in R.

Table 2. All models with tested combinations of variables.

Model	Canopy	Visibility	ForestAge	ForestType	TreeSpecies	Water	Elevation	Slope
Topogeographical models								
Mod 1							*	*
Environmental models								
Mod 1			*	*		*		
Mod 2				*	*	*		
Mod 3			*		*	*		
Mod 4			*	*	*			
Mod 5		*	*			*		
Mod 6		*		*		*		
Mod 7	*			*		*		
Mod 8		*	*	*				
Mod 9	*			*	*			
Mod 10	*				*	*		
Mod 11	*		*	*				
Mod 12	*		*			*		
Mod 13	*		*		*			
Mod 14		*	*		*			
Mod 15		*			*	*		
Mod 16		*		*	*			
Mod 17	*	*				*		
Mod 18	*	*		*				
Mod 19	*	*	*					
Mod 20	*	*			*			
Mixed models without canopy and visibility								
Mod 1			*	*	*			
Mod 2			*		*	*		
Mod 3				*	*	*		
Mod 4			*	*		*		

3. Results

3.1 Den types and environment

The most common den types were ‘Boulder / caves’ (45%) and ‘Under or by tree roots’ (17.5%) (see Table 3 for complete summary). The ‘Boulder/caves’ dens varied in structure, with some being natural cave-like openings in rock formations or overhangs, while others were dens excavated beneath large boulders (Fig. 4-5). Dens categorized as ‘Under or by tree roots’ were in some cases beneath the roots of a toppled tree, creating a sheltered space (Fig. 4C). In other cases, the den was at the base of a standing tree, with the tree’s branches providing a canopy of cover for the den (Fig. 5C). ‘Anthill’dens (10%) showed variation as well. Two of the dens were dug out in a similar manner to some bear dens (Fig. 5B), while the other two were open at the top with the ridge of the anthill providing shelter (Fig. 4B). Only two dens were excavated in sand (Fig. 4D), and one den was previously used by a bear (Fig. 5D, See Supplementary S1 for more detailed den picture). Signs of previous wolf activity, such as older excavations in the soil and older remnants of prey (i.e. bones) were observed at several of the den sites. In some cases, well-trodden paths were still discernible around the den. The presence of nearby water sources varied between dens and control plots. Seven dens (17.5%) had a water source within the 10-meter radius, compared to 37 at the control plots. Matching the plotID’s to its corresponding den, thus increasing the radius to 60 meters, showed that 18 dens (45%) had a water source in nearby vicinity of the denning area.

The following results described are from the dens (n=35) used in the analysis. Spruce was the predominant tree species surrounding both den sites and control plots. It was most common at 80% of the den sites, and 60% of the control plots. Pine was the second most common species, with 20% at dens and 27.8% at the control plot. The last 12.9% at the control plots were birch. Dens located in mixed-age forests counted 28 (80%), while seven (20%) were in evenly aged forest. Similarly, 111 control plots (79.28%) were in mixed age forest compared to 29 (20.71%) in evenly aged forest.

