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Master thesis

Micro-scale selection of winter dens by brown bear (*Ursus arctos*) males in Southeastern Norway

Master in Applied Ecology

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Abstract

Den selection is a component of habitat selection, which occurs on several spatial scales. Brown bears (*Ursus arctos*) in the northern latitudes hibernate in dens during winter, which is their way to survive the period of cold conditions when food is scarce. On the smallest scale habitat selection is the most subtle, and for brown bears it has been found to be more linked to finding security than food. Microscale den site properties can also be important for the thermal conditions in the winter den. A successful denning period is important for the survival and reproduction of bears, which makes it essential to gain knowledge about the possible denning sites for the management of brown bear populations. In this study I examined whether male brown bears in Hedmark Southeastern Norway select for security, food and/or better thermal insulation when choosing a den site on the microhabitat scale. I also studied which factors in the denning habitat may affect the den type and occurrence of ant mounds (*Formica* spp., Hymenoptera), in which many brown bears use for denning. I used 41 winter dens used by male brown bears between 2001 and 2014 and 160 control points which were placed in the near surroundings of the winter dens. I did all my habitat measurements in the field without using GIS-based habitat data. I found evidence that the male bears in Hedmark selected for security in terms of horizontal consealment, either in the form of an ant mound or surrounding forest. The bears seemed to select for more horizontal concealment when choosing an open den. On the other hand, the bears seemed to select for less vertical cover when choosing an open den, which is probably due to the benefit gained from the thermal insulation from the snow cover. The presence of ant mounds was positively associated with selected den sites and within the denning habitat, ant mounds were more likely to be found in areas with bilberry dominance and in edge habitat.

Table of contents

1. Introduction

Habitat selection is a process in which individual organisms choose their preferred areas from a heterogeneous environment to feed and reproduce to increase their fitness and survival (Brown, Laundré & Gurung 1999; Morris 2003; Mueller & Fagan 2008). Habitat selection is a crucial ecological process since it has an influence on the interactions and distribution of species, population regulation, origin and maintenance of biodiversity and the assembly of ecological communities (Morris 2003). Individual organisms choose habitat by movement across multiple scales in space and time, and how and why that happens is one of the fundamental questions of ecological research (Nathan *et al.* 2008).

Habitat selection is a hierarchical process that occurs at multiple spatial scales (Johnson 1980). The individual first selects a home range and then within that range it decides which areas to use for different purposes, such as mating, denning and eating (Johnson 1980). Scale-dependency in ecological processes and patterns is increasingly appreciated among ecologists, which also means that what might be observed on one scale is not always transferrable to other scales (Wiens 1989; Levin 1992; Schneider 1994). Although ecological data gathered on the microhabitat scale are rarely used, such can strengthen the understanding of habitat selection processes by providing more detailed information about the microscale characteristics, such as concealment cover and food availability (Vroom, Herrero & Ogilvie 1980; Schwartz, Miller & Franzmann 1987; Sahlén, Støen & Swenson 2011; Pigeon, Côté & Stenhouse 2016).

Brown bears (*Ursus arctos*) are habitat generalists and widely distributed in the northern hemisphere (Hodder *et al.* 2014). Bears have adapted to winter conditions in areas of high latitude by hibernation, which helps them to overcome the season of scarce food availability and low temperatures (Hodder *et al.* 2014) . In Scandinavia, the bear spends approximately 6 months in the winter den (on average 161 days for males in the southern population) (Manchi & Swenson 2005). During the denning period its metabolism decreases to 50-60% and heart rate to 20-40% of normal levels and it can lose a third of its' body weight (Hellgren 1998; Manchi & Swenson 2005; Tøien *et al.* 2011). The time of den entry has been reported to be driven primarily by environmental factors, such as declining ambient temperature and arrival of snow (Evans *et al.* 2016).

The denning is important for the survival and reproduction of brown bears, which makes it important to the management authorities and land owners to understand, what is necessary for the preservation of potential denning habitat (Hodder *et al.* 2014). Additionally, most of the rare but still reported brown bear-human encounters in Scandinavia occur during the den entry period, and furthermore, the abandonment of bear dens has been suggested to be mainly due to human activity around the den site (Swenson *et al.* 1997). In cases of den abandonment bears move up to 30 km to den again, which has been documented to have a fitness cost (Swenson *et al.* 1997). Perhaps as a consequence, brown bears in Scandinavia have been reported to be sensitive to disturbance within a 1000 m radius from the den and especially vulnerable when the disturbance is occurring within a 200 m radius (Linnell *et al.* 2000).

Cover around the bear den is used as a measurement for security, since it can reduce predation risk and human disturbance (Wielgus & Bunnell 1995; Ordiz *et al.* 2011). The micro-habitat characteristics and den type can mitigate both disturbance and the weather effects and thus have been reported as important den selection factors (Hayes & Pelton 1994; Weaver & Pelton 1994; Hightower, Wagner & Pace III 2002). Bears also seem to select for increased snow cover, which improves thermal insulation (Vroom, Herrero & Ogilvie 1980).

Den type along other microhabitat characteristics influences the den selection by mitigating the effects of disturbance and cold weather (Hayes & Pelton 1994; Weaver & Pelton 1994; Hightower, Wagner & Pace III 2002). Brown bears have been shown to prefer excavated dens for stability, that are dug into ant mounds or under tree roots (Linnell *et al.* 2000). Open dens do not provide a barrier around the bear to protect it from weather or disturbance from humans and other animals. However, the microhabitat around an open den can provide insulation and concealment, which may be vital for the hibernating bear in terms of energy preservation, cub survival and den abandonment (Hellgren & Vaughan 1989). The importance of den type in offering physical protection and acoustic-, thermal- and maybe also odor- insulation, and the effect of these factors on the reproduction of bears and their vulnerability to disturbance have been speculated, but definitive conclusions remain unclear (Smith 1986; Oli, Jacobson & Leopold 1997; McDonald Jr & Fuller 1998; Linnell *et al.* 2000). In Sweden, adult male bears select for open nest dens over ant mounds compared to other age-sex classes (Elfström & Swenson 2009).

