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John - Like me, I am sure you don't need more to read, but I had been trying to track down this 2015 thesis from Finland, "Den site characteristics of female wolverine (*Gulo gulo*) in Scandinavian forested landscape." Audrey had a copy. Note the discussion section and use of GIS-based models. Please do not distribute.

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DEN SITE CHARACTERISTICS OF FEMALE WOLVERINE (*GULO GULO*) IN
SCANDINAVIAN FOREST LANDSCAPE

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1 INTRODUCTION

For species with a low reproductive rate, such as the wolverine (*Gulo gulo*), the survival of reproductive females and their offspring has crucial effect on population growth (Persson *et al.* 2006), and habitat with suitable characteristics for denning may have a significant effect on wolverine reproductive success (Banci 1994, Landa *et al.* 1998a, May *et al.* 2012). Being able to recognize and possibly quantify suitable denning habitat for reproductive female wolverines provides valuable information for management of the species.

Female wolverine den site selection in alpine and tundra habitat has been described in previous studies in Finland (Pulliainen 1968), North America (Magoun & Copeland 1998), Norway (May *et al.* 2012) and Sweden (Mattsing 2008). However, little is known about the den site characteristics in the southern boreal forest. Den sites in forest habitat were pooled together with the dens in alpine and tundra habitats in one Norwegian study (May *et al.* 2012), and a Canadian study by Dawson *et al.* (2010) described denning habitat for a single den site in boreal forest of Ontario.

Wolverines are considered to be snow-dependent since their worldwide distribution is correlated with the distribution of persistent snow cover, presumably due to the importance of snow for suitable den sites and for efficiency of food caching (Copeland *et al.* 2010, McKelvey *et al.* 2011, Inman *et al.* 2012a). Timing in birth differs from other northern non-hibernating carnivores, since wolverines give birth during February-March (Inman *et al.* 2012a) in den sites dug in the snow that provides insulation and protection from predators (Pulliainen 1968, Magoun & Copeland 1998, Persson *et al.* 2003). Therefore, a warming climate may have effects on these northern alpine habitats (McCarthy 2001) and negative effects on wolverine reproductive rate (Copeland *et al.* 2010, McKelvey *et al.* 2011, Inman *et al.* 2012a). Studying the female wolverine reproductive den site selection at the southern edge of wolverine distribution can improve our understanding of wolverines reproductive potential under conditions that can be described as an exception from what is currently known as suitable wolverine denning habitat (Magoun & Copeland 1998, May 2007, May *et al.* 2012).

1.1 General description of the study species

Wolverines occupy the northern arctic and subarctic areas, boreal forests and alpine regions globally (Landa *et al.* 1998b, Krebs *et al.* 2007, Copeland *et al.* 2010). As scavengers they are well adapted to remote, low productive and cold habitat both physically and behaviorally (Banci 1994, Inman *et al.* 2012b). Their relatively small body (males 12-18kg, females 8-12 kg) and wide paws are well suited for travelling long distances (30-40km daily) in all seasons (Banci 1994). Thus wolverines are capable of retrieving food from various types of habitats (Rauset *et al.* 2013) by hunting small game such as rodents, forest birds, hare and even ungulates (Landa *et al.* 1997, Mattisson *et al.* 2011, Koskela *et al.* 2013b). They are also very efficient using the carrion left by other predators (Mattisson *et al.* 2011, Koskela *et al.* 2013b) and caching food throughout the year for their food source (Mattisson *et al.* 2011, Inman *et al.* 2012b, Koskela *et al.* 2013b). Wolverines are territorial and maintain large home ranges (males mean 669 km², females mean 170 km² (Persson *et al.* 2010), that are intra-sexual and mostly temporarily exclusive with some spatial overlap (Persson *et al.* 2010, Inman *et al.* 2012b). Boundaries are maintained by scent marking, urinating (Pulliainen & Ovaskainen 1975) and patrolling regularly (Inman *et al.* 2012b).

1.2 Habitat selection

Suitable wolverine habitat is associated with high elevation alpine areas, sub alpine forested areas and rocky and rugged terrains in remote areas (May *et al.* 2006, Copeland *et al.* 2007, May *et al.* 2008, Rauset *et al.* 2013). Some wolverines display minor seasonal shifts in habitat preference (Hornocker & Hash 1981, Landa *et al.* 1998a, Copeland *et al.* 2007, Krebs *et al.* 2007, Inman *et al.* 2012b), where in general, wolverines use higher elevations and alpine rocky habitats in the summer and in the winter preference shifts to lower elevation forest habitats (Copeland *et al.* 2007, Krebs *et al.* 2007, Inman *et al.* 2012b). Human activities are avoided in both seasons (May *et al.* 2006, Krebs *et al.* 2007, May *et al.* 2008, Koskela *et al.* 2013a, Rauset *et al.* 2013).

Wolverines are known to benefit from carrion left by other guild members such as brown bear (*Ursus arctos*), European lynx (*Lynx lynx*) and grey wolves (*Canis lupus*) (May *et al.* 2008, Mattisson *et al.* 2011, Rauset *et al.* 2013, Koskela *et al.* 2013a). However, some avoidance is detected (Copeland *et al.* 2007, Krebs *et al.* 2007, May *et al.* 2008), but on the other hand, there is also spatial overlap with these other large carnivores (May *et al.* 2008,

Mattisson *et al.* 2011, Koskela *et al.* 2013a). In boreal forests wolverines showed similar patterns as in alpine and tundra habitats by avoiding human settlements but favoring wolf presence (Koskela *et al.* 2013a).

Between sexes, male habitat selection is mostly driven by food supply in all spatial scales (Krebs *et al.* 2007), whereas female habitat selection is more complex as they have to balance food availability, risk of predation and human disturbance for cubs (Krebs *et al.* 2007). Similar to males, females also express seasonal shifts in their habitat preferences and are driven mostly by food supply (Krebs *et al.* 2007, May *et al.* 2010) but they show more clear avoidance for human disturbance than males (Krebs *et al.* 2007, Dawson *et al.* 2010, May *et al.* 2010). When looking closer to female wolverine habitat selection during the winter, Krebs (2007) noted that risk of human disturbance and predation seems to have an effect when selecting territory, but within their territory food availability may become more important (Krebs *et al.* 2007).

1.3 Reproductive ecology

Wolverines have a low reproductive rate with mean annual birth rate of 0.74 cubs per female and mean litter size of 1.88 (Persson *et al.* 2006). Females can reproduce between the age of 2 and 13 years, but mean age for first reproduction is 3.4 (Persson *et al.* 2006). They are capable of producing a litter every year but reproductive success is highly dependent on food availability (Persson 2005, Rauset 2013).

Wolverines have a polygamous mating system in which males can mate with several females during the mating season (Hedmark *et al.* 2007). They are delayed implanters where mating season is from May to August with a peak in June (Inman *et al.* 2012a) but birth is not until mid-winter. Females give birth in February to mid-March in general, with few reported exceptions both earlier and later (Inman *et al.* 2012a).

Harsh weather creates resources for scavengers (Wilmers *et al.* 2003), which limits competition for resources among other large carnivores or predators (Inman *et al.* 2012a). However, these weather conditions set a challenge for females to provide thermoregulatory cover for their offspring. Cubs stay in dens until weaning (10 weeks), but females are known to continue nursing up to late May and June (Inman *et al.* 2012a). During this denning period, females move their cubs between primary and secondary den sites, although reasons for this behavior are still largely unknown. Possible reasons can be the

changes in the thermal conditions and human disturbance (Magoun & Copeland 1998, Persson *et al.* 2003, Inman *et al.* 2012a), but other known threats for cubs are infanticide (Persson *et al.* 2003) and intraguild predation (Boles 1977, Banci 1994).

1.4 Den site characteristics

Successful reproductive wolverine dens require thermoregulatory cover, dry shelter (Pulliainen 1968, Magoun & Copeland 1998, Mattsing 2008) and safety from predators and human disturbance (Magoun & Copeland 1998, Krebs *et al.* 2007, Mattsing 2008, May *et al.* 2012). Snow provides thermoregulatory insulation and protects from most predators (Boles 1977, Banci 1994). Therefore, characteristics supporting the presence of a deep snow bank have a high impact on the female wolverine den site selection (Pulliainen 1968, Banci 1994, Magoun & Copeland 1998, May *et al.* 2012). Dens have been located in relatively high elevations, close to alpine tree line (Magoun & Copeland 1998, Landa *et al.* 1998a, Mattsing 2008, May *et al.* 2012) on steep slopes in rugged terrain with rocks, where snow can accumulate (Pulliainen 1968, Magoun & Copeland 1998, May *et al.* 2012). Recent study in Norway found a preference for north facing slopes (May *et al.* 2012) and a study in Sweden found preference for slopes facing to the direction where snow accumulates (Mattsing 2008). However, some of these habitat characteristics associated with deep snow bank such as higher elevation, steep slopes and rugged terrain, are also associated with remote and safe locations for den sites, to avoid intraguild predation (Magoun & Copeland 1998, May *et al.* 2008) and human disturbance (May *et al.* 2006, Dawson *et al.* 2010, May *et al.* 2012).

Magoun & Copeland (1998) suggest wolverines require deep snow bank and persistent snow cover (> 1 m) throughout the whole denning period from February to May, and Copeland *et al.* (2010) suggests that spring snow coverage (up to 24th April-15th of May) is important for reproductive dens. However, in southern boreal forests persistent snow cover is not a reliable source for thermoregulatory cover and safe shelter for cubs (SMHI 2014, Appendix 3). Therefore in forest regions other characteristics should be found to provide the same conditions. Dawson *et al.* (2010) suggested that in lower elevation boreal forests, additional cover provided by boulders, trees and other suitable structures is critical, due to the lack of snow drifts which are typical for alpine and tundra habitat.

For providing thermoregulatory cover den sites would need to be found in a habitat type that would stay dry throughout the denning season. Pulliainen (1968) described three snow

covered den sites with additional structures, which were located at peat bogs. However, it can be suggested that this type of habitat might not provide dry shelter in early spring thaw. He also noticed that in snow dens, wolverines avoid putting cubs against cold rocks. In snow dens this could be avoided with snow layer as Copeland et al (1998) found in their study. Tunnels at dens did not reach ground, but beds were found on hard packed snow (Magoun & Copeland 1998). With unreliable snow conditions, the ground cover at site could have a meaning for insulation for cubs if snowbank does not allow digging tunnels. Also, without snow, the den structures would need to form a cover from the weather. Good solid structures would also provide safety from predators and infanticide, and alternative entrances would provide possible escape route for the female, as found in snow dens (Pulliainen 1968, Magoun & Copeland 1998).

Remote and inaccessible areas are important for safety from human disturbance. These are rare in southern boreal forest, due to the high abundance of logging roads (Figure 1), but during the winter, usage of these roads is lower. Most of the small private roads are not plowed, and are used only by snowmobiles or occasional skiers. Wolverines are known to use smaller roads and trails as travelling routes (Copeland *et al.* 2007), therefore smaller roads might not be avoided, but major, plowed roads used during the winter might be avoided. Remoteness might also be related to the abundance of human settlements within the area. Recreational cabins are abundant even in the remote areas, but are not necessarily used during the winter, at least not on a regular basis. However, more stable human settlements occupied all year round would be avoided by the wolverines as much as possible. In addition to linear distance to human settlements, remoteness in this study area could mean inaccessible rugged terrain and steep slopes that are inaccessible to humans. If truly remote areas far from human settlements and roads within their territory cannot be found, den sites would have to provide good solid structures to keep cubs safe from possible disturbance.

The aim of this thesis is to study wolverine den site selection in the forest landscape in central Sweden by focusing on two associated research questions 1) **What are the typical characteristics of female wolverine reproductive den sites in boreal forests?** For this, den sites registered within the national wolverine-monitoring program (Naturvårdsverket 2014) were visited to describe a typical den site and habitat characteristics. 2) **What habitat characteristics do female wolverines choose for reproductive den sites in boreal forests?** Resource selection function (Johnson 1980, Manly *et al.* 1992) is used to

quantify the use of resources in relation to availability within female's territory. It is predicted that characteristics found on the female wolverine den sites in the forest habitat would provide cover and safety in all weather conditions and den sites are situated in remote, rugged areas, far from human settlements and major roads.