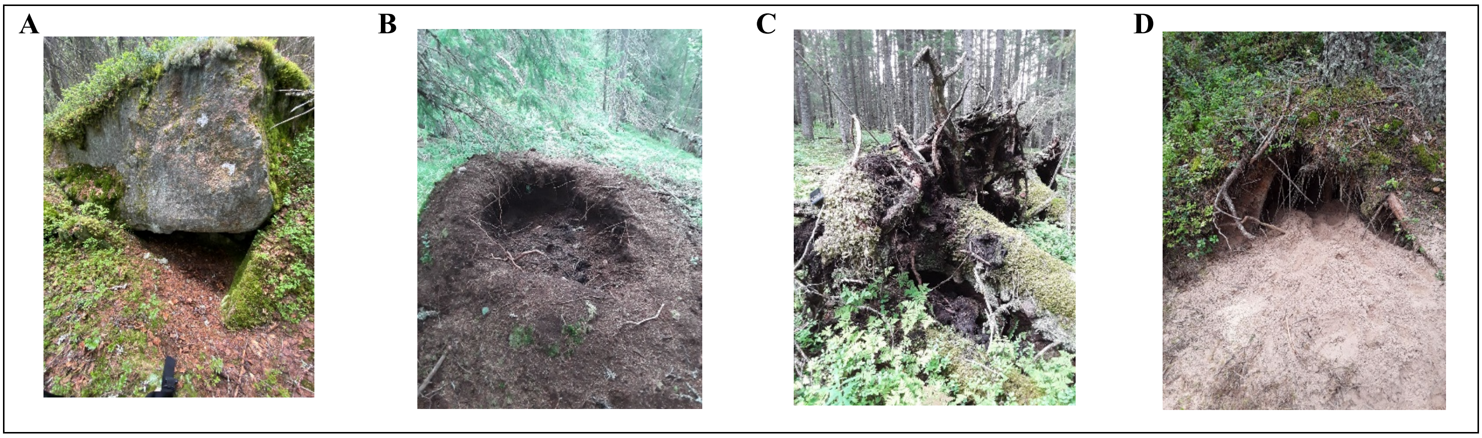

Figure 4. Variation in den types. **A)** Den dug out beneath a boulder. **B)** Open anthill. **C)** Under fallen tree root. **D)** Den excavated in sand /gravel.

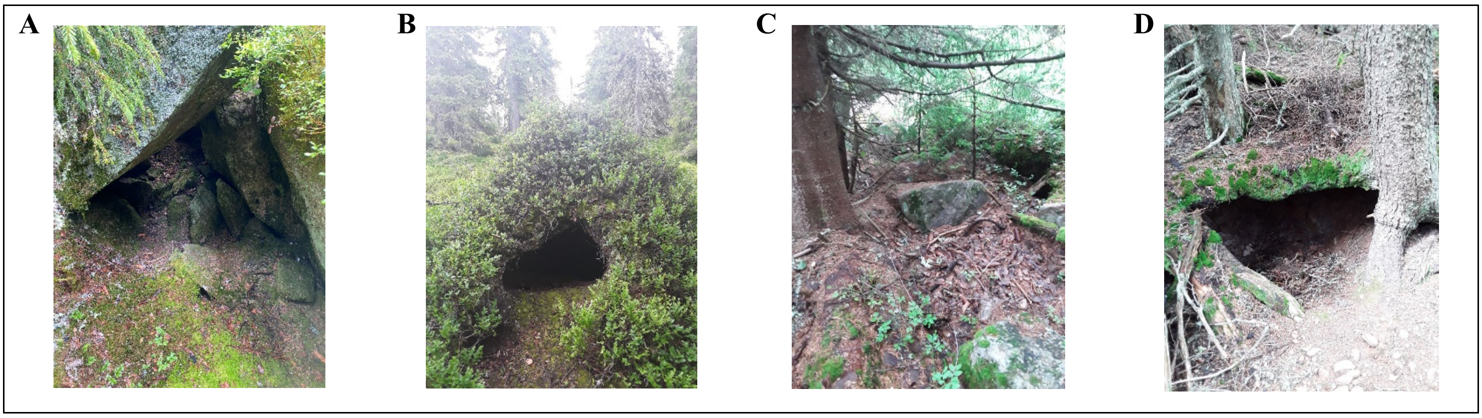

Figure 5. Variations in den types. **A)** Natural cave opening between boulders. **B)** Den in anthill in similar style as some bear dens. **C)** By tree root/base of tree. **D)** Den previously used by bear.

Table 3. Summary of the different den types including all visited dens.