The red wood ants (*Formica* sp.) are important predators, scavengers and turners of soil comprising up to 10% of animal biomass in the Eurasian forests (Hölldobler & Wilson 1990). The availability of ant mounds is essential for the denning of brown bears, since bears prefer to dig their dens inside them for stability (Linnell *et al.* 2000). The occurrence of ant mounds has been reported to be associated with high soil fertility, forest fragmentation and presence of edge habitats (Punttila & Kilpelainen 2009). In Finland, the presence of mound-building ant species have been reported to be higher in old (140-year-old) Norway spruce forest and a young (5-year-old) clear cut areas compared to 20-year-old Scots pine stands and the mounds have been reported to be bigger in volume and taller in old forest than in young forest (Domisch, Finér & Jurgensen 2005).

The main objective of this study was to identify the main factors that influence the bear den site selection at the microhabitat scale. Specifically, I was interested in variables describing, concealment cover (visibility, tree age, dominant tree species, edge habitat), food availability (vegetation type, dominant berry species) and insulating properties (canopy cover, which is assumed to limit snowfall, is a proxy for the insulating properties of the snow cover) (Sturm *et al.* 1997). I predicted that bears select areas with more for concealment, which with my variables would mean less visibility from the den, older trees, more spruces compared to other tree species and no edge habitat present. I predicted variables associated with food availability, i.e. vegetation type or dominant berry species, not to effect the den site selection on this scale. I predicted that bears select for less canopy cover, and no branches directly above the den. I also predicted the occurrance of ant mounds and skirt spruces would be prefered by the bears compared to what is available. My objective was also to compare whether the microhabitat around open dens differs from ant mound dens, and I predicted that since the ant mound dens provide more security by themselves, the bears that use open dens select for more horizontal concealment from the surrounding vegetation, but less canopy cover to maximize the insulating snow cover. I also studied, which factors affect the distribution of ant mounds in these denning areas to find out whether the bears' apparent preferences are an artefact of the habitat selection of ants. In addition, I measured the bearings of the cavity openings of the ant mounds and tested whether there is a bias toward specific directions. Finally, I assessed whether the opening directions had more concealment cover from the surrounding trees compared to other directions of the ant mound dens.

2. Materials and methods

2.1 Study area

The study was done in Hedmark County in South-Eastern Norway (Fig. 1), which covers an area of 27 388 km^2, (61°N, 11°E). Hedmark borders with Sør-Trøndelag in the north, Oppland in the west, Akershus in the south, and Sweden in the east. The county is located in the boreal forest zone with dominance a of commercial coniferous Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) accompanied with smaller densities of deciduous trees, such as birch (*Betula* spp.). River Glomma runs through Hedmark from north to south. Higher elevations are in the northern Hedmark with mountains rising to above 2000 m.a.s.l. The lowest areas are in valley bottoms, which may be lower than 300 m.a.s.l. The climate is continental with warm summer temperatures rises up to 30°C and winter temperatures sinking down to -40°C, but the average temperatures are more moderate.

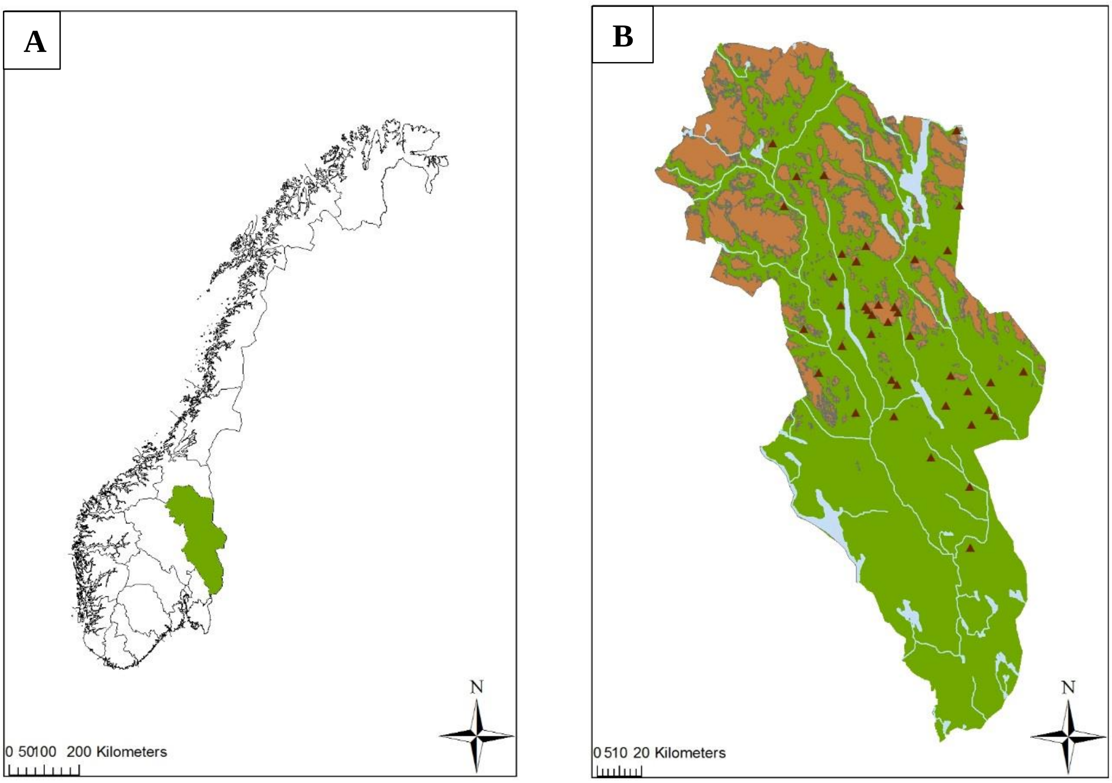

Figure 1: Hedmark County situated in Norway (A), and location of 41 bear dens used by brown bear males between 2001-2014 in Hedmark (B). Brown color represents the mountain areas above the tree line and blue color represents the rivers and lakes. Dark brown triangles represent the brown bear winter dens.