2 MATERIAL AND METHODS

2.1 Study area

The wolverine den survey was done in parts of Jämtland and Västernorrland counties in Sweden (Figure 1). The habitat is mainly a mixture of managed boreal forests dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), and mires, lakes and human settlements. Elevation ranges from 158 m to 1032 m above sea level (Lantmäteriet 2010). Yearly medium temperature is 1.9 °C ranging from minimum -38.5 °C to maximum 28.8 °C (SMHI 2015). Forestry has a high impact to the forest structure by creating a mosaic of highly managed forest patches and wide spread network of forest logging roads.

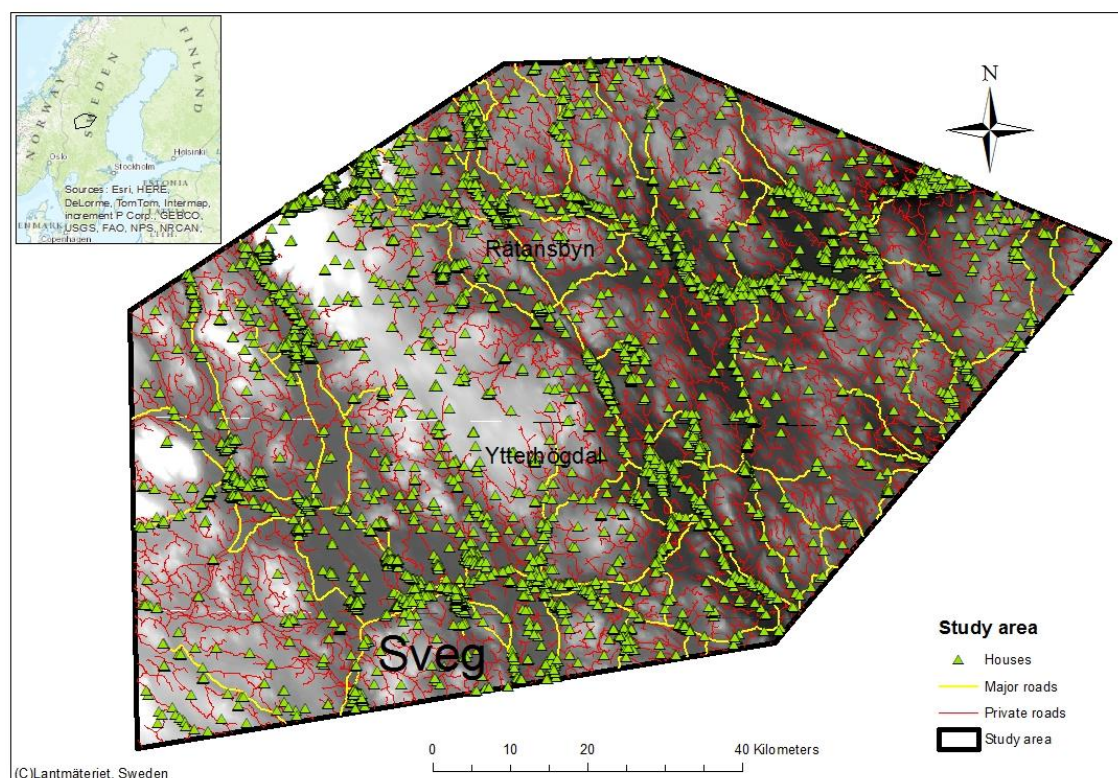


Figure 1. Map with background of +50m Digital elevation map (DEM) representing the study area in Sweden with locations of all houses (excluding cabins and huts) and private and major roads from National Road map provided by Lantmäteriet (Lantmäteriet 2010, Lantmäteriet 2014).

There are no large national parks or nature preserves in the area, but there are several very small, unconnected preserves focusing on rare nature types or certain species (Länsstyrelsen 2015, Lantmäteriet 2014). The potential prey for the wolverine in the area, are moose (*Alces alces*), tetraonids, beaver (*Castor fiber*), mountain hare (*Lepus timidus*) roe deer (*Capreolus capreolus*) and rodents. Semi-domestic reindeer (*Rangifer tarandus*) is present in the western part of the study area. Wolves (*Canis lupus*), brown bears (*Ursus arctos*), Eurasian lynx (*Lynx lynx*) and red fox (*Vulpes vulpes*) occur in the area.

2.2 Resource selection function

Johnson (1980) suggested that species in general select habitat in hierarchical manner. He described selection as a process of selecting suitable habitat including components or characteristics that can be defined. Species select their geographical distribution range (first order selection), home range within that distributional range (second order selection), a habitat components such as feeding site or a rest site within their home range (third order selection) and certain items at that site (fourth order selection) (Johnson 1980).

Manly *et al.* (1992) introduced resource selection function (RSF) method to quantify the use of resources in relation to availability. When resource is observed to be used more than what is available, it is then favored i.e. selected. Contrary, if resource is used less than what is available, it is avoided (Manly *et al.* 1992). The type of RSF study design depends on the species ecology, available data and type of the resources. In this study when individuals are known and resource availability is restricted by territoriality of animals, resource selection is done for each individual within their territory (third order selection) and used and available resource units are sampled independently. This way comparison is done between individuals and individual based variation in used and available resources is taken into account (Manly *et al.* 1992).

2.3 Data

The reproductive events of Swedish wolverine population are monitored yearly by County Administrative Board field personnel (Karlsson & Eklund 2014). Monitoring is performed from February to June and registered reproductions are based on documentation of den site, tracks of females with young and visual observations of young after den abandonment (Naturvårdsverket 2014). Furthermore, DNA-samples from scats and secretions are collected to identify the reproducing female. Due to this intensive effort, information about

den site locations, the individuals associated with each den, and the sequential use of dens within the year for females that changed den sites, is known. In cases when female used multiple den sites during the same year the first den found for that year were classified as the primary den and all the dens used after that were secondary dens.

For each surveyed den site, three random locations were generated and surveyed to compare used vs. available locations. Random locations were selected at a distance of over one kilometer (1 km) from the den site, because female wolverine's den area can be very large (mean = 80 m (May *et al.* 2012). The availability differed for primary and secondary dens, therefore random locations for primary dens were chosen within a 5 km radius from the observed den site. The 5 km buffer zone represents an average female territory during the denning season with the assumption that when choosing the first den, the whole territory is available. Also, in the used data set, 5 km was the minimum distance between primary dens for different females during the same year. For secondary dens, random locations were chosen within 2 km radius from the previous den site (for example, if 2nd den, the random location was chosen within 2 km from the primary den and if 3rd den, 2 km from the 2nd etc.) The 2 km distance is based on the longest distance between consecutive den sites used by the same female within the same year in this study area, representing the reduced available area when female has to move with dependent young.

Den site characteristics were recorded according to a field protocol (Appendix 1) and described for both den sites and random locations. Simple descriptive statistics were carried out using R-program 3.1.2 (R Core Team 2014) and presented in tables for both den sites and random locations. It is important to notice that no statistical tests were conducted to compare means and therefore, no estimations of differences or selection of certain characteristics were done based on descriptive statistics. Instead, resource selection function was used to quantify the differences in use and availability.

From collected data, only variables recorded within 20 m radius in addition with GIS – based variables (Appendix 2) were used within a RSF framework to investigate the used-available -relation within female's territory (third order selection). Generalized linear mixed models (GLMM) are flexible to deal with unbalanced sample size, non-normal distribution and dependent samples, with random effects and link –functions (Bolker *et al.* 2009, Bates 2013). In this study, both dens and random locations depend on the individual

and also on the year. *A priori* models were generated based on knowledge of wolverine ecology and previous research on den site selection.

2.4 A priori models

The *a priori* models were formed based on three possible causes of threats for female wolverines and their cubs; highly variable weather conditions during the denning season, intraguild and interspecific predation, and disturbance caused by human activities. Three sets of models, Cover and safety –models (CS), Disturbance –models (D) and models with variables extracted from GIS –layers (G) were constructed based on predictions of suitable characteristics.

2.4.1 Cover and safety –models

If cover and safety from weather and predation is the driving force for female wolverines when selecting a suitable den site, dens would be found on dry habitat with rocky, rugged terrain that includes a high number of boulders for cover and safety. Therefore the simplest CS-model would include HABITAT+ROCKS+TRE+BOULDERS for cover and ELEVATION as a safety from intraguild members (May *et al.* 2008) (see Appendix 2 for details about variables). If there are areas that are too rugged and as such a risk for cubs safety, then CS -models with estimated terrain ruggedness with quadratic effect would perform better with HABITAT+ROCKS+TRE+TRE²+BOULDERS+ELEVATION. Also, it could be expected that if high elevation areas are not available, den sites at lower elevations would have higher ruggedness to provide additional cover for safety. Therefore CS -model with interaction term HABITAT+ROCKS+TRE+BOULDERS+ELEVATION+TRE*ELEVATION is added. Even though it was not expected that snow would be a significant provider for cover and safety in this study area due to unreliable weather conditions during the winter, to test this, a model with HABITAT+TRE+ELEVATION+ASPECT was added. Choosing alpine habitat with rugged sites at high elevation with north facing hillsides or to a direction where snow accumulates and spring thaw is late, would indicate importance of snow cover for denning.

2.4.2 Disturbance -models

Den sites were expected to be located in remote, rugged areas, far from human settlements and major roads (Figure 2). If human disturbance is the only factor here, simple D -model including ROAD+SETTLEMENT would perform well. Since rugged areas with steep slopes are often inaccessible for humans especially during the winter, D -model including SLOPE and TRE (ROAD+SETTLEMENT+SLOPE+TRE) would perform better. When taking account that totally remote areas are rare in this study area, interaction terms between both distance to major roads and human settlements against terrain ruggedness and slope should be included in models. This would indicate that when den sites are closer to major roads or human settlements, sites would have higher ruggedness or steeper slopes to compensate, with addition of higher number of boulders (BOULDERS).

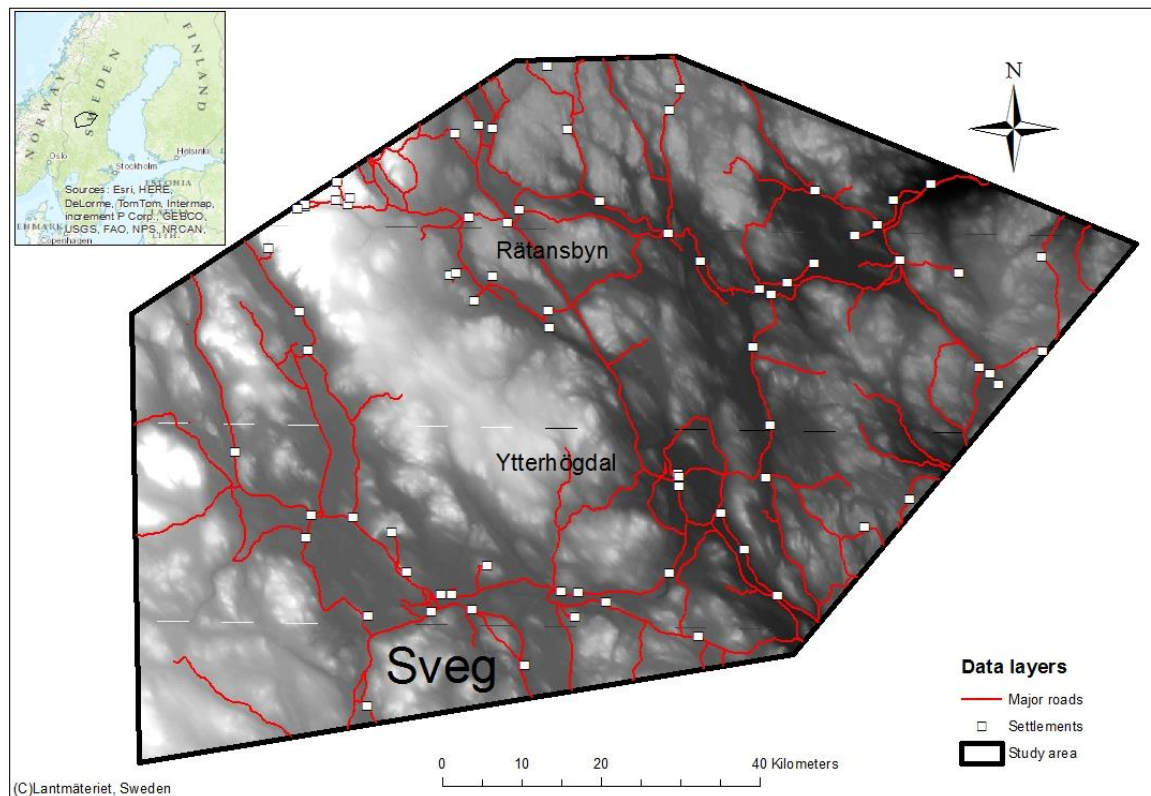


Figure 2. Map with background of +50 m digital elevation map (DEM) representing the study area in Sweden with human settlements and major roads that are likely used during the winter, from national road map provided by Lantmäteriet (Lantmäteriet 2010, Lantmäteriet 2014).