Den types	Number of dens	Percentage
Boulder /caves	18	45 %
Under or by tree roots	7	17.50 %
Anthill	4	10 %
Sand / gravel	2	5 %
Pitch / sink	1	2.50 %
Den used by other spec	1	2.50 %
Den not visible	7	17.50 %
Total	**40**	**100 %**

3.2 Selection of denning areas within wolf territories

The denning areas (n=38) had a mean distance of 2961 meters to the closest building and a mean distance of 558 meters to the closest road (Fig. 6). In comparison, the mean distance from random points to the closest building and road was 2436 m and 494 m respectively . The denning area furthest away from the closest road was 2631 meters and the closest was 92 meters. The one furthest away from any building was 9878 meters with the closest being 331 meters. The result from the GLMM showed significant relationships between den presence and all predictors (Fig. 7, Tab. 5). There was a non-linear relationship for the distance to gravel roads, with both the linear (p=0.003) and the quadratic (p=0.033) terms for distance to gravel roads being significant. There was an increase in odd ratio up to 1.5 kilometers, before decreasing. The model showed a positive relationship for distance to buildings (p=0.025), Tree density (p=<0.001) showed a strong positive effect on the odds for den area being present, slope (p<0.001) was also positively related.

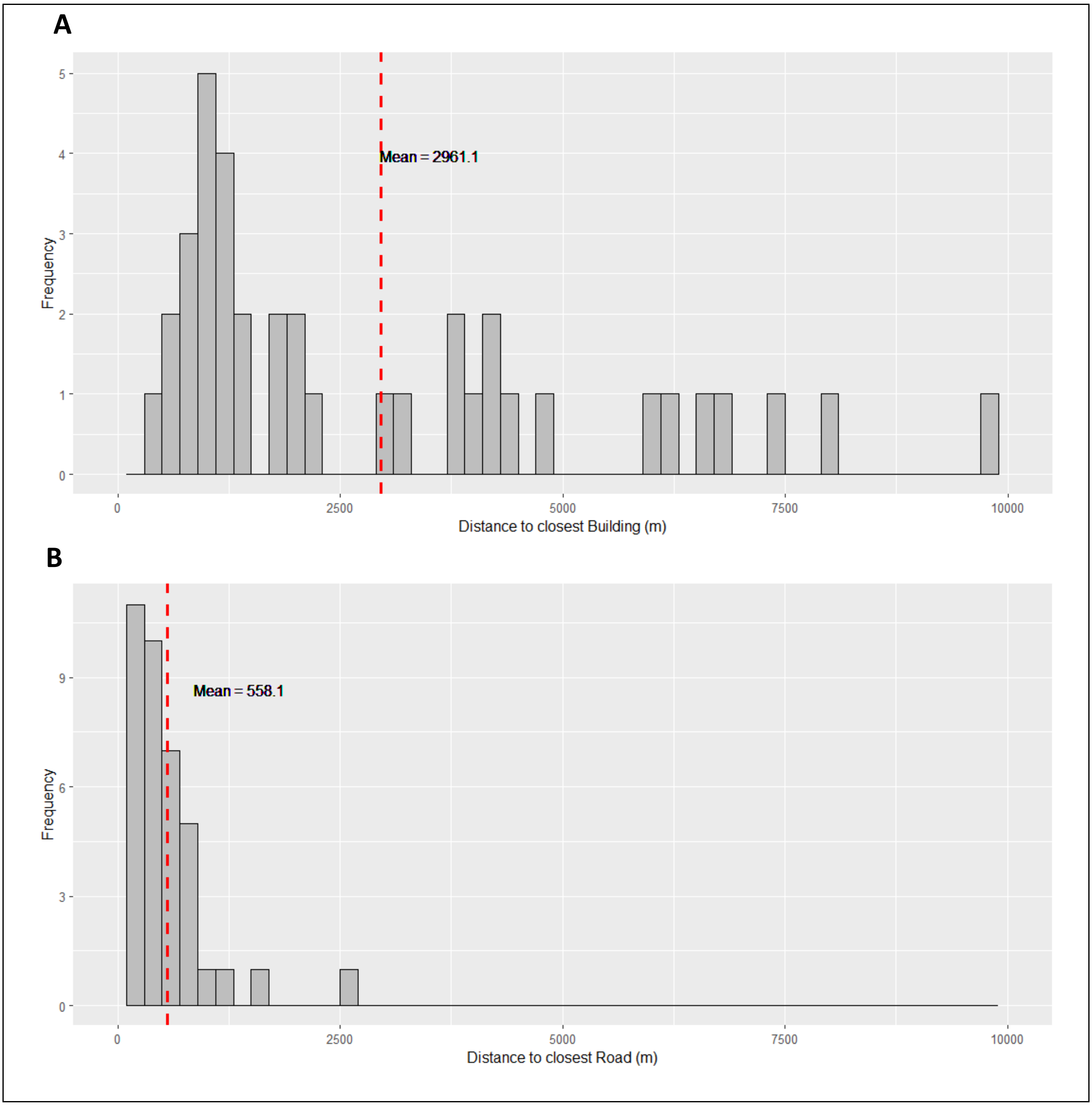

Figure 6. Histogram displaying the frequency distribution of distance from wolf dens to **A)** the closest building, and **B)** the closest road. The red lines represent the mean distance value.

Table 4. Top ranked GLMM model for habitat at wolf den sites compared to random points following AIC values.

Nr	Model	df	AIC	AIC Weight
2	**DenPresence ~ DistGravelKM + I(DistGravelKM^2) + DistBuildKM + slope + treedens + (1 | DenID)**	**7**	**539.87**	**0.3174**
3	DenPresence ~ DistGravelKM + I(DistGravelKM^2) + DistBuildKM + ElevKM + slope + treedens + (1 | DenID)	8	539.11	0.4657
1	DenPresence ~ DistGravelKM + I(DistGravelKM^2) + DistBuildKM + ElevKM + I(ElevKM^2) + Slope + treedens + (1 | DenID)	9	540.63	0.2168

Table 5. . Estimates for the model for habitat comparison between dens and random points.

Predictor	Estimate	Std.Error	z-value	p-value
Intercept	-11.98848	1.02909	-11.650	< 0.001
DistanceGravelKM	2.3866	0.9280	2.572	0.010
I(DistanceGravelKM^2)	-0.9110	0.4545	-2.004	0.045
DistBuildKM	0.1352	0.0594	2.273	0.023
ElevKM	1.9869	1.1910	1.668	0.095
slope	0.1361	0.0232	5.861	< 0.001
treedens	3.4586	0.8850	3.908	< 0.001