Urban settlements cover 0.4% of the study area, and the human population density is low with 7,5 persons per km^2 (Statistics 2017). Due to commercial logging for the past two centuries the forest gravel road network is extensive (0.68 km/km^2).

2.2 Study population

The number of brown bears in Norway in the mid-1800's was estimated by bounty records to be around 3,100 and the whole Scandinavian population was estimated to 4,750 individuals (Swenson *et al.* 1995). After a bottleneck in the 1920-1930s due to management policies, with a subsequent increase from the 1970s, the joint Swedish-Norwegian brown bear population is now centred on the Swedish side of the border. The population consists of four subpopulations, of which the bears in Hedmark are mostly young males dispersing from the southernmost Swedish subpopulation (Swenson, Sandegren & SO-Derberg 1998). Hedmark is at the expansion front of the population, and due to the low bear density and male-skewed sex ratio, bears in this peripheral area may differ in behaviour and habitat selection from the core population, by e. g. differences in home range size and -use (Wabakken *et al.* 1992; Wabakken & Maartmann 1994). The brown bears in Hedmark are the most numerous in Norway, but the bear density is still relatively low (Swenson 2000).

2.3 Data collection

In Hedmark county brown bear dens have been monitored since the 1970s, but I included only dens used by males from 2001 and onwards. The dens were located independently of telemetry, mostly by snow tracking in spring, and the coordinates were recorded using a handheld GPS (Global Positioning System) device. The initial sample consisted of 42 male brown bear winter dens used in 2001-2014, each used by different individuals and the den selected for the study was always the most recently used by each male. One den was discarded since the area had been logged after denning, leaving 41 dens for the analyses. Each den was compared to four systemically created control sites, placed to each cardinal direction, 50 meters from the actual den. I discarded 4 control points due to recent logging leaving a total of 160 control points.

I visited each den during the period in June-October 2016, and recorded different variables possibly influencing the micro-habitat selection of male brown bears in the periphery of their range. In addition, the same variables were recorded at all the control sites, namely visibility, tree age, dominant tree species, presence of edge habitat, vegetation type, dominant berry species, canopy cover, branch above the data spot, presence of skirt spruce, presence of ant mounds, den type and bearing of the cavity opening (if measurable) (Tab. 1).

Table 1. Micro-habitat habitat characteristics recorded at each den and control site. Vegetation type, canopy cover, tree age, and dominant berry- and tree species were measured within a 100m^2 circle around each data point.

Variable name	**Variable type**	**Definition of the measured variable**
Visibility	Continuous	Mean of the distances to next obstacle to each cardinal direction (m).
sq Visibility	Continuous	Quadratic effect of the visibility.
Tree age	Categorical	Tree age; young, medium, old, “other”.
Tree	Categorical	Dominant tree species; spruce, pine, birch, “other”.
Edge	Binomial	Edge habitat; whether the habitat changes within 50 m around the den or control site.
Veg. type	Categorical	Vegetation type; A, B, E, L and “other”. A, B and E are woodland vegetation and L is swamp. A is lichen/bryophyte and dwarf-shrub woodland, B is low-herb woodland and E is swamp woodland (Fremstad 1997).
Berry	Binomial	Dominant ground vegetation on the sample plot, in two classes; bilberry and other species.
Canopy cover	Categorical	Canopy cover above the data point, 0-25%, 25-50%, 50-75%, 75-100%.
Branch	Binomial	Whether a branch covers the den or control point exactly above
Spruce	Binomial	Presence of skirt spruces within the visual range of the data point.
Ant m.	Binomial	Presence of ant mounds within the visual range of the data point.
d.type	Binomial	Den type; ant mound, open.
Bearing	Categorical	Bearing of the cavity opening of the ant mound dens; N, E, S, W.

The visibility was measured in a straight line from each data point to all four cardinal directions, approximately 1 m from the ground. It was measured as the number of meters to the nearest obstacle that obstructed the visibility, usually trunks or branches of surrounding trees. The mean of the distances to the four directions was calculated for each data point. Finally, the mean of the visibility of the four control points was compared to the one of the den. In the models, I also tested the quadratic effect of visibility in addition to the linear effect. Tree age was classified first to five groups (Solbraa 2001), and then I reduced the groups into four categories: 1 and 2 were considered young, 3 medium and 4 and 5 were considered old forest. Sampling plots that were not in forest were classified as “other”. Dominant tree species was recorded within a 5.64 m radius (100 m^2) around each data point and classified to four categories (Tab. 1). Edge habitat was defined within 50 meters from the den or control point or within visual range. The distance of 50 meters was selected since the abiotic edge effects, such as variation in air temperature and light intensity have been estimated to vanish over a distance of 50 m (Murcia 1995). The edge was most often to a swamp, but could also be to a logging site or different forest habitat.

Vegetation type was detected within a 5.64 m radius (100 m^2) around the dens and control sites and classified into five categories (Tab. 1). Dominant berry species was detected within 5,64 m radius (100 m^2) around the den and control sites. The areas that did not have a berry species as dominant species, were classified as “other”. I reduced the dominant berry -variable to only include two categories; bilberry (*Vaccinium myrtillus*) and “other”, since rest of the categories had very few data points. Dominant berry species that I grouped to “other” were crowberry (*Empetrum* nigrum), bog blueberry (*Vaccinium uliginosum*), cloudberry (*Rubus chamaemorus*) and lingonberry (*Vaccinium vitis-idaea*).

I used two proxies for possible snow fall which I assumed would influence the thermal insulation. One was the canopy cover over dens and control points. Canopy cover was estimated by eye within a 5.64 m radius (100 m^2) around the data points to four ordinal categories 0-25%, 25-50%, 50-75% and 75-100%. The other proxy for the possible snow fall was whether or not there was a branch exactly above the data points. When a branch was very small and the tree species was birch, it was not considered as a cover since a deciduous branch loses its leaves in the winter. The occurrence of a branch was measured from approximately 1 m above the ground.