To see if both human disturbance and risk from intraguild predation are high, model with elevation as an indicator of habitat differentiation with guild members (ROAD +SETTLEMENT+ELEVATION) was added in the set. This model would also perform better with TRE, SLOPE or BOULDERS, if ruggedness provides additional cover in high

risk areas. Model with interaction term SETTLEMENT*TRE would reveal higher impact from human disturbance and ELEVATION*TRE higher risk from intraguild predation.

2.4.3 GIS -based models

Since TRE and SLOPE were measured at site and were not extracted from GIS-layers, models including only GIS-based variables were added to test how well this type of data performs when predicting the locations of the den sites. If models with GIS-data give reliable estimates of locations of den sites, predictive habitat maps created for larger areas could be used without conducting high amount of field work. Instead of TRE, vector ruggedness measure (VRM) was calculated to indicate ruggedness (Sappington *et al.* 2007) and GISslope was extracted from digital elevation model for each location (see appendix 2 for variable details). Used-available relation and locations were kept the same as in previous models. Similarly, G-models were constructed based on predictions of cover and safety, remoteness and human disturbance with possible quadratic effects and interaction terms.

2.4.4 Variable relevance

A correlation test among variables revealed collinearity between variables ROCKS and TRE (Spearman, $r = 0.78$), TRE and SLOPE ($r = 0.54$), but also between ROAD and ELEVATION ($r = 0.61$) and VRM and GISslope ($r = 0.51$). Variable ROCKS was excluded from the analysis since the proportional amount of rocks at present does not indicate the amount of cover or structure that is at interest here. The proportional amount of rocks at site can be high, but since this is recorded with or without vegetation on top, there can be pure, flat bedrock or rocks covered with moss and vegetation with no access underneath. The TRE instead represents better the overall ruggedness and structure of the location thus with higher ruggedness, there is more likely suitable cover at present. For the same reason SLOPE was excluded. Steep slopes might indicate inaccessibility for humans, but does not necessarily provide structures for cover, although, correlation indicates that there is a connection between these two. The TRE indicates ruggedness with such a small scale that even relatively flat areas can have structures such as boulders, and therefore get higher value of TRE.

For G-models, VRM and GISslope were kept in different models since the aim was to find out which of these variables could be used to create predictive maps for management

purposes. Therefore the correlation between the ELEVATION and the ROAD was handled similarly by separating these into different models. The SETTLEMENT and the ROAD were not significantly correlated ($r = 0.41$) and therefore the combination of these two could be seen as a good indicator of human disturbance, although with the ROAD, there are some uncertainties about the amount of disturbance during the winter without the certain knowledge of plowed roads. The ELEVATION can be seen as a good indicator of avoidance of intraguild members (May *et al.* 2008) and it is possibly related to snow cover (Rauset 2013).

Table 1. *A priori* models for resource selection function based on hypotheses of cover and safety from intraguild predation (CS-models), human disturbance (D-models) and models with same underlying hypotheses formed with GIS-based variables (G-models). In models, $I(x^2)$ indicates quadratic effect and asterisk (*) interaction with variables. See appendix 2 for variable details.

CS and D Models
CSg: TRE+ $I(TRE^2)$ +ASP+ELEVATION+SETTLEMENT+SETTLEMENT*TRE+E*TRE
Dg: TRE+ $I(TRE^2)$ +ASP+SETTLEMENT+ROAD+SETTLEMENT*TRE+ROAD*TRE
CSMod1: TRE+ELEVATION
CSmod2: TRE+ $I(TRE^2)$ +ELEVATION
CSmod3: E+TRE+ $I(TRE^2)$ +ELEVATION*TRE
CSmod4: TRE+ $I(TRE^2)$ +ELEVATION+ASPECT
Dmod5: SETTLEMENT+ROAD
Dmod6: SETTLEMENT+ROAD+TRE+ $I(TRE^2)$
Dmod7: SETTLEMENT+ROAD+TRE+ $I(TRE^2)$ +SETTLEMENT*TRE+ROAD*TRE
Dmod8: SETTLEMENT+ROAD+TRE+ $I(TRE^2)$ +SETTLEMENT*TRE
Dmod9: SETTLEMENT+ROAD+TRE+ $I(TRE^2)$ +ROAD*TRE
Dmod10: SETTLEMENT+ELEVATION
Dmod11: SETTLEMENT+ELEVATION+TRE+ $I(cTRE^2)$
Dmod12: SETTLEMENT+ELEVATION+TRE+ $I(TRE^2)$ +SETTLEMENT*TRE+ELEVATION*TRE
Dmod13: SETTLEMENT+ELEVATION+TRE+ $I(cTRE^2)$ +ELEVATION*TRE
Dmod14: SETTLEMENT+ELEVATION+TRE+ $I(TRE^2)$ +SETTLEMENT*TRE
Dmod26: ROAD+TRE+ $I(TRE^2)$
Dmod27: ROAD+TRE+ $I(TRE^2)$ +ROAD*TRE
Gmodels
Gglobal15: VRM+ELEVATION+SETTLEMENT+SETTLEMENT*VRM+ELEVATION*VRM
Gmod16: VRM+SETTLEMENT+ROAD+SETTLEMENT*VRM+ROAD*VRM
Gmod17: VRM+ELEVATION
Gmod18: VRM+ELEVATION+ELEVATION*VRM
Gmod19: VRM+SETTLEMENT+ROAD
Gmod20: VRM+SETTLEMENT+ROAD+SETT*VRM
Gmod21: VRM+SETTLEMENT+ROAD+ROAD*VRM
Gmod22: GISsl+SETTLEMENT+ROAD
Gmod23: GISsl+SETTLEMENT+ROAD+SETTLEMENT*GISsl+ROAD*GISsl
Gmod24: GISsl+SETTLEMENT+ROAD+SETTLEMENT*GISsl
Gmod25: GISsl+SETTLEMENT+ROAD+ROAD*GISsl

Variance inflation factor (VIF) indicated collinearity in TRE and BOULDERS (VIF value for TRE: 4.64, for BOULDERS: 4.97) when associated with all other variables. When BOULDERS was removed from the set, all variables were under VIF threshold 3, recommended by Zuur *et al.* (2010). Categorical variable HABITAT had no variation in den group (all dens were in forest) and it was dropped out from the model set. Based on the rest of the suitable variables, three global models, one with ELEVATION (CSglobal), one with ROADS (Dglobal) and one with GIS -variables (Gglobal15) were formed (Table 1) for goodness-of-fit tests. Also, 27 *a priori* candidate models (Table 1) were reconstructed for further analysis and due to numerous interaction terms, variables were centered to avoid misinterpretation of the between groups -effect (Schielzeth 2010).

The sets of *a priori* candidate models were compared using the Akaike Information Criterion (AIC) with a second order correction for sample size (AIC_c) (Hurvich & Tsai 1989, Burnham & Anderson 2002). Burnham and Anderson (2002) recommends to use AIC_c if ratio for the global model n/K is < 40 (n = sample size, K = number of parameters), here 11.5 (n = 197 and K = 17). AIC_c weights (w_i) were used to determine the relative strength of support for each candidate model and also to generate model averaged estimates (MAE) with standard errors and 95% confidence levels for each explanatory variable (Burnham & Anderson 2002) in the most parsimonious models ($\Delta AIC_c < 2$). Model average estimates are interpreted such that if 95% confidence intervals include zero, the variable does not affect the models predictive ability, therefore being irrelevant for the selection of the den site in this area. The predictive value of the most parsimonious model and each variable was tested by using modified k-fold cross-validation technique (Boyce *et al.* 2002) with Relative Operating Characteristics (ROC) and area under roc curve (AUC) values (Metz 1978, Pearce & Ferrier 2000). In cross-validation, individuals were divided in to five groups and mean AUC values with 95% confidence levels for 1000 repetitions were calculated to test in 4 to1 relation how well model separates the den sites from individual's sampled locations (4 group's data predicted the fifth group's den sites). Since cross-validation models are entered without random effects, using each individual as a grouping term, variation among individuals is taken into account. ROC and mean AUC values for individual variables were used to compare predictive ability and to evaluate variable importance (to interpret AUC values for predictive ability 1= perfect separation, > 0.90 = excellent, > 0.80 = good, > 0.70 = fair, > 0.60 = poor, 0 -0.50 = fail). Finally, to evaluate the habitat selection, the predictive performance (i.e. the ability to predict den site usage) of

the important variables in top models were plotted with 2*standard errors (approximately equaling the 95% confidence levels). The associated variables in the model were standardized at their mean values.

3 RESULTS

In this study, forty-nine ($n = 49$) den sites were investigated within the study area during the summer 2014 (June to August). The den sites were from years 2008–2014 and all dens were confirmed to be reproductive dens used by cub rearing female wolverines. Some dens sites were used in multiple years and some females changed the den site during the denning period (i.e. same year).

3.1 Typical characteristics of wolverine reproductive den sites in boreal forests

Characteristics for typical den sites in this area are boulder complexes in mature coniferous mixed forest with several different sized holes and caves formed by boulders. Holes were often connected with multiple entrances from different directions.

3.1.1 Den site characteristics in 20 m radius

All dens ($n = 49$) were found in forest habitat and 76% of these were in mature or old growth forest habitat (mature $n = 24$, old growth $n = 13$, Table 2). In all cases ($n = 49$), berry shrub was the main ground cover (Table 3). From dens, 31 were found in coniferous mixed forest (63%) and dominating tree species were pine (15%), and spruce (10%) (Table 4, see classification (Hagner & Reese 2007)).

Table 2. Estimated forest age for female wolverine reproductive den sites in forest landscape with number of den sites (N) and proportions of den sites (%) found on each forest age category.

Forest age (years)	N	%
Old growth >80	13	27
Mature 30-80	24	49
Young 10-30	11	22
Succession 0-10	1	2

Table 3. Ground cover type for female wolverine reproductive den sites in forest landscape categorized for 20 m radius and estimated minimum area size with proportion of dens (%) within these categories.

Ground cover	Den		Den	
	20m Radius	%	minimum area	%
Herbacious	0	0	0	0
Grass	0	0	0	0
Berry shrub	49	100	37	76
Moss	0	0	6	12
Lichen	0	0	6	12
Sphagnum	0	0	0	0

Table 4. Main forest type for female wolverine reproductive den sites in forest landscape with number of den sites (N) and proportions of den sites (%) found on each forest type category. The forest type is categorized to single species forest when the proportion of dominating tree species exceeds 70% and to mixed forest when proportion of deciduous trees is between 31-69%.

Main Forest type		
Species >70% of trees	N	%
Spruce	5	10
Pine	7	15
Contorta	2	4
Birch	4	8
Mixed	31	63

Mean of estimated proportion of rocks on ground was 41% (SE $\pm$ 3.23) and mean of estimated terrain ruggedness (TRE) at the location was 0.21 (SE $\pm$ 0.01) (Table 5). For den sites, mean elevation was 495 m (DEM, SE $\pm$ 11.68) and mean distance from road was 4.00 km (SE $\pm$ 0.32) and from houses 6.18 km (SE $\pm$ 0.43). Based on plotted measured aspects, no particular aspect was selected (Figure 3 a). Mean slope for hillside was 20° (SE $\pm$ 1.68). From 50 m digital elevation model, GISslope was lower with mean of 8° (SE $\pm$ 0.84).