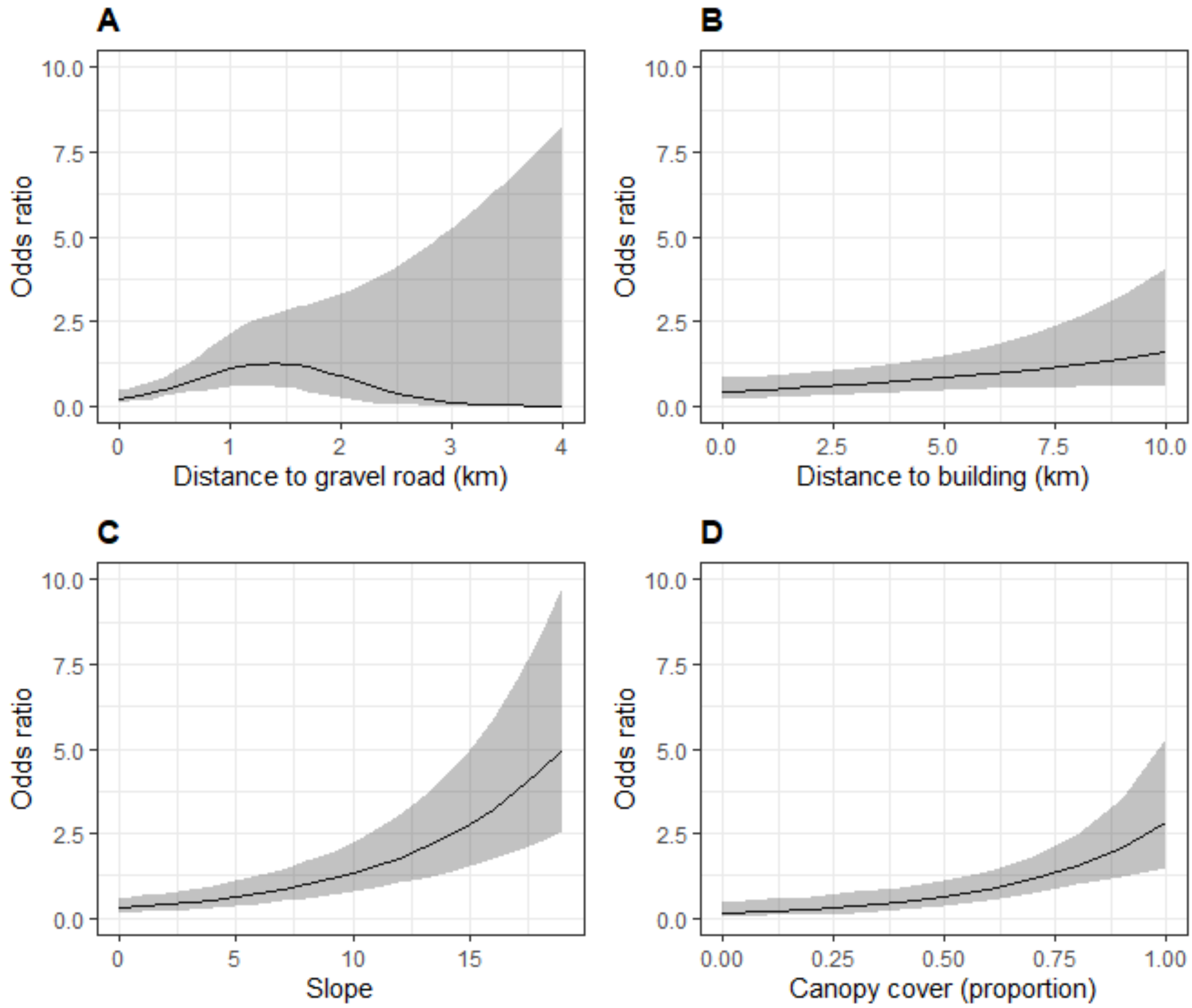

Figure 7. Odds ratio for den site presence. Black line shows the odds ratio of den site being used for each predictor variable, with the grey field representing the 95% confidence interval. **A)** Distance to gravel road (km), **B)** Distance to buildings (km), **C)** Slope, and **D)** Tree density (Canopy cover).

3.4 Den site selection at a micro-habitat scale

Canopy cover (p=0.003) and visibility (p= <0.001) had the biggest effect on the probability of a den site being present and were significant across all models (Tab. 6). Tree species (p=0.059) influenced the den presence to some degree, though not statistically significant (Tab. 6-7, Fig. 8) The ground cover within the 1.78 m radius varied for the different dens depending on the surrounding terrain, tree species, forest age and den types (Tab. 8). The mean canopy coverage for dens was 68.9% (SE ±2.1) and 52.2% for control plots (SE ±2.01), (Tab. 8). Only three den sites had a canopy cover below 40 %, those being Rotna2013, Slettås2013, and Osdalen2009.The mean visibility was 9.6 m (SE ±1.2) at the dens, and 15.8 m (SE ± 0.7) at the control plots, (Tab. 8).

Table 6. Top ranked GLMM model for micro-habitat at wolf den sites compared control plots following AICc values.

Nr	Model	df	AICc	AICc Weight	ΔAICc
1	**DenPresence ~ Canopy + Visibility + Tree_Species + (1 | DenID)**	**2**	**147.78**	**0.4895**	**0.000**
2	DenPresence ~ Canopy + Visibility + Northness + (1 | DenID)	2	149.76	0.1818	1.980
3	DenPresence ~ Canopy + Visibility + ForestAge + (1 | DenID)	2	149.83	0.1755	2.050
4	DenPresence ~ Canopy + Visibility + Elevation + (1 | DenID)	2	150.10	0.153	2.325

Table 7. Estimates for the model for habitat comparison between dens and control plots.