The presence of skirt spruces and ant mounds were detected within visual range of each sampling point. All sizes of ant mounds were recorded, since the factor is an indicator of the properties of the habitat sustaining ant mounds and not of the presence of available denning mounds at the sampling time. Skirt spruces were defined as spruces of which branches reached the ground creating a space resembling a hut between the trunk and the branches.

I measured the bearings of the cavity openings to assess whether these were evenly distributed. A bias to certain direction could indicate a thermal effect of digging into the ant mound from these directions. Bearing of the cavity opening was measurable for 26 ant mound dens. Fourteen of them had collapsed and lost their structure, but the opening was still measurable. Eight ant mound dens had lost their structure so that the opening direction was not possible to identify.

2.4 Data analysis

I did all the data analyses using RStudio 3.2.5. I ran three sets of models, including the variables listed in Tab. 1; visibility, quadratic effect of visibility, tree age, dominant tree species, edge habitat, vegetation type, dominant berry species, canopy cover, branch above the data point, presence of skirt spruces and presence of ant mounds. In the analysis where the presence of ant mounds was the response variable, it was not included as an explanatory variable. First, to compare the den sites to their respective control sites, I used conditional logistic regression models from the R package survival (Therneau 2014) and created resource selection functions (RSFs) (Manly *et al.* 2007). The response variable was a binary term with den locations coded as 1 and control locations coded as 0, and the total sample size was 201 (41 dens and 160 control points). Secondly, in the den type analyses I used generalized linear models (Nelder & Baker 1972). The sample size of the den type analysis was 40 (34 ant mound dens and 6 open dens), and did not include the control points. The response variable was a binary term with ant mound dens coded as 1 and open dens coded as 0. Finally, I did a post-hoc analysis of the presence of ant mounds using logistic generalized linear mixed models (Dougles Bates 2017), with the 201 locations from the den site models. The presence of ant mounds was the binary response with ant mounds present coded as 1 and no ant mounds present coded as 0. The random effect in this third set of models was the cluster ID, since the data were clustered into groups of five data points (one den and four control sites). Within the clusters, the dens and control sites were treated equally in this last set of models. The ant mound dens were not included in the count of ant mounds, and the same ant mounds could possibly be counted from more than one data points due to the study design.

I calculated the variance inflation factor (VIF) of all 10 explanatory variables using the car package (Fox 2016) in R to test for collinearity between the variables. For selecting the model I used a backward stepwise model selection procedure. The final models were selected according to the Akaike Information Criterion (AIC), and among the models with $\Delta AIC < 2$, I selected the simples model according to the principle of parsimony.

Model validation was performed by K-fold cross-validation (Boyce *et al.* 2002) to evaluate the predictive power of the selected models for den sites vs. control sites and the occurrence of ant mounds. The selected den type model was not possible to validate due to the small sample size, especially of open dens (Fig. 2). In both validation processes I split the data into two sets, a validating set and a training set. In the conditional regression model the validating set included 10 randomly selected den and their corresponding control points. The remaining data set of 31 dens and their corresponding control points was used as a training set. I ran the selected model with the training set and used the coefficients to predict the RSF values of the data point in the validating set. The five observations per den in the validation set were ranked from 1 to 5 based on the RSF value, and one control point was selected randomly for each den to compare the rank value to that of the den. I repeated this process 100 times, giving rank values for ten dens and ten corresponding control sites from each iteration. The RSF rank indicates how well the selected model predicts, whether a certain location according to its micro-habitat characteristics is a selected winter den. The predictive power of the model was finally assessed by comparing the 1000 den rank values to the corresponding control rank values using a Wilcoxon Signed Rank Test. This indicates whether the selected model consistently predicts higher RSF value for the den sites than for the corresponding control sites. The output of this test is a V statistic representing the sum of the ranks of the pairs in which the RSF rank was higher for the den than for the control sites. For the generalized linear mixed model, I split the data into a validating set containing 41 randomly selected data points, and a training set containing the remaining 160 data points. I ran the selected model with the training set and used the coefficients to predict the RSF values of the data points in the validating set. Because the selected model only included two binomial explanatory variables, the model could give only four different predicted values. I hence sorted the data points in the validating set into four ranked bins labelled 1-4 based on the predicted RSF values, with bin number 1 including the data points with the lowest predicted value and 4 including the data points with the highest predicted value. I then calculated the Spearman rank correlation coefficient (r_s) of the bin ranks and the proportions of ant mounds in the bins. I repeated this process 100 times, giving rank values and proportion of ant mounds for four bins calculated from 41 data points at each iteration. Finally, I calculated the average of the 100 Spearman rank correlation coefficients. A high mean r_s would indicate that the data points with ant mounds present generally get higher predicted values than the data points with no ant mounds present, i.e. that the model has good predictive power.

I reported the R^2 value of each model as a measure of how much of the variation in the data was explained by the model. For the glmm I report both the marginal R^2, which describes the proportion of variation explained by only the fixed factors and the conditional R^2, which describes the proportion of the variation explained by both the fixed and random factors.

I grouped the bearings of the den cavity openings into the four main cardinal directions. To investigate if there was a significant difference in frequency of these four directions, I conducted a chi-square test with an alpha level of 0.05. I calculated the mean of the visibility factor towards the tree directions that were not to the direction of the opening of the den. Then I ran a paired Wilcoxon test to see if the cavity opening is dug from a direction which has more horizontal cover from the surroundings compared to the other directions around the den.

3. Results

3.1 Male brown bear denning sites

The 41 brown bear dens were used by male bears between 2001 and 2014. The dataset contained one den per male and a total of 2-5 dens from each year (Fig. 2).