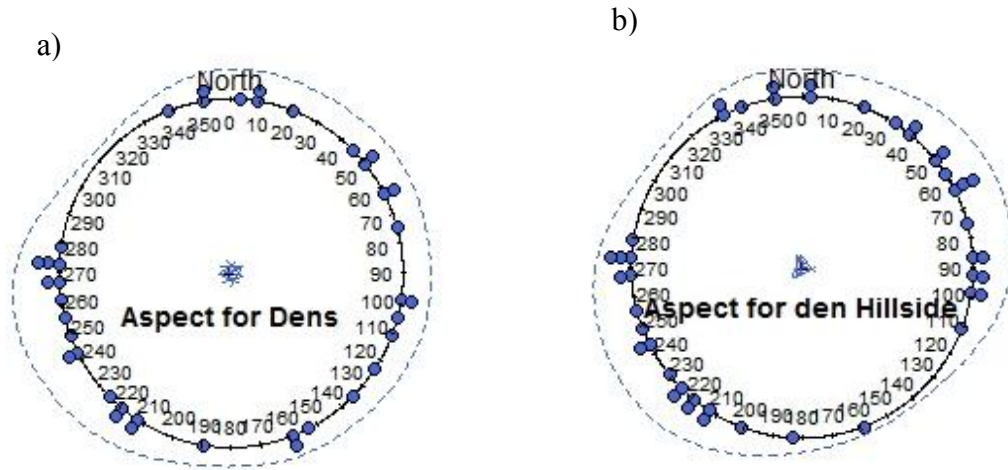


Figure 3. Plotted values for measured aspect (360° blue circles) a) at the den site and b) the hillside for female wolverine reproductive den sites in forest landscape.

Table 5. Descriptive statistics for measured habitat variables in female wolverine reproductive den sites and associated random locations in forest landscape with mean values, 95% confidence levels (95% CI), standard errors (SE) and number of sites (N). See Appendices 1 and 2 for details of measured habitat variables.

Variable	Den sites				Random locations			
	Mean	95% CI	SE ±	N	Mean	95% CI	SE ±	N
Minimum area size (m)	29	5.75	2.85	42	–	–	–	–
ELEVATION (m)	495	23.49	11.68	49	475	13.29	6.72	147
Rocks (%)	41	6.50	3.23	49	6.86	2.32	1.17	147
Slope Hillside (Degrees)	20	3.38	1.68	49	8.4	1.35	0.68	147
Slope site (Degrees)	17	3.53	1.76	49	7.12	1.3	0.66	147
GISslope (Degrees)	8	1.68	0.84	49	4.28	0.69	0.35	147
Estimated Terrain Ruggedness (TRE)	0.21	0.02	0.01	49	0.06	0.01	0.00	147
Canopy cover (%)	20	8.80	4.38	49	14.49	3.21	1.62	146
Distance to major roads (km) (ROAD)	4.00	0.65	0.32	49	3.44	0.39	0.20	147
Distance to human settlements (m) (SETTLEMENT)	6.18	0.87	0.43	49	5.8	0.5	0.25	147
VRM	0.010	0.005	0.003	49	0.005	0.002	0.001	147

3.1.2 Den site characteristics for estimated minimum area size

Minimum area size (see Appendix 1 for details) was estimated for 42 dens based on sings of use and the mean was 29 m (SE $\pm$ 2.85, Table 5). Similarly to the 20 m radius, berry shrubs was the major ground cover type (76%) but other types such as, lichen (12%) and moss (12%) were found at some sites (Table 3). Similarly to 20m scale, no particular aspect was selected (Figure 3), but mean slope measured at den site was 17° (SE $\pm$ 1.76) which was lower than for the hillside at 20 m scale. Canopy cover was estimated at the center of the den site and mean canopy cover was 20% (SE $\pm$ 4.38, Table 5).

3.1.3 Structures

Main structure at den sites was boulder (n = 46) or a rock wall (n = 3) (Table 6). Boulders were found at all den sites and 41 (84%) of them had 5 or more boulders (Table 7). Six dens (12%) had boulders combined with fallen logs, and dens with rock wall as a main structure (n = 3), also had other structures present (boulders 3/3, logs 2/3, standing trees 2/3, Table 6). Standing spruce trees were present at nine dens (18%, Table 6), and trees were usually in close proximity to the estimated center of the den or providing cover to the center. All dens (n = 49) provided cover for the cubs without snow, although there were differences how much cover was available.

Table 6. Main structure type for number of dens (N) and proportion of dens (%) and number and proportion of dens where structure types were present at female wolverine reproductive den sites in forest landscape. See Appendix 1. for details on survey protocol.

Main structure type	N	%	Structure type present	N	%
Boulder	46	94		49	100
Rock wall	3	6		3	6
Log	0	0		6	12
Hole in the ground	0	0		0	0
Other	0	0	Standing spruce tree	9	18

Table 7. Number of boulders at female wolverine reproductive den sites in forest landscape with the number of dens (N) and proportion of dens (%) in each category. See Appendix 1 for details on survey protocol.

Number of boulders	N	%
1-5	8	16
5-20	22	45
>20	19	39

3.2 Female wolverines den site selection in boreal forests

Two global models, CSg and Dg including all variables used in *a priori* candidate models set, performed relatively well using cross validation and ROC as a goodness-of-fit test (cover and safety global model: CSg mean AUC = 0.84, disturbance global model: Dg mean AUC = 0.85, see Figure 4). Therefore the set of candidate models based on these variables should also perform well to represent the data. The global model in G -model set, Gglobal15, received mean AUC = 0.62, which indicates very poor predictive ability and therefore sub-models based on those variables might not perform any better. Therefore, G-models were kept in separate analysis. For the CS and D model sets, models including TRE with quadratic effect performed surprisingly well and therefore this was tested separately (Table 8). Due to a high support on quadratic term, it was included into all models with TRE.

Table 8. Comparison of resource selection function models with quadratic estimated terrain ruggedness (QTRE) and linear estimated terrain ruggedness (LinTRE) to quantify the use of den sites (n = 49) in relation to availability (n = 147) within female wolverine's territory in forest landscape. Models with number of parameters (K) are compared using Akaike information criterion with second order correction for sample size (AIC_c) and Akaike weights (w_i).

Model	K	AIC _c	Δ AIC _c	w_i
mQTRE	5	110.17	0	0.93
mLinTRE	4	115.45	5.28	0.07

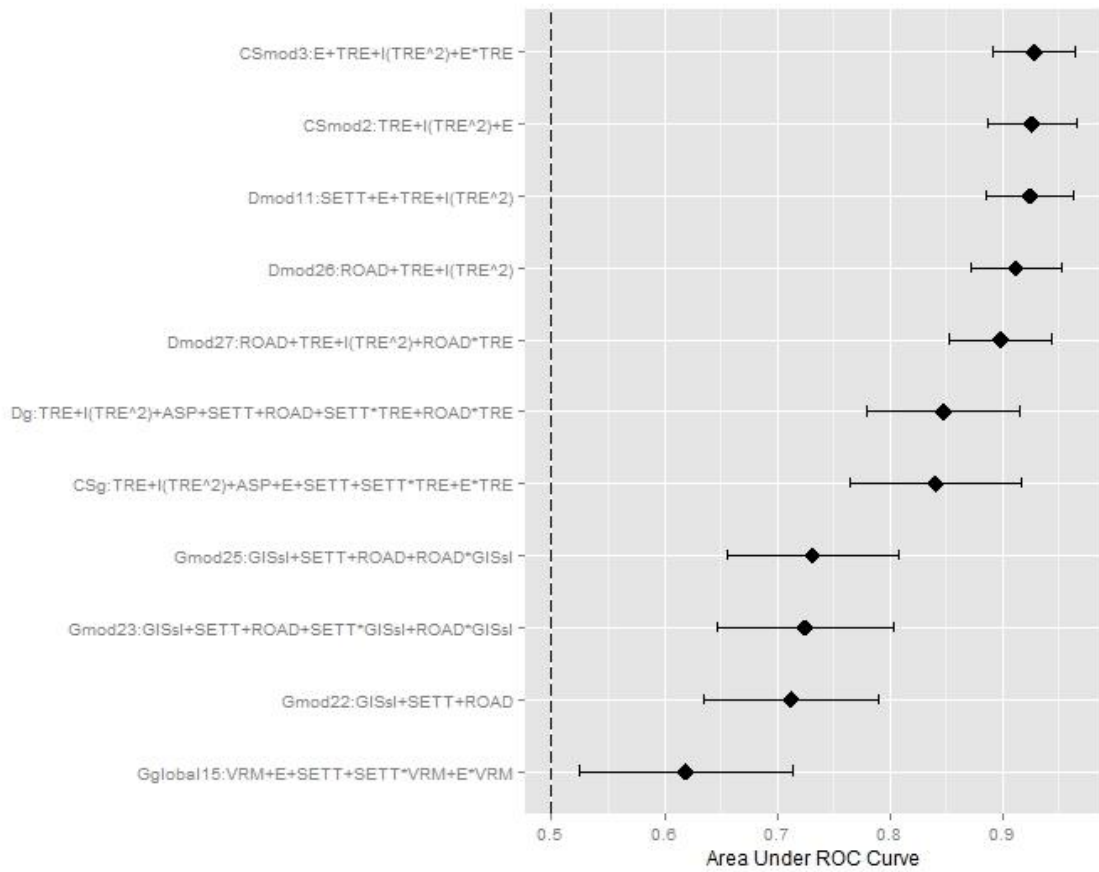


Figure 4. Forest plot representing the modified k-fold cross-validation goodness-of-fit, predictive value of the top models with relative operating characteristics (ROC) and area under roc curve mean (AUC, $\blacklozenge$) with upper and lower 95% confidence levels. See Methods for the criteria of predictive ability of AUC values. In models, $I(x^2)$ indicates quadratic effect and asterisk (*) interaction term.

Table 9. Comparison of the most parsimonious ($\Delta AIC_c < 2$) resource selection function models in the cover and safety (CS), and disturbance (D) model sets representing the use of den sites ($n = 49$) in relation to availability ($n = 147$) within female wolverine's territory in forest landscape. Models with number of parameters (K) are compared using Akaike information criterion with second order correction for sample size (AIC_c), Akaike weights (w_i) and evidence ratios (w_1/w_i) based on Akaike weights. In models, $I(x^2)$ indicates quadratic effect and asterisk (*) interaction term.

Model	K	AIC_c	ΔAIC_c	w_i	w_1/w_i
CSmod2: TRE+I(TRE^2)+ELEVATION	6	109.19	0	0.32	
CSmod3:ELEVATION+TRE+I(TRE^2)+ELEVATION*TRE	7	109.78	0.59	0.24	1.33
Dmod26:ROAD+TRE+I(TRE^2)	6	110.38	1.18	0.18	1.78
Dmod11:SETTLEMENT+ELEVATION+TRE+I(TRE^2)	7	110.85	1.66	0.14	2.29
Dmod27:ROAD+TRE+I(TRE^2)+ROAD*TRE	7	111.12	1.93	0.12	2.67

Two models, CSmodel2 and CSmodel3 performed nearly equally well in explaining the den site selection for female wolverines in this area (Table 9). Altogether, 14 models got some support ($\Delta AIC_c < 10$), and after removing models with $\Delta AIC_c > 10$, five models got substantial empirical support ($\Delta AIC_c < 2$). When comparing between those five, two models had higher weight of evidence (Akaike weights, w_i) compared to the rest of the models. The most parsimonious model, CSmodel2 TRE+TRE²+ELEVATION had the lowest AIC_c value ($AIC_c = 109.19$) and the highest Akaike weight ($w_i = 0.32$). The second most parsimonious model ($AIC_c = 109.78$, $w_i = 0.24$) was CSmodel3 with interaction term ELEVATION*TRE. Both models suggested that terrain ruggedness and elevation explained the den site selection in this area. The second most parsimonious models interaction term indicated compensation with higher ruggedness when in lower elevation areas. Four models had excellent (> 0.90) predictive value based on AUC values, with marginal differences (CSmod3: mean AUC = 0.928, CSmod2: mean AUC = 0.926, Dmod11: mean AUC = 0.924, and Dmod26: mean AUC = 0.912; Figure 4). The second most parsimonious model CSmod3 had the best predictive value although it had lower weight when comparing between models (Figure 4).