Predictor	Estimate	Std. Error	z-value	p-value
Intercept	-1.49826	1.22568	-1.222	0.221560
Canopy	0.00431	0.0146	2.947	0.0032
Visibility	-0.12627	0.0359	-3.511	< 0.001
Tree_Species	-0.78027	0.41430	-1.883	0.0596

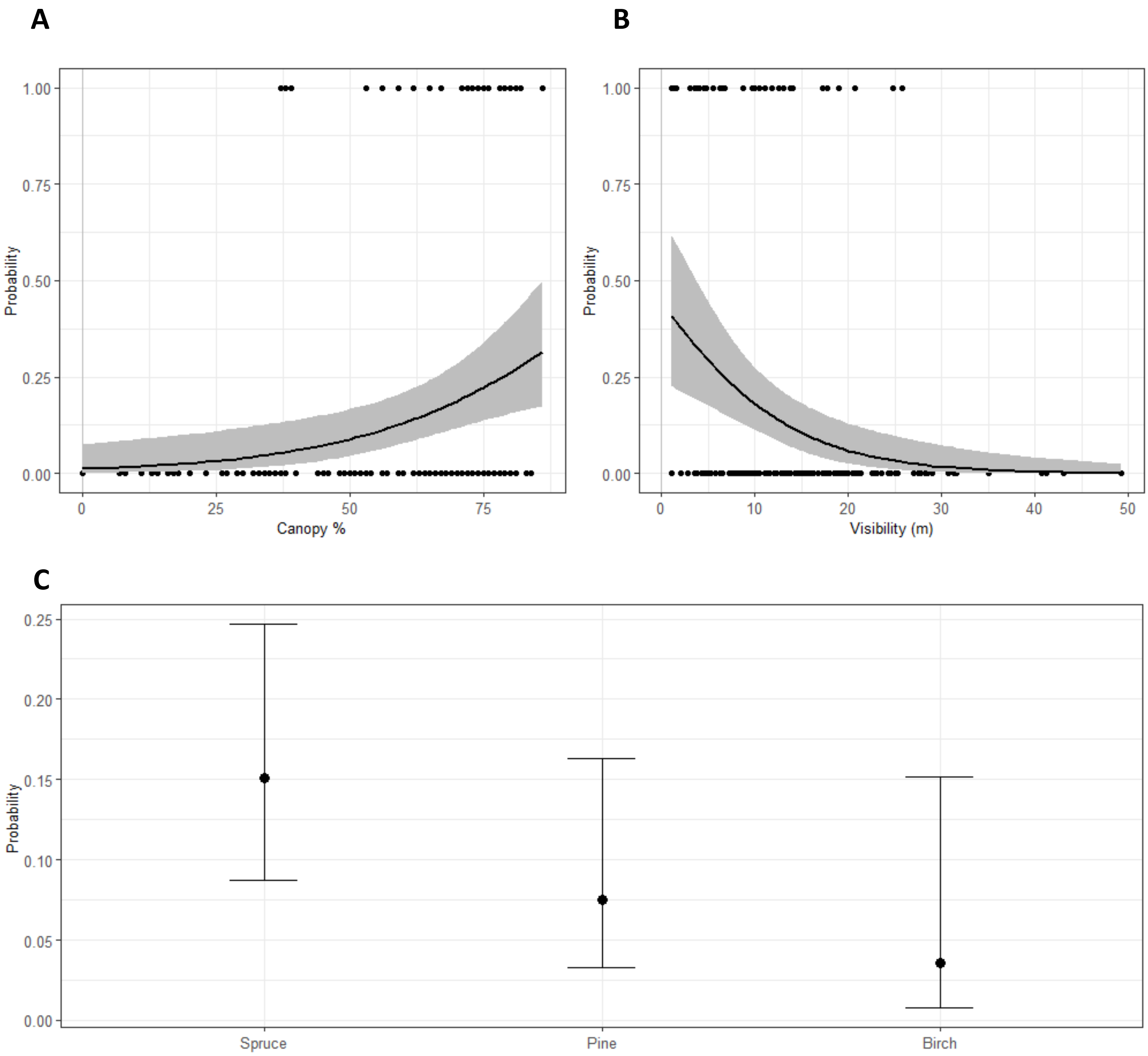

Figure 8. Predictions for the best model used to explain wolf habitat selection for den sites in Scandinavia. Black line shows the predicted probability of den site being used, with the grey field representing the 95% confidence interval. Black dots show the absence and presence (den and control plots). **A)** Canopy had a positive effect on den site being selected (p=0.003) . **B)** Visibility (p= <0.001) had a positive effect on den site being selected. **C)** The presence of different tree species (p=0.059) had no significant effect on den presence.