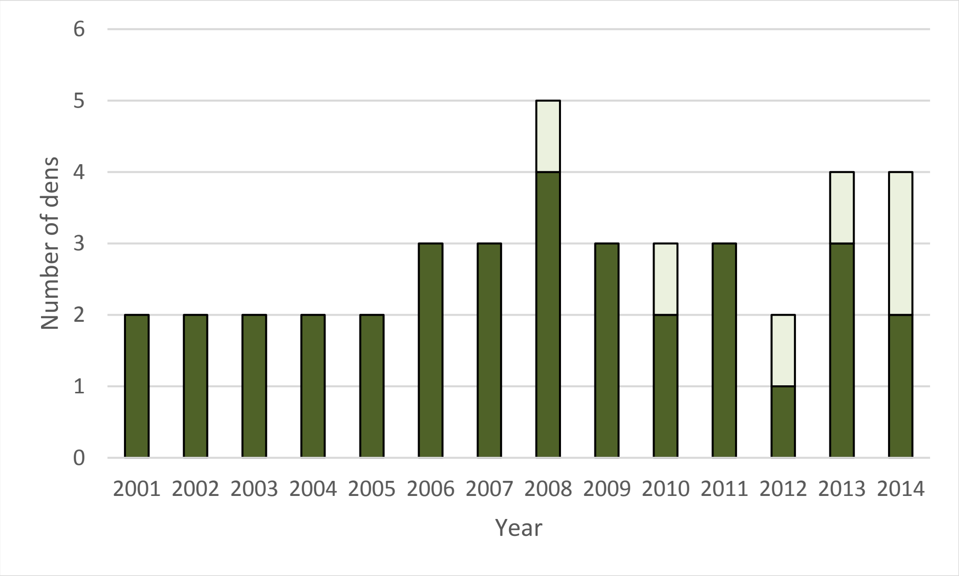

Figure 2: Number of dens of the two den types in different years used by different male brown bear individual in Hedmark County. Dark colour represents ant mound dens and light colour represents open dens.

I grouped the dens into two categories, open dens and ant mound dens (Fig. 2). In the data set one den was dug into the ground, so it did not suit to either of the groups. In the den type analysis this den was discarded, and the resulting sample size was 40.

3.2 Micro-habitat selection of denning sites

I included all predictors in the initial, full conditional logistic regression model (Tab. 2) because there was no significant collinearity among them (VIF < 5). The most parsimonious model included three variables; visibility, the presence of ant mounds, and the presence of a branch above the data point (m9, Tab. 2)

Table 2: The stepwise model selection for conditional logistic regression models comparing each den site to four control points placed 50 m from the den in each cardinal direction.

Model	Visibility	sq. Visibility	Tree age	Tree	Edge	Veg. type	Berry	Canopy cover	Branch	Spruce	Ant m.	AIC	ΔAIC
m1	*										*	126.58	19.57
m2											*	120.83	13.83
m3									.		**	115.31	8.30
m4									*		**	111.44	4.43
m5									*	.	**	112.29	5.28
m6									*	.	**	110.39	3.39
m7									*	.	**	108.65	1.64
m8	**								*	.	**	107.01	0.00
m9	**								*		**	108.16	1.15

According to the selected model, the relative likelihood of a site selected for denning by male brown bears decreased with increasing visibility (Tab. 3, Fig. 3A). The dens were more likely to have a branch straight above the sampling point, and to have ant mounds present in the area, compared to the control points (Tab. 3, Fig. 3B and C). These three variables were also the only ones that were statistically significant throughout the whole model selection process (Tab. 1). In addition, the presence of skirt spruces was included in the model with the lowest AIC (m8 Tab.2, estimate = 0.99561, SE = 0.57027). Within the models with ΔAIC < 2 the quadratic effect of the visibility was included (m7 Tab.2, estimate = -0.004250, SE = 0.007713).