Table 10. Model average estimates (MAE) with unconditional standard errors (Unc SE) and 95% confidence levels for each explanatory variable in the most parsimonious ($\Delta AIC_c < 2$) resource selection function models in the combined CS and D-model set representing the den site selection within female wolverine's territory in forest landscape. Variables with MAE values 95% confidence intervals not including zero and therefore having an effect on den site selection of the den site in this area, are highlighted. In models, I(x²) indicates quadratic effect and asterisk (*) interaction term.

Variable	MAE	95% CI		Unc SE
		Low	Upper	
ROAD*TRE	-0.37	-0.96	0.21	0.30
ELEVATION*TRE	-0.35	-0.88	0.18	0.27
SETTLEMENT	-0.21	-0.80	0.38	0.30
ROAD	0.37	-0.25	1.00	0.32
ELEVATION	0.49	-0.06	1.05	0.28
TRE	3.64	2.39	4.88	0.64
TRE²	-0.80	-1.32	-0.27	0.27

All five models got substantial empirical support, the evidence ratios (w_1/w_i) between the most parsimonious model and the rest of the four models were very small indicating almost equal support explaining the den site selection in this area, and there were no big differences in the predictive ability of the models according to AUC values (Figure 4). Therefore model average estimates for individual variables were used to estimate the uncertainty brought to each model by certain variable. This helps to estimate the value of each variable in the top models and use them as indicators of better model. Model averaged estimates (MAE, Table 10) for variables indicated that the TRE and the TRE² were the only variables that were relevant (95%CI not including zero) in the most parsimonious models, with MAE for TRE = 3.55 (95%CI 2.3 < > 4.81 SE=0.64) and TRE² -0.81 (95%CI -1.32 < > -0.27 SE=0.27), therefore having an effect on the den site selection in this area. This was shown also in the predictive performance of TRE in the top model (CSmod2) (see Figure 5) where the probability of a site to be classified as a den site rose clearly with higher values of TRE, but it also showed that the quadratic effect was clear. With intermediate values of TRE, the probability for a site to be a den was high, but when approaching the highest and the lowest values of TRE, the probability was lower. Especially with high values of TRE, standard error expanded causing higher uncertainty to the prediction. The elevation was related to a very small rise in the predicted usage when approaching the maximum values. It was very unlikely to find a den site at the low elevation areas but the standard error expanded a lot when elevation gets higher values, indicating that both random locations and den sites can be found in higher elevations.

In the set of G-models, two models got substantial empirical support ($\Delta AIC_c < 2$). Gmod25 with $AIC_c = 204.66$ was the most parsimonious with $w_i = 0.50$ (Table 11). The second most parsimonious model Gmod23 had $AIC_c = 205.44$ and $w_i = 0.34$. Both most parsimonious models indicated that the distance to major roads and human settlements together with the slopes explained the female wolverine den site selection in this area. The most parsimonious model indicated possible compensation with slope, when den sites are situated closer to road. Gmod23 had an interaction for both settlements and roads with slope.

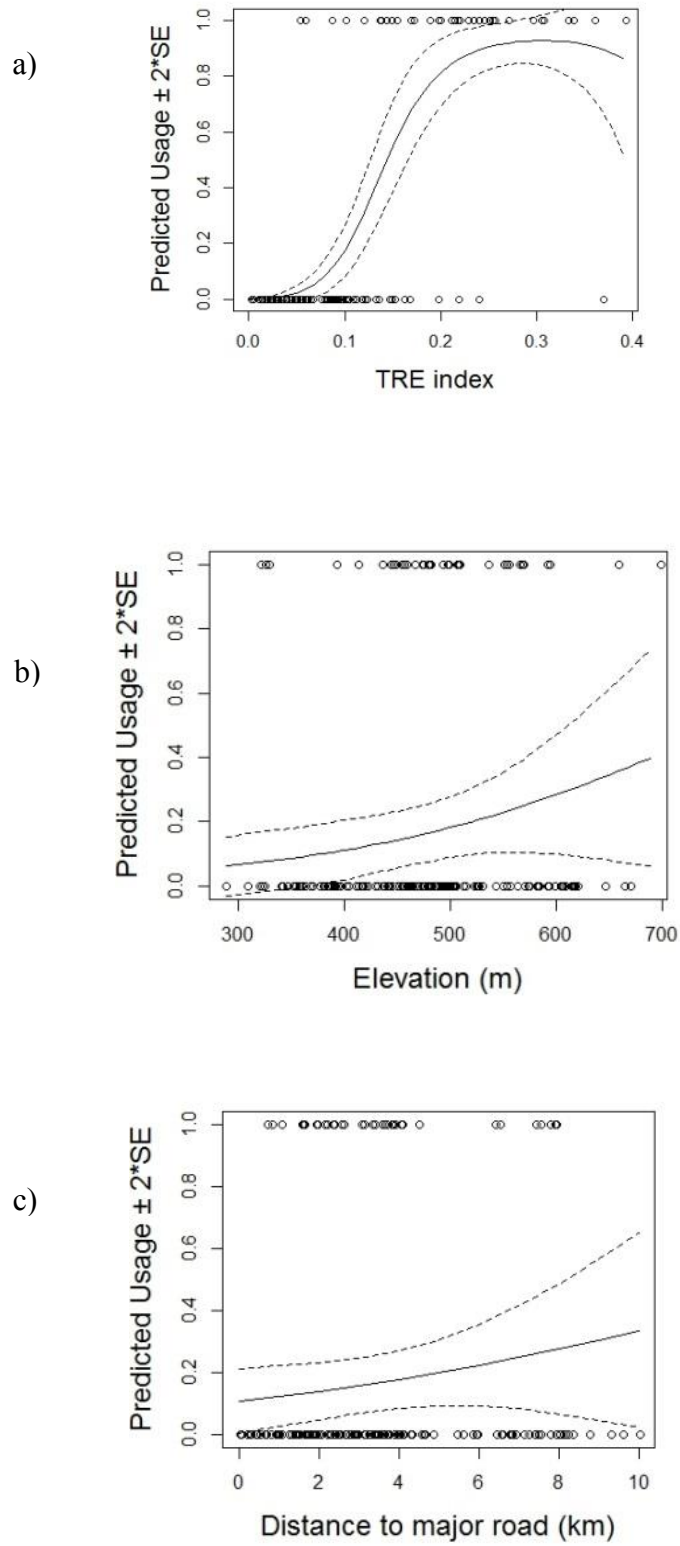


Figure 5. Predicted usage with $\pm 2*SE$ in relation to a) estimated terrain ruggedness (TRE), b) elevation in the most parsimonious model (CSmod2) and c) distance to major roads in the most parsimonious disturbance model (Dmod26). Associated variables standardized to a mean.

The evidence ratio for the most parsimonious model compared to the second model (Gmod23 $w_1/w_i = 1.47$) indicated almost equal support, so both models can explain the den site selection in this area. The goodness-of-fit and model predictive ability based on AUC value were fair (mean AUC >0.70) for both top models (Gmod25 mean AUC = 0.732, Gmod23 mean AUC = 0.725, Figure 4) and based on MAE, all variables in the most parsimonious model Gmod25 were relevant, except for SETTLEMENT which had MAE - 0.2 with 95%CI -0.66 < > 0.27 (SE =0.24) (Table 12). The predictive performance of settlements (Figure 6 a) indicated that the further the settlements were, the lower was the probability of the site to be classified as a den site, which indicated selecting locations closer to settlements instead of avoidance. Although, even when closer to settlements the probability to find a den site was very low indicating that the effect of settlements to den site selection in this area is very low. Therefore slope, distance to road and an interaction between slope and distance to road had an effect on den site selection in this area.

The predictive performance of the GISslope in top model (Gmod25) supported the interpretation of the model average estimates (Figure 6 b). It showed that when slope exceeded 15° the predicted usage was over 0.8. The predictive performance of distance to major roads showed weaker pattern, but the probability of a site to be classified as a den clearly got higher with longer distances to major roads (Figure 6 c).

Table 11. Comparison of the most parsimonious ($\Delta AIC_c < 2$) resource selection function models in the GIS- based (G) model set representing the use of den sites (n = 49) in relation to availability (n = 147) within female wolverine's territory in forest landscape. Models with number of parameters (K) are compared using Akaike information criterion with second order correction for sample size (AIC_c), Akaike weights (w_i) and evidence ratios (w_1/w_i) based on Akaike weights. In models, asterisk (*) indicates interaction term.

Model	K	AIC_c	ΔAIC_c	w_i	w_1/w_i
Gmod25:GISslope+SETTLEMENT+ROAD+ROAD*GISslope	7	204.7	0	0.6	0.60
Gmod23:GISslope+SETTLEMENT+ROAD+SETT*GISslope+ROAD*GISslope	8	205.4	0.78	0.4	1.50

Table 12. Model average estimates (MAE) with unconditional standard errors (SE) and 95% confidence levels for each explanatory variable in the most parsimonious ($\Delta AIC_c < 2$) resource selection function models in G-model set representing den site selection within female wolverine's territory in forest landscape. Variables with MAE values 95% confidence intervals not including zero and therefore having an effect on den site selection of the den site in this area, are highlighted. Asterisk (*) indicates interaction term.

Variable	MAE	95% CI		Unc SE
		Low	Upper	
GISslope	1.24	0.69	1.79	0.28
ROAD	0.77	0.30	1.24	0.24
SETTLEMENT	-0.20	-0.66	0.27	0.24
SETTLEMENT*GISslope	-0.24	-0.63	0.14	0.20
ROAD*GISslope	0.65	0.05	1.25	0.31

4 DISCUSSION

In this study the aim was to describe a typical female wolverine reproductive den site in Scandinavian boreal forest and to quantify the use of the resources in relation to the availability within their territories. The expected characteristics at the typical wolverine den sites would provide cover and safety in all weather conditions and the den sites would be found in remote, rugged areas, far from human settlements and major roads.

The typical descriptive characteristics for the female wolverine den sites were forested rocky areas with rugged terrain and all the dens had rock formed structures at present. The resource selection function showed that the terrain ruggedness and the elevation could explain the den site selection in this area and from the GIS –based models, the slope and the distance to major roads had an effect on the den site selection.