Table 8. Environmental variables with the mean values and standard error

Variable	Den site	(n=35)	Control plot	(n=140)
	mean	SE	mean	SE
Canopy	68.94	2.13	52.24	2.01
Visibility	9.62	1.18	15.82	0.74
Sand/Gravel	12.86	4.19	1.79	0.79
Heather	16.43	3.79	32.77	2.28
Moss/lichen	18.43	2.59	34.61	2.06
Shrubs	4.14	1.97	7.18	1.40
Rocks	29.86	5.24	6.50	1.38
Grass	0.14	0.14	6.50	1.43
Deadwood	18.14	4.02	10.71	1.47

4. Discussion

In this study, I investigated which factors are important on different scales for wolves when selecting den sites using data collected from 40 wolf dens in Norway and Sweden. According to my first hypothesis H1: the wolves selected their denning areas away from human infrastructure, though the distance varied between the different den sites. I also hypothesized that H2: Shelter and concealment were the most decisive factors at a micro habitat scale. The wolves selected for den sites in areas with high canopy and low visibility.

Following my first prediction 1) both distance to buildings and roads had a negative effect on den presence. Distance to building had a significant but low effect. The relationship between distance to road and den site was non-linear, and not conclusive. Distance to road varied for all dens, and this variation for both can suggest that wolves may be selecting and adapting to human induced changes or activity when selecting den sites, as not all roads or buildings equal human presence. Consistent with my second prediction 2) wolves selected for denning areas with high tree density compared to random points within the simulated territory. The tree density used in the analysis represents density as of 2018, so there is some uncertainty when it comes to accuracy. Still, it should be representative for the area on a larger scale. My third prediction was also supported 3), with canopy cover being higher and visibility lower at the den sites compared to the control plots. While both were significant, visibility in particular had a big impact on the selection of den sites. Though density and visibility will vary depending on the tree species, spruce was the dominating tree species at 80% of the den sites, and 60% of the control plots, usually providing low visibility in contrast to planted stands of pine trees commonly found throughout the study area due to the commercial forestry. In cases where pine was the most dominating tree species, one or more spruce close to the den would affect both canopy and visibility. As such, while the wolves chose denning areas with higher tree density, they generally selected even more dense areas for their den sites.

My last prediction 4), while hard to quantify, was supported by their choice of den types. The wolves showed a preference for dens located in between or under boulders (45%), which were hard to identify as dens, thus providing further concealment. Additionally, visibility was often limited in multiple directions due to the size of the boulders. Dens by, or under tree roots could potentially be easier to spot, except those under dense spruce or at ground level between roots. While few, the two anthill dens with open tops were easier to spot, though both cases were next to large trees providing either canopy or limited visibility. The excavated hollow anthills on the other hand would only be identified as a den from the front, while quickly mistaken for an overgrown anthill from the other side. Though when the den was active, more visible dirt excavated from the anthill would be visible in front or potentially from the sides. While surprisingly few dens in my study were excavated in sand or moraine, all of which are abundant throughout the study area, it was also the den type easiest to spot. The fresh light-colored sand sticking out would stand in stark contrast to the ground vegetation surrounding it (Fig. 4D). Except for the joint protection from both parents, or in many cases the pack, nothing stops a potential predator or competitor from smelling, and seeking out the den sites. In comparison, humans could in many cases walk straight by the den sites at a distance. When fresh, and as the den sites age (assuming no further use), many of the dens would be indistinguishable from the environment if one were not knowledgeable about its characteristics or environment.