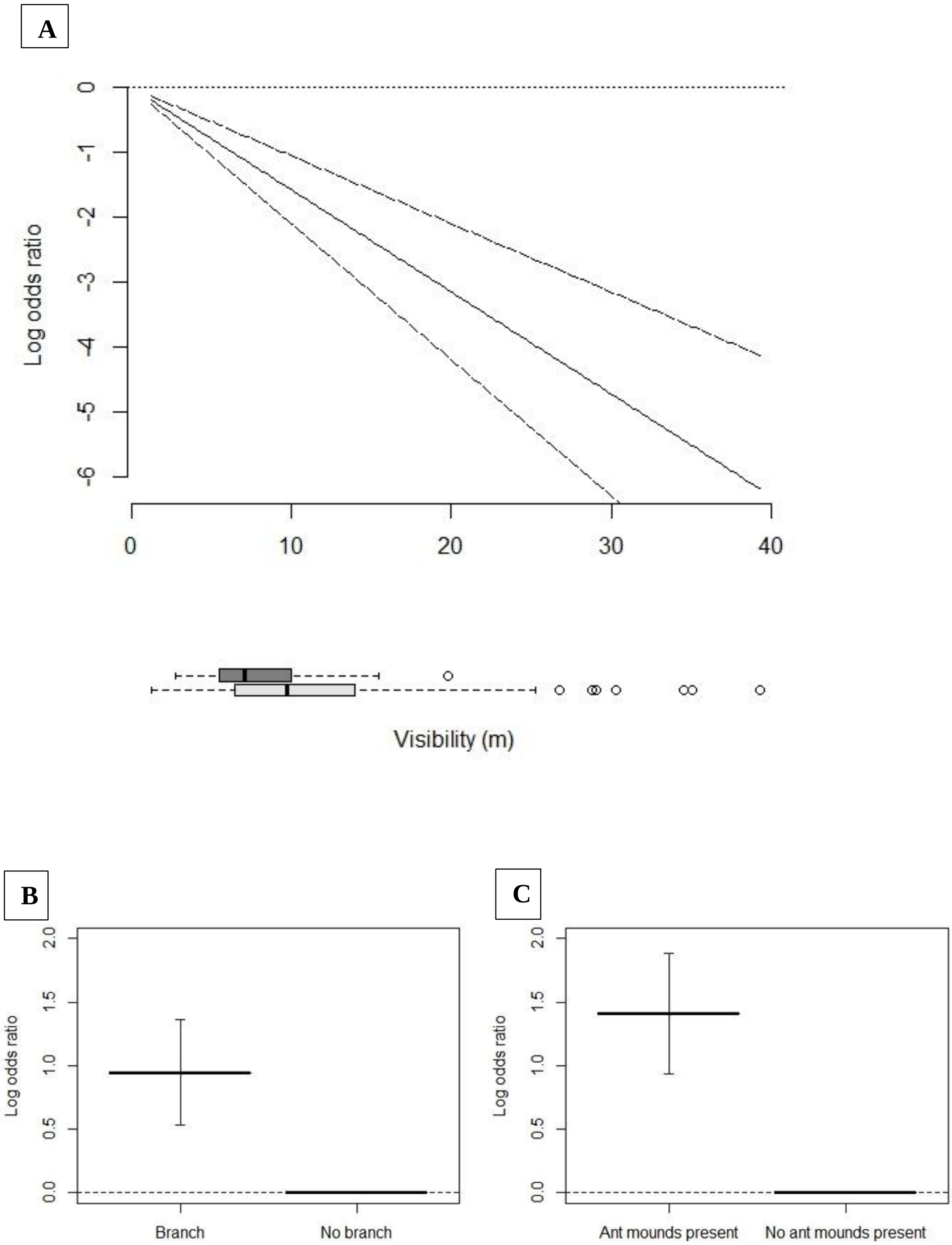

Figure 3: Predicted RSF score for brown bear den site selection at the micro-habitat scale in Hedmark County, Norway. A) Visibility (m) measured as sightability in the four cardinal directions. Spotted line represents the standard error. Dark horizontal box plot represents the distribution of den sites and lighter plot represents the distribution of the control sites. B) Presence of a branch above the den site; and C) Presence of ant mounds near the sampling plot. Vertical lines represent the standard error.

Table 3. Results of the selected conditional logistic regression comparing each den site to four control points placed 50 m from the den in each cardinal direction (m9, Tab.2).

Variable	Estimate	SE	Z	P
Visibility	-0.15776	0.05253	-3.003	0.00267
Branch	0.94600	0.41536	2.278	0.02275
Ant m.	1.41282	0.47426	2.979	0.00289

The R^2 of the final model was 0.13 with the possible maximum of 0.476. The K-fold cross-validation to determine the predictive power of the selected conditional logistic regression model showed a higher rank for the den sites compared to the respective control points (Fig. 4) with Wilcoxon signed rank V = 385310, p < 0.001.

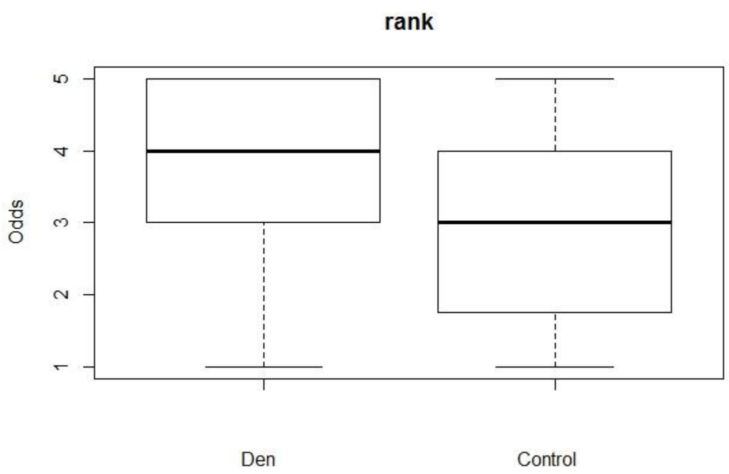

Figure 4: The rank of the dens compared to the rank of one randomly selected control point for each den in the K-fold cross validation of the selected conditional logistic regression comparing each den site to four control points placed 50 m from the den in each cardinal direction.

3.3 Den type selection

All the variables except the quadratic effect of the visibility were included in the initial full model because there was no significant collinearity among them (VIF < 5). The quadratic effect of visibility was discarded due to estimation problems. After conducting the model selection following the backward stepwise procedure, three models; m7, m8 and m9 (Tab. 4) were within ΔAIC < 2, and m9 was selected according to my criteria. The selected model included canopy cover and visibility (Tab. 4).

Table 4: The stepwise model selection for the logistic generalized linear model comparing the microhabitat characteristics around ant mound dens and open dens.

Model	Visibility	Tree age	Tree	Edge	Veg. type	Berry	Canopy cover	Branch	Spruce	Ant m.	AIC	ΔAIC
m1	*										45.56	13.08
m2	*										39.56	7.08
m3	*										37.83	5.35
m4	*										35.85	3.38
m5	.						.				36.89	4.41
m6	.						*				34.62	2.15
m7	.						*				32.65	0.17
m8	*						*				32.74	0.27
m9	.						*				32.48	0.00

According to the selected model, the relative likelihood of a den to be an ant mound den rather than an open den increased with increasing visibility (Fig. 5A, Tab. 5) and when the canopy cover above the den was more than 25% (Fig. 5B & 6). In addition to having the smallest number of predictors, the selected model was also the model with lowest AIC. Within ΔAIC < 2 were also models which included branch above the sampling spot (m7 Tab. 4, estimate = 2.7778, SE = 2.4078) and the presence of ant mounds (estimate = -1.4716, SE = 1.5084).