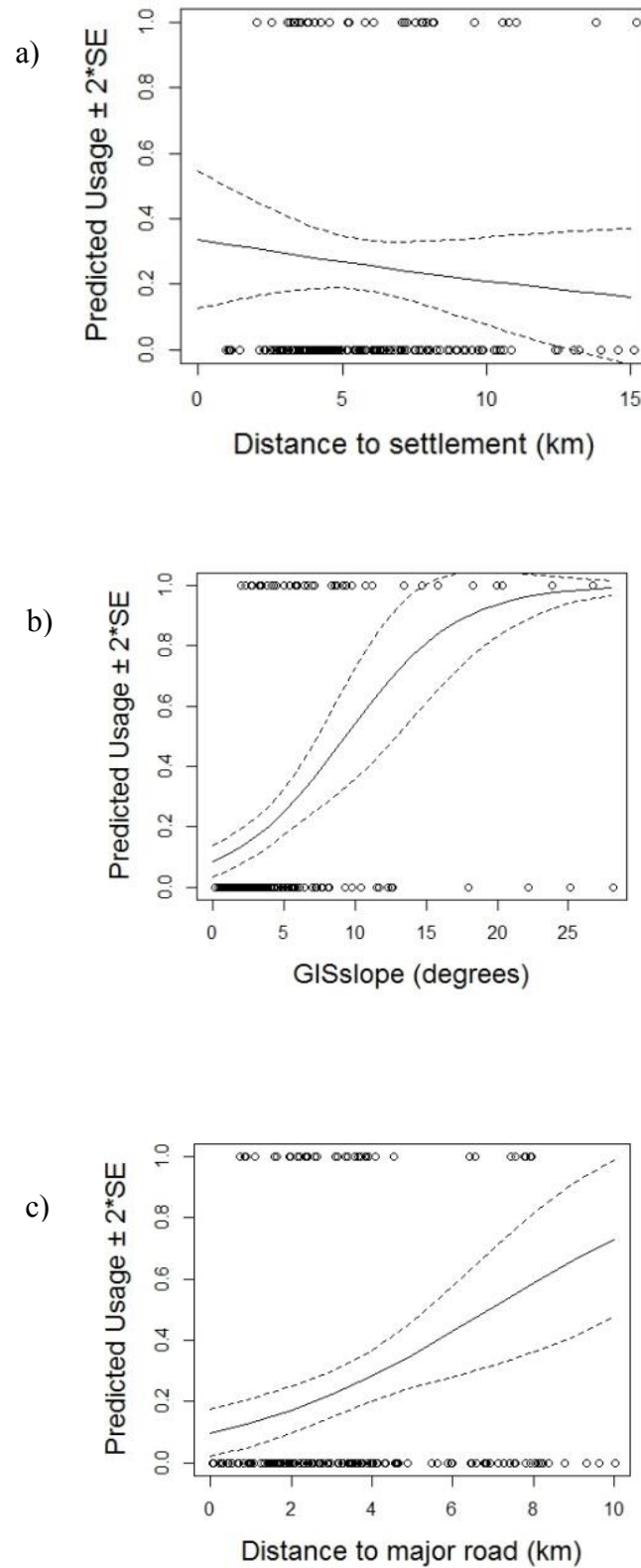


Figure 6. Predicted usage with $\pm 2 \text{SE}$ in relation to a) distance to human settlements, b) slope extracted from digital elevation model and c) distance to major roads in the most parsimonious model (Gmod25). Associated variables standardized to a mean.

4.1 Den site characteristics

The main habitat for dens was a forest which was also the main habitat for random locations (Figure 7). It is not surprising that dens were found in the forest since the amount of alpine and tundra habitat is limited in this area and majority of these are around the western region of the study area. However, in previous studies done on wolverine den site selection in alpine and tundra habitat types, dens are often found in more open habitat types when located close to alpine tree line or even above the tree line (Magoun & Copeland 1998, Landa *et al.* 1998b, Mattsing 2008, May *et al.* 2012). Therefore it is surprising that dens were not found in open habitats such as boulder fields or clear cuts, but this would indicate that these treeless or open habitats in alpine and tundra regions are

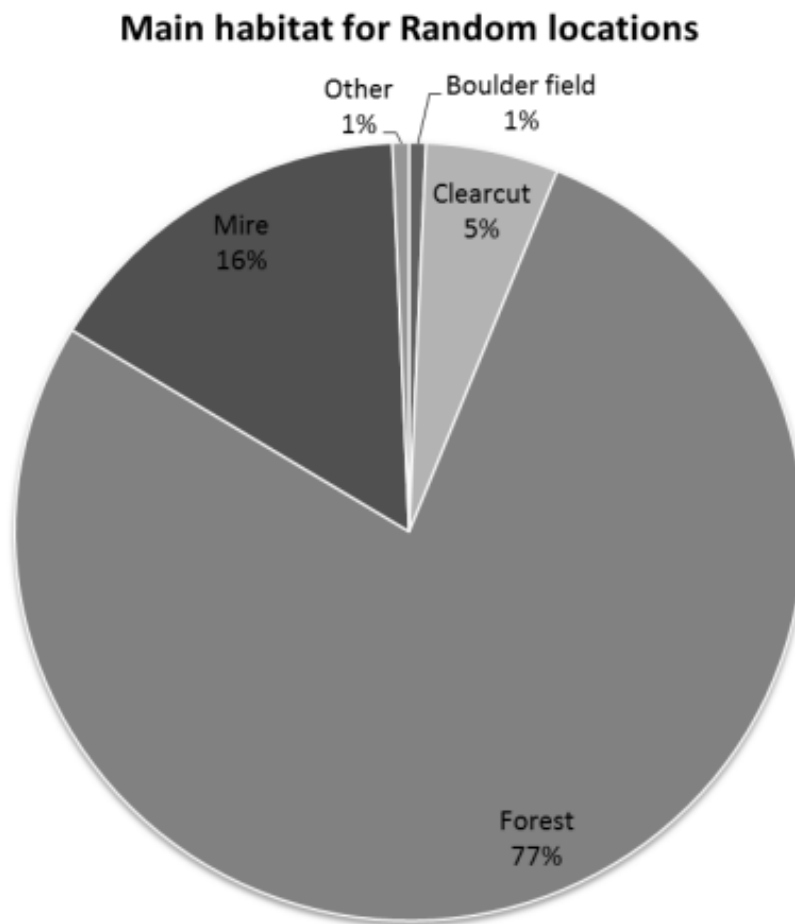


Figure 7. Proportions of categorized main habitat types for random locations (n = 147) within 20m radius from the center of the site. All dens (n = 49) were in forest habitat (100%).

selected for other characteristics, not for the openness itself. In Norwegian study (May *et al.* 2008) discuss that this type of habitat is likely chosen due to heavy human disturbance. Therefore open habitats might be chosen only because it correlates with the high altitude areas away from humans (May *et al.* 2006, May *et al.* 2008).

The dens were mostly found in mature (30-80 years) or old growth (>80) forests and the dominating forest type was a coniferous mixed forest. In this area an intensive forestry has a major impact on a forest structure. In highly managed areas, single species forests are favored by the forest industry and the forest age and a stand structure is regulated by repeated, intensive maintenance (Loman 2010). It seems though that wolverines are capable of finding these mixed coniferous forest stands despite the intensive forestry, since only 29% of the dens were in coniferous single species forest (spruce 10%, pine 15%, contorta 4%; Table 4).

In this study it was hypothesized that wolverines would prefer habitats that would stay dry throughout the denning season and therefore the mires would not be suitable places for dens. None of the dens were in the mire habitat, as expected, even though it is abundant in this area. In this study, mires were not used possibly because there were better sites available or mires and bogs in this area did not offer needed dry habitat with structures. On the other hand, large boulder fields would have been expected to provide a perfect dry habitat including cover and safety formed by boulders. The mean for the proportion of rocks at the den sites was very high (Table 5) and several of the dens were very close proximity to a habitat that could have been classified as boulder field, but this was not recorded in the protocol. It is also noticeable that only one random location was classified as a boulder field, i.e. the proportions of the large boulder fields in the area in general might not be very high. Also, possibly there may be some characteristics at the boulder fields that wolverines avoid, or forest as a habitat provides something more, that is important for successful denning.

Structures were present at all den sites as expected. Boulders were in a major role as a structure type and number of boulders was high as they were found on every den site, even though they were not the main structure type for all den sites (Table 7). Logs were present at multiple locations but were never the only structure providing cover at the site. It is possible that due to the lack of snow covered tunnels with early snow melt, boulder complexes with several entrances from different directions form a good combination of

cover and alternative entrances that are necessary characteristics for a good and safe den site. Rock walls were the main structure at three den sites, (one was used twice in consecutive years) but boulders were found in these sites also. Even though the number of the boulders was high, the amount of cover provided by structures varied a lot even though all den sites provided cover without snow. This could be due to differences in availability of suitable den sites within female's territory. If availability of den sites with good structures is restricted when in need for alternative den site, females might need to compromise finding suitable places close enough their previous den site.

4.2 Den site selection

Based on resource selection function the terrain ruggedness and the elevation had an effect on den site selection for female wolverines in this study area. Both two most parsimonious models represented the cover and safety hypothesis, indicating that the cover from weather and safety from intraguild predation were important. In this study, high elevation was seen as an indicator of difference in habitat selection from guild members. Rugged terrain, with addition that all den sites had cover for cubs without snow, indicated cover from the weather. The interaction term indicated selection for more rugged places when den sites were located in lower elevation areas. Based on the model selection, wolverines seem to favor rugged high elevation areas similarly to previous studies. If these are seen as indicators of avoidance of intraguild members in lower areas (May *et al.* 2008) it is possible that risk of intraguild predation is high in this area and therefore effects female wolverine den site selection.

Three disturbance models (Dmod26, Dmod11 and Dmod27) were also in the $\Delta AIC_c < 2$ group, and thus able to explain the den site selection in this area (Table 9). The most parsimonious disturbance model included distance to major roads with terrain ruggedness and therefore is very similar to the most parsimonious CS -model. It is worth noticing that the distance to major roads and the elevation were highly correlated and thus kept in separate models. Both of them seem to perform very well explaining the den site selection in this area, since they are both in the top 5 models and they perform equally well predicting the den sites based on AUC values (elevation mean AUC = 0.57 (95%CI 0.48 < > 0.66); roads mean AUC = 0.57 (95%CI 0.48 < > 0.66); Figure 8) and the predictive performance of usage is very similar. With such a high correlation, one variable could represent the other. If one of these would have been excluded in the analysis, the support

for the most parsimonious model would have likely been higher, since then the support would not be divided between models that were all almost as good (Burnham & Anderson 2002).

When looking at the importance of variables for CS and D-models based on model averaged estimates, only TRE linear and TRE with quadratic term have an effect on the selection of the den sites. The terrain ruggedness as an index represents very small scale ruggedness and places with high ruggedness in this study most often had a high amount of additional cover. The importance might be due to the fact that such places provide all needed elements: cover from weather and safety from predation and human disturbance. The elevation and distance to major roads does not have a strong effect, but based on predicted usage (Figure 6 c), major roads were avoided and high elevation areas favored to some extent. The poor predictive performance based on AUC values (Figure 8) also supports the interpretation that these two variables do not have strong effect on den site selection in this area.

With separated G -model set, two models stand out with $\Delta AIC_c < 2$ (Table 11). The most parsimonious model indicated that slope, distance to roads and human settlements have an effect to den site selection. The difference between the two top models was small, with only addition of interaction term indicating selection for steeper slopes when closer to settlements. Based on model average estimates and predicted usage, similarly to previous studies, steep slopes were favored and major roads avoided (Table 12, Figure 6), except for SETTLEMENT and SETTLEMENT*GISslope. Distance to settlements would have been expected to have an effect based on the clear avoidance shown in previous den site and habitat selection studies on wolverines, but based on MAE value, it does not seem to have an effect in the den site selection in forest landscape. Mean AUC was >0.5 which indicates poor predictive performance when separating dens and random locations (Figure 8) and predicted usage plot for SETTLEMENT (Figure 6 a) supports the interpretation from AUC values. It is possible that since random locations are selected within females' assumed territory, if they choose to place their territories far from human settlements, the sampled random locations are within similar distances from the settlements. In this study especially, random locations for secondary den sites were only 2 km from the den site. The predicted usage (Figure 6 a) shows no clear selection for or against the settlements since slope of the line is near zero.