My results are consistent with previous studies from North America, which identified canopy and visibility as significant factors influencing den site selection at smaller scales (Person & Russell, 2009b; Trapp et al., 2008). Matteson (1992) suggested that, while not statistically significant, canopy plays a role in den selection at scales less than 0.03 km^2. The previously mentioned study from Poland found no significant difference in canopy cover at den sites compared to random points but suggested that protection provided by certain habitat types depends on their choice of den type. While I did not analyze distance to water beyond a 60-meter radius, 18 dens (45%) had a water source within this distance, and literature have shown that water tend to be in close range to natal dens (Ahmadi et al., 2014; Packard, 2003; Person & Russell, 2009b; Trapp et al., 2008). Though with the substantial number of bogs, small springs and ponds throughout the study area, water is always somewhat available from a wolfs perspective. Lastly, slope proved to have positive effect on breeding areas. Den site selection in steep terrain have been reported in multiple studies and is often attributed to the perceived risk of human presence (Ahmadi et al., 2014; Fuller, 1989; Llaneza et al., 2012). Person and Russel and Ahmadi et al found elevations and slopes to be most important on a small scale within the denning area in two separate studies. Additionally, Stephenson found a tendency for dens to be in warm south-facing slopes, which often are the first places the snow melts during spring and provides potential warmth for both adults and offspring. Based on person observations during data collection at the den sites, dens in steep terrain were harder to spot before getting close compared to dens in flatter areas. At the same time, this selection of den sites on elevations or steep terrain within the denning area also provides a possible vantage point for the wolves around the den.

Den site preparations may in some cases start as early as autumn and mid-winter (Thiel et al., 1997), or as early as one month prior to parturition while preparing multiple dens (Ryon, 1977; Thiel et al., 1997). To my knowledge, no such cases of early den preparations have been documented in Scandinavia. After parturition, the pups stay around the den for their first eight weeks, though the amount of time spent at the same den varies between wolf packs (Packard, 2003). The significance of concealment might only be important in the first few weeks, as the age of the pups have been found to affect the degree of tolerance (Frame et al., 2007), and as the mother can move pups between dens and various rendezvous sites during this period (Packard, 2003; Stephenson, 1974). Despite relying on concealment, denning wolves have been reported to be tolerant of different degrees of human disturbance (Person & Russell, 2009b; Thiel et al., 1998b). While not a prerequisite for successful denning (i.e. pup survival), experience might impact the choice of den sites (Fuller, 1989; Packard, 2003), As such, their den site selection might be a result of previous experience with human presence such as in their natal territory (Milleret et al., 2019b) and can be a possible explanation for not only the variation in distance between den sites and buildings along with road density, but also their general selection of den sites in steep terrain and the varying degree of concealment by the environment. Road density rather than distance alone might be a better indicator of human activity affecting den site selection. While I did not include paved roads due to them never being the closest, other studies have found them to have a negative effect on den locations (See Ahmadi et al., 2014 and Kaartinen et al., 2010).

To the extent that denning areas and den sites are chosen on the basis of human presence, choosing to stay or leave the dens is also influenced by abiotic factors as well due to the altricial state of the pups. Staying over longer periods could very well increase risk of detection from humans or other predators, while simultaneously increase risks in the den due to accumulation of scats and parasites (Ausband et al., 2016). The degree of shelter provided for the pups can also be assumed to be relative to the den type. Whereas dens in caves or boulders provide what would be considered good shelter, other dens such as open anthills or by tree roots may not be adequate during heavy rain or high temperatures. Thus, the cases of high tolerance of human disturbance might be a trade-off in favor of good denning areas, and could explain the large difference in both tolerance and den site variations found in my study, and others.

Management implications

To the extent that my results are representative for the choice of denning habitat for the Scandinavian wolf population, small scale habitat selection surrounding den sites should not be considered the sole decisive factor due to the adaptive nature of wolves and potential impact of other factors. While steep dense forest and degree of visibility can help identify potential den sites, both previous and current, the human aspect and abiotic factors should be considered at different scales. Combined with studies on wolves' habitat selection for den sites on a larger scale, these results can potentially assist future research and management of Scandinavian wolf population.

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Supplementary S1