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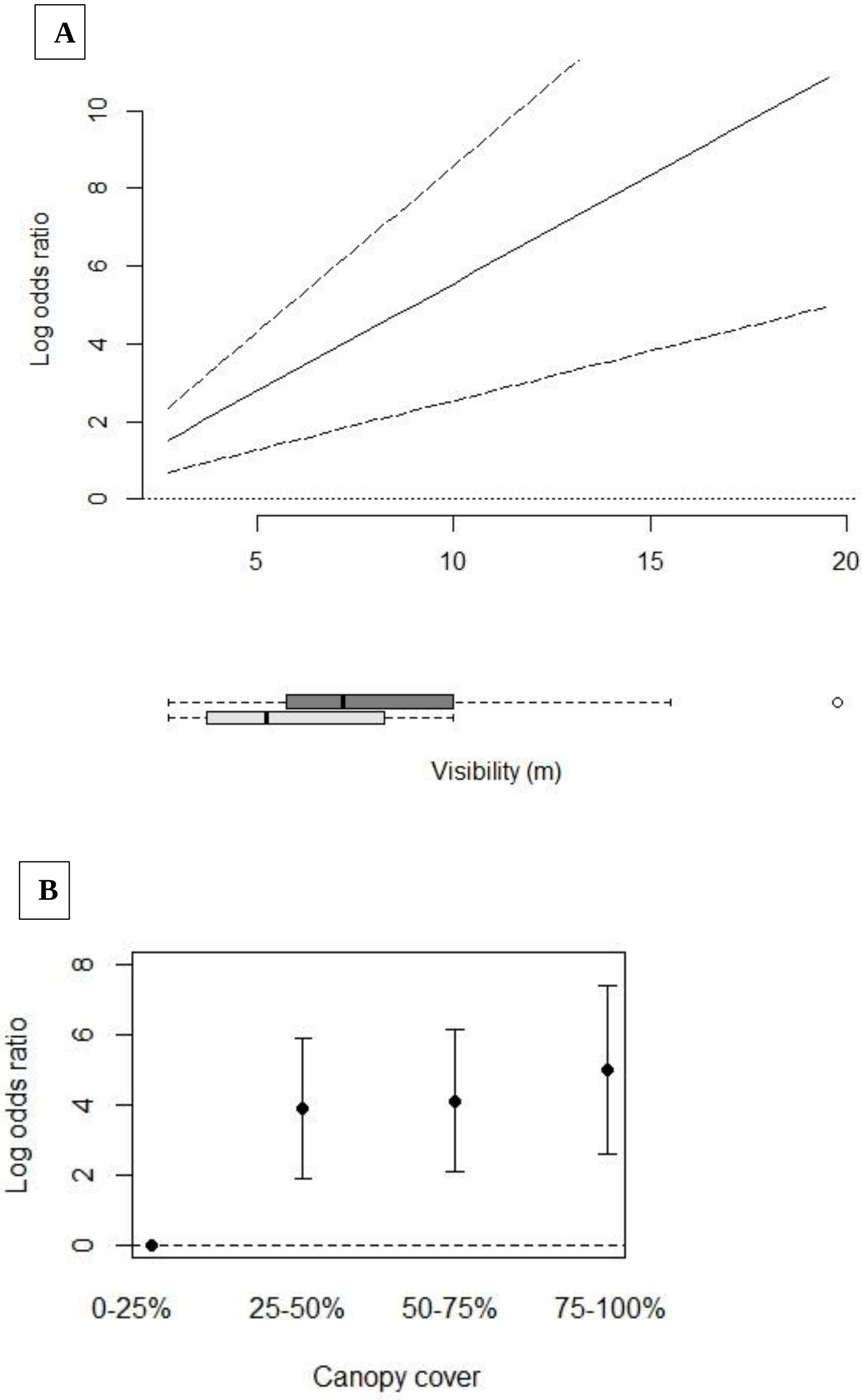

Figure 5: RSF scores of the covariates in the selected logistic generalized linear model comparing ant mound dens and open dens. A: Visibility measured as distance (m) to nearest obstacle blocking the visibility around the dens. Spotted lines represent the standard error. Dark horizontal box plot represents the distribution of ant mound dens and lighter plot represents the open dens. B: Canopy cover above the dens. Error bars represent the standard error.

The selected logistic generalized linear model had an R^2 = 0.3354. This is, the variation explained by the explanatory factors was 33.5%.

Table 5. Results of the selected generalized linear regression comparing ant mound den to open dens (m9, Tab.4).

Variable	**Estimate**	**SE**	**Z**	**P**
Intercept	-5.2715	3.1788	-1.658	0.0972
visibility	0.5556	0.3018	1.841	0.0656
c.cover 25-50%	3.8897	1.9882	1.956	0.0504
c.cover 50-75%	4.1154	2.0128	2.045	0.0409
c.cover 75-100%	4.9794	2.3993	2.075	0.0380

The first category of 0-25% canopy cover the proportion of both den types is equal and in the rest of three canopy cover categories most of the brown bear dens were ant mound dens (Fig. 6).

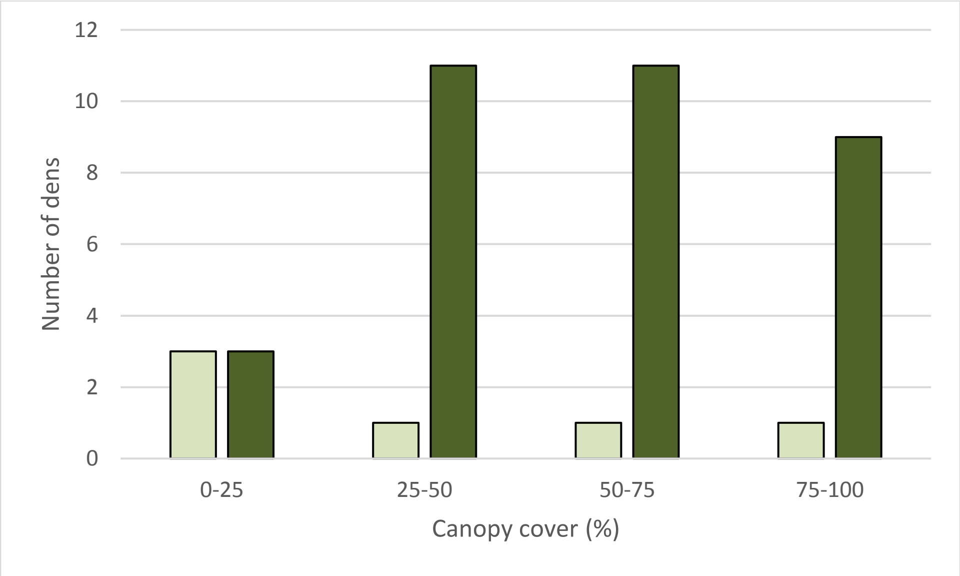

Figure 6: The distribution of brown bear den types to four canopy cover categories (measured in %). Dark bars represent the ant mound dens and light bars represent the open dens.