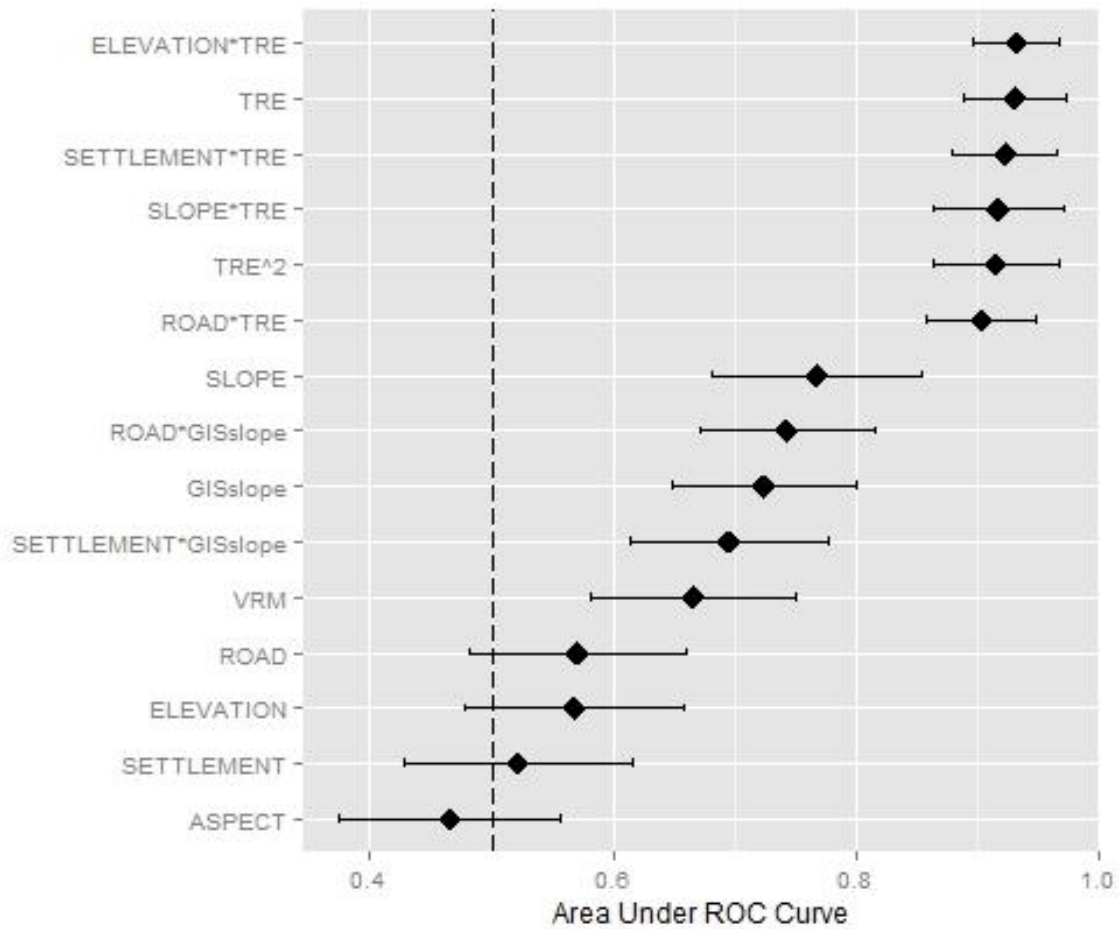


Figure 8. Forest plot representing the modified k-fold cross-validation goodness-of-fit, predictive value of the explanatory variables with relative operating characteristics (ROC) and area under roc curve mean (AUC, $\blacklozenge$) with upper and lower 95% confidence levels. See Methods for the criteria of predictive ability of AUC values. In models, $I(x^2)$ indicates quadratic effect and asterisk (*) interaction term.

The Global models' (CSglobal, Dglobal and Gglobal15) goodness-of-fit was not as high as would have been expected, which indicates that they are far too complex or they include variables that are not meaningful. Based on AUC for individual variables (Figure 8), it seems that if the threshold for prediction ability is > 0.7 (fair), only Gisslope, slope hillside, both TRE's and nearly all interaction terms have fair or better predictive value. It is interesting that all interaction terms get excellent predictive value even though based on MAE, only ROAD*GISslope had an effect on den site selection. It is unclear, if this is due to individual variation in availability or preference. With GLMM individual and year were random factors, but when testing the model's predictive performance, it is entered and run without random factors. Also it may have something to do with the fact that TRE and GISslope have such a high explanatory value, that even with variables that have only fair

predictive value, they make it possible to separate the den sites from the random locations. However, it is possible that when there are big differences in what is available for individuals it is hard to detect a preference with model averaged estimates (Beyer *et al.* 2010).

The snow model (CSmod4) including terrain ruggedness, elevation and aspect got very little support compared to the most parsimonious models ($AIC_c w_i = 0.01$). Both elevation and aspect as individual variables had poor predictive value. Aspect was not included in any of the most parsimonious models and with ROC curves, it failed to predict the separation of den sites and random locations (mean AUC = 0.465 (CI 95% $0.37 < 0.56$ Figure 8)). The aspect plots (Figure 3) reveal that no particular aspect was selected even though the plot for aspect for den sites shows that sites are accumulated slightly both towards northeast and southwest. This could indicate the overall orientation of the topographic features in this area. Ridge lines follow the northwest- southeast line (Figure 1) and therefore, hillsides are found on the opposite sides of this line. Therefore it is possible that hillsides were selected for the slope or the ruggedness, not for the orientation towards the aspect where snow accumulates or where late spring thaw occurs. Otherwise it would have been expected to see more clear selection for the aspect that correlates with snow accumulation in this area.

From variables, terrain ruggedness measured at site (TRE) had the strongest predictive ability but when compared to VRM which was distracted from GIS layers, they are not highly correlated. VRM's predictive ability is much lower than that for TRE and it was not included in the most parsimonious models in the G-model set. This indicates that these small patches of boulder complexes or rock walls with enough cover for cubs are important but these do not show up through VRM. This makes creating predictive maps based on GIS layers very complicated. This could be due to the fact that VRM was calculated from +50 m grid digital elevation model. VRM might perform better if calculated for example from 5 m. It still might fail to detect these small rugged patches that were found by visiting these sites and measuring TRE on ground, but when combined with other GIS-based variables that have an effect on den site selection, it could improve the accuracy when creating predictive habitat maps for female wolverines.

4.3 Evaluation

The amount of collected data was quite high and not all was used in this study. Most of the data will be used in future studies and therefore was not included in this thesis, but it was collected by the author to be able to collect as much data as possible by visiting sites at once. Many of the variables in field protocol are subjective estimations that can be affected by individual differences, if collected by several persons. In this study, all sampled den sites and majority of random locations (92%) were visited and measured by author herself and this minimizes the variation caused by subjectivity and therefore adds the reliability of the interpretations.

The food availability was not part of this study as an indicator of a suitable characteristic for a den site, even though Landa *et al.* (1997) already speculated that the variation in reproductive success is related to habitat quality between den sites and that food availability is a good indicator of quality. Food availability has an effect for reproduction success for wolverines (Persson 2005) and it has an effect on the habitat selection of female wolverines at least in larger spatial scales (see section 1.2). Thus it could be argued that in this study, one important aspect of den site selection is neglected. On the other hand, Rauset *et al.* (2013) suggest in their habitat selection study within wolverine home ranges (territories) that since wolverines are capable of caching, scavenging and travel long distances they are not so much restricted by food availability within their territory. Therefore, even though females with cubs restrict their movements during the denning period (Landa *et al.* 1998a) they are still capable of using their whole territory while leaving cubs in the den. This effective space use and caching behavior allows them to focus on other aspects such as providing safety and shelter for cubs, when selecting a den site.

4.4 Conclusions

In overall, wolverines in boreal forests show selection for similar characteristics as they show in other studies in different habitat types. However, there were also some differences in preference. Rugged terrain with steep slopes was favored, but the preference for high elevation and avoidance of human disturbance was not as clear as was expected based on the previous studies. Due to differences in availability and characteristics in this study area compared to alpine and tundra habitat, the underlying reasons for these preferences might be different. In alpine and tundra habitats the snow possibly plays an important role in the denning and reproduction success. Therefore, these similar characteristics in those habitats

might be selected due to the support for the snow accumulation and late spring thaw and thus the additional cover provided by structures may not be needed due to deep snow cover. In this study, the importance of structures in forest landscape was shown both in the descriptive study and in the form of TRE in the resource selection function.

For territorial animals available denning habitat is only what is found within their territory. Differences between territories can be significant and some individuals might need to compromise with some criteria to find suitable sites. If sites with good solid structures are rare within females' territory, boulder complexes close to settlements or roads or small holes under rocks might be the only structures available. In this trade of situation (Mysterud & Ims 1998) wolverines need to compromise for example for the remoteness of the site to find enough cover for the cubs.

The purpose of the G -model set was to see if variables based on GIS- layers could be used to create predictive habitat selection maps for den sites for female wolverines without intensive field work as in this study. With AUC values, top G-models got fair predictive value and based on the model average estimates, maps with slopes and distance to roads could be created to get an average idea of the amount of suitable habitats within forest region. Using smaller scale digital elevation map could improve the accuracy and predictive ability of the variables based on DEM and GIS-models in general.

4.5 Future studies

Restricting the study area mainly in forest region gives a good description on what are the typical characteristics in this habitat. May et al. (2012) had den sites both in forest and alpine habitats, but probably the low number of dens in the forest region did not give an opportunity to detect possible differences in den site selection. To expand to this type of study, with known individuals with territories including both habitat types, would make it possible to see which of these habitat types is preferred when both are available. This might clarify the reasons behind the preference whether the habitat type itself is significant or the remoteness or the provided cover and safety for the cubs is more important.

Since wolverines express some seasonal habitat shifts and especially females seem to be sensitive to human disturbance during the denning season, the wolverine habitat selection in different spatial scales in boreal forests needs to be studied further and consider more carefully how to quantify the human disturbance in this type of a habitat, where the

disturbance is highly variable between seasons. In this study, the used variable was a linear distance to human settlements and those settlements were selected based on the assumption that when classified as settlement, it is likely to have all year round use. Settlements with multiple houses are not guaranteed to be used all year round and therefore, not avoided. In these areas, with abundant human use, it might be more revealing to use house and road density instead of linear distance to quantify the disturbance. Especially for houses, the disturbance is likely higher in areas with higher density and more occasional or even absent, in lower density and therefore, would give more realistic estimation for the disturbance. Also, linear distance does not take into account possible geographical boundaries such as lakes, rivers or hills between den sites and roads and houses.

Wolverines are said to be limited by environmental factors such as persistent snow cover and their preference for alpine and tundra habitat (Copeland *et al.* 2010, McKelvey *et al.* 2011). On the other hand, they seem to be able to find suitable den sites outside alpine and tundra habitat and reproduce successfully, since they are observed to occupy their old distribution range now (Chapron *et al.* 2014) even though boreal forests are areas which face the most rapid changes with warming climate (Parry 2007). On the other hand, May *et al.* (2006) stated that human disturbance has the highest impact on wolverine habitat selection in all spatial scales. Their worldwide distribution is limited to the most remote areas with low human impact, but also within this range, their individual territories are selected by their remoteness, not by habitat type (May *et al.* 2006). Also, the use of habitat within their territories indicates avoidance of human disturbance (Rauset *et al.* 2013) especially on females (Krebs *et al.* 2007). Copeland (2007) speculates whether this is due to the preference of wolverines to this cold and rugged high elevation habitat type itself, or if it is really selected because of the fact that there are no humans. There are not enough studies done on habitat selection of wolverines in different types of habitats other than alpine and tundra regions for proper comparison of the habitat preferences. It is difficult to quantify the snow cover at site reliably due to high variation in snow accumulation between locations and between years to be able to study the true importance of snow cover for wolverine reproduction success. It is also difficult to quantify the human disturbance reliably. The knowledge of whether the limiting factor for wolverine distribution and population growth is the climate change or human disturbance would be valuable information for the future management of the species.

What ultimately defines a suitable den site is the reproduction success and cub survival rate. These monitored dens were signed as reproductive den sites but there was no follow up if these cubs survived or not. A long term ecological studies in the forest region are needed to be able to link habitat characteristics to higher cub survival rate. This would give tools for species management and habitat management within the wolverine distribution range.

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Appendix 1: Field Protocol

Following protocol and data sheet was used to collect data from all survey locations. Same protocol was used both known den sites and associated random locations so that all sample sites were treated the same.

Pictures:

Pictures were taken from all sites, first to identify the location and then to four bearings, North, East, South and West. From known den sites, photos from all interesting details and structures, but also overall surroundings were taken, to get a better description of each den.

Coordinates:

Survey coordinates: Location coordinates from den site inventory or created random locations to find the place.

Assumed den site: New coordinates were taken at the actual den site centre, if location, based on signs of use, differed from survey coordinates.

Minimum area size: Rough estimation of the minimum den site area based on signs of use (toilets, daybeds, prey remains) as m². Size was not estimated for random locations and if no signs were present. This was recorded to estimate the difference of the den site area between individuals and between primary and secondary dens.

Collector Initials: These were recorded to be able to detect possible measurement errors between field personnel. If measurement errors exist later in a large data set, this can be taken into account when analysing the data.

HABITAT CHARACTERISTICS:

All these were recorded within 20 m radius from the center of the site.

Main habitat:

Habitats were categorized to Forest, mire, boulder field, alpine, clearcut, other. If site found in other, habitat type is specified.

Distance to productive forest: Nearest distance to the edge of a forest if, site is not in productive forest habitat. Measured with GPS.

Rocks %: Proportion of rocks with or without vegetation on in 20 m area.

Ground cover: Vegetation class that makes up the majority of the ground cover at site. This is categorized as herbs, grasses, berry shrubs, moss, lichen or sphagnum.

FOREST: When site is at forest, this data is recorded at site. If site is not in the forest, recorded from the nearest forest.

Forest type %: Proportions of different tree species present. For each tree species, (spruce, pine, contorta pine, birch, other deciduous) the proportions are estimated separately. Total number equals 100%.

Ground cover in the forest: Vegetation class that makes up the majority of the ground cover classified as herbs, grasses, berry shrubs, moss, lichen or sphagnum. This is repeated here due to the possibility that actual site is in other type of habitat than forest, and ground cover is different in the nearby forest.

Age: Forest age is estimated from major tree species in four categories: successional (0-10), young forest (10-30 years), mature (30-80), old growth > 80

Height: Height of the average tree constituting the forest measured with height meter.

Basal area: Measured with relascope by standing in the middle of the site and holding the string close to your eye and pointing the relascope towards nearest tree at breast height. If the tree fills the hole in relascope, it is counted. If there is space between the inner edges of the relascope and the tree trunk, it's not counted. Turn around 360 degrees estimating all trees in the area and count how many trees are big enough to fit in the relascope. Basal area: N of trees*Basal area factor (1 in this study) (Department of Environment, Climate Change and Water 2010).

DEN SITE: characteristics at the estimated minimum area size or in 5m distance from the estimated center of the site.

Aspect Site: Compass bearing at the site, measured by compass standing at the center of the site, back against the slope and facing the open side. If on flat ground, aspect is 0.

Aspect Hillside: Compass bearing at the hillside (broader scale), measured by compass standing at the hillside back against the slope and facing the open side. If on flat ground, aspect is 0.

Slope Site: The angle of the slope is measured with clinometer at the center of the site. If on flat ground, slope is 0.

Slope Hillside: The angle of the slope measured with clinometer at the hillside. If site is on flat ground, slope is 0

Canopy cover %: Estimation of the winter canopy cover at the center of the site with densiometer (4 cm diameter, 7.5 cm long tube), by setting densiometer directly above and estimating the proportion of canopy cover covering the 4cm diameter hole. Estimation is done without leaves.

Estimated terrain ruggedness (TRE): TRE is a sum of linear distances measured with 10 m rope from the center of the site uphill (or north if flat surface) by following the shape of the terrain. Measure the straight length from the center to the 10m mark in the rope with measuring tape. Repeat this to all four directions, downhill (south), and perpendicular to right and left (or east and west). Length is relative to the maximum possible distance (40 m). TRE index is calculated ($TRE = ((40-L)/40)$) (May *et al.* 2012).

Ground cover: Vegetation class that makes up the majority of the ground cover in minimum area or 5m distance. This is categorized as herbs, grasses, berry shrubs, moss, lichen or sphagnum.

DEN STRUCTURE:

Structures are recorded at the minimum area size or at 5m radius from the center of the site.

Main den structure: The main structure providing cover or forming the site. Categorized as Boulder, Rock wall, Log, Hole or Other. If other, then specified.

Boulder: Counted number of boulders categorized as 1-5, -20 >20

Rock wall: Continuous solid rock walls that are not formed from boulders. Width and height of the wall are measured or estimated if can't be measured

Log: Structures that are dead or live trees down on the ground forming cover for the site. Number of the logs (up to 10) is counted.

Hole in the ground: Structure is counted as a hole in the ground if it is completely formed from ground and no rocks are forming any part of the hole. (If there are rocks, then recorded as boulder). Width and height and depth of the hole are measured.

Other: Other structures at present. Only structures at the minimum area size or at the 5m radius from the center are recorded.

Part of the site open (in summer): Categorized as YES or NO. Categorized as yes if there is cover only when snow is at present. Categorized as No if structures at present provide full coverage at the site for cubs.

Comments and findings: Drawing or description, notes of interesting details and findings at the site.

FWP den site protocol					Coordinates:	
Den ID:		Survey coordinates:		N:	E:	
		Assumed den site:		N:	E:	
Minimum area size:	Elevation GPS:	Date:		Collector Initials:		
Habitat characteristics 20m						
Main habitat:		Distance to forest:				
Forest		Mire	Boulder field	Alpine	Clearcut	Other
Rocks %		Ground cover				
		H	G	BS	M	L SP
Forest						
Forest type	Spruce%	Pine%	Contorta%	Birch%	Other deciduous%	
Ground cover	Forest age:		0-10	Height		Basal area:
	10-30	30-80	>80			
Den site						
Aspect (den)		Aspect (hillside)		Slope (den site):		Slope (hillside):
TRI:	Up/N:	Down/S:	Left/E:	Right/W:		
Ground cover						CanCo %
H	G	BS	M	L	SP	
Den Structure (main den structure X)						
Boulder	number	Average boulder		Largest boulder		
		width/height		width/height		
	1-5, -20, >20					
Rock wall:		Width		Height		
Log:	number	Width (at den)		Length	Species	
Hole in the ground	width/height	min. depth		Describe in comment		
Other						
Site modification				Part of den site open (without snow)		
Y / N How:						
Comments and findings:						

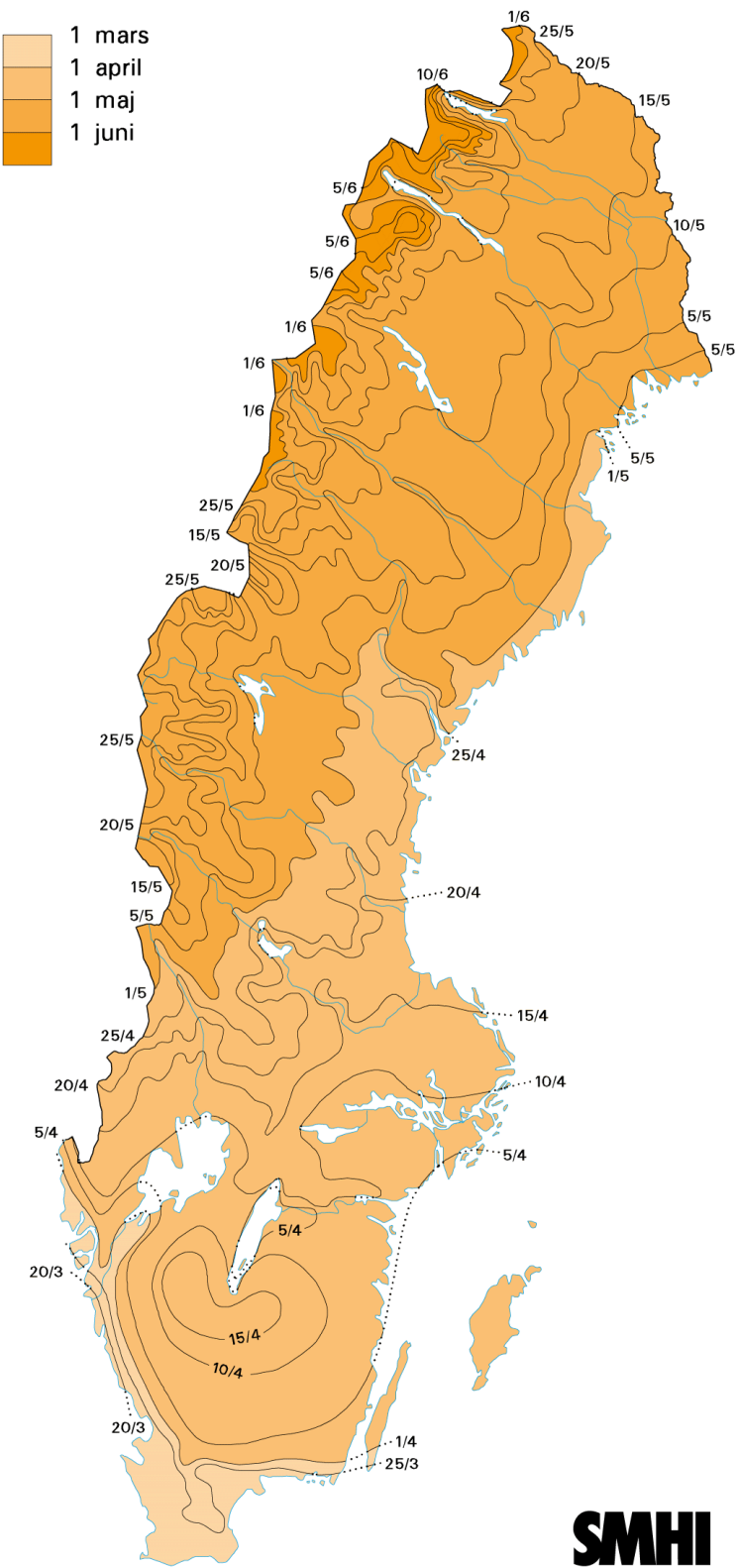
Appendix 2. Variable table

Variables used in resource selection function to quantify the use of resources in relation to availability and reproductive den site selection within the female wolverine (*Gulo gulo*) territory.

Variable	Type	Value	Description
Usage	Nominal	Binomial	0=random site, 1=Den site
Individual	Nominal	Individual ID	ID number of the wolverine using the den site from National wolverine monitoring program. For random sites, the ID of the individual using the den site for which the random location is created for.
Main Habitat (HABITAT)	Nominal	Categories	Main habitat type in 20m: Forest, Mire, Boulder field, Alpine, other
Rocks %	Proportional	%	Proportion of rock with or without vegetation on top
Slope Hillside (SLOPE)	Measurement	Degrees	Slope measured with clinometer. On flat ground =0 (see details on Protocol)
Estimated Terrain Ruggedness (TRE)	Measurement	Index	Sum of 4 measurements with 10 m rope from the center point put in to relation with max distance (40m) 0 non rugged, max 1
Nmbr of boulders (BOULDERS)	Nominal	Categories	Number of boulders at site , 1-5, -20, >20
ELEVATION	Measurement	m	Extracted from 50m digital elevation model (DEM) for each point (Lantmäteriet 2010).
ASPECT	Nominal	Categories	Compass bearings measured at site categorized as 315°-45°=N, 46°-135°=E, 136°-225°=S, 226°-314° =W, No aspect=Flat
GISslope	Measurement	Degrees	Extracted from 50m digital elevation model (DEM) for each point (Lantmäteriet 2010).
Distance to Road (ROAD)	Measurement	km	From vector form road map provided by Swedish Lantmäteriet (Lantmäteriet 2014), only roads classified as major roads, that are likely to be plowed during the winter were selected to create distance raster. The distance for dens and random locations to major roads was extracted from this layer (Figure 2).
Distance to human settlements (SETTLEMENT)	Measurement	km	From point layer with buildings in vector form road map provided by Swedish Lantmäteriet (Lantmäteriet 2014), only points classified as settlements with several houses that are likely to be inhabited during the winter (excluding cabins and huts) were selected to create distance raster. The distance for dens and random locations to human settlements was extracted from this layer (Figure 2).
Vector ruggedness measure (VRM)	Measurement	Index	Vector ruggedness measure (VRM) is an index calculated from 50m grid Digital Elevation Model including slope and aspect. VRM indicates well areas that are both rugged and steep, but gives lower values to areas that are only steep, but not rugged (Sappington <i>et al.</i> 2007).

Appendix 3. Snow data

Climate map illustrating the medium value for last day with snow cover for normal period 1961-1990 defined by World Meteorological Organisation. The black circle representing the approximate location of the study area. (SMHI 2014)



Snow depth (cm) from Ytterhögdal, Jämtland County, Sweden (see Figure 2. for location). Time period from 1.1.2012 to 31.5.2014 (SMHI 2015) .