3.4 Presence of ant mounds

I initially included all predictors in the full generalized linear mixed analysis (Tab. 6) because, like in the two previous analyses, there was no multicollinearity between the variables (VIF < 5). The most parsimonious model (m9) included two binomial variables; dominant berry species and presence of edge habitat (Tab. 6).

Visibility (estimate = 0.05758, SE = 0.03299,) and dominant tree species (old: estimate = 0.50725, SE = 0.47279; other: estimate = -15.82148, SE = 980.68461; young: estimate = -0.14731, SE =0.75376) were within the $\Delta AIC < 2$.

Table 6: The stepwise model selection for generalized linear mixed model for presence of ant mounds.

Model	Visibility	sq. Visibility	Tree age	Tree	Edge	Veg. type	Berry	Canopy cover	Branch	Spruce	AIC	ΔAIC
m1	.				.		*				191.68	18.11
m2	.				.		*				185.51	11.95
m3					*		*				181.90	18.11
m4					*		*				178.34	4.77
m5	.				*		*				176.57	3.01
m6	.				*		*				174.90	1.33
m7	.				*		*				173.57	0.00
m8					*		*				174.70	1.14
m9					*		*				174.51	0.94

The relative probability of the occurrence of ant mounds at a site decreased when the dominant berry species was something other than bilberry, and increased with presence of edge habitat (Fig. 7, Tab. 6).

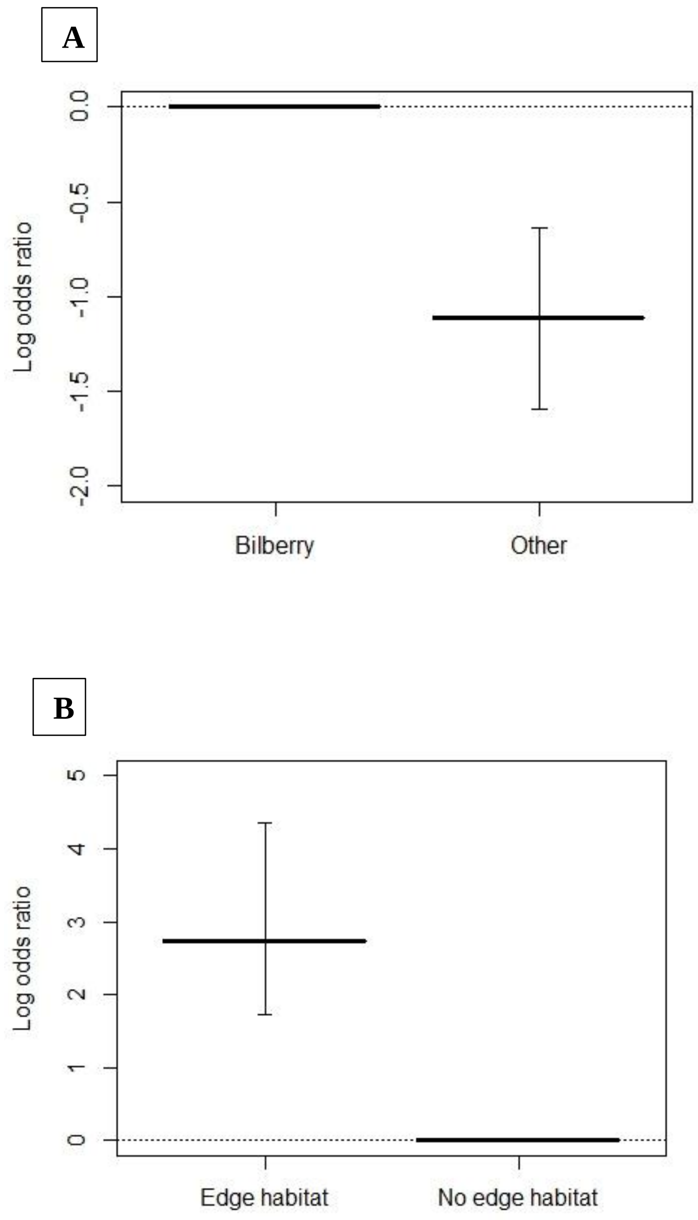

Figure 7: RSF scores of the covariates in the selected model for the occurrence of ant mounds A: Bilberry and other dominant berry species. B: Presence of edge habitat within 50 meters. Error bars represent the standard error.

Tree age and linear effect of visibility were included in the model with the lowest AIC. Within a Δ AIC < 2 the quadratic effect of visibility was also included.

The marginal R^2 value of the m9 was 0.11 and the conditional R^2 value was 0.18.

Table 7: Results of the selected generalized linear mixed regression comparing sampling site with the presence of ant mounds to sampling sites with no presence of ant mounds (m9, Tab.4).

Variable	Estimate	SE	Z	P
intercept	-1.6625	0.3238	-5.135	2.82e-07
berry other	-1.1148	0.4770	-2.337	0.0194
e. habitat	1.0080	0.4646	2.170	0.0300

The r_s values from the cross-validation had an average of 0.51 and standard deviation of 0.51.

3.5 Cavity opening

The cavity openings showed no significant difference from an even distribution between the four cardinal directions (X^2 = 1.0256, df = 3, p = 0.795). From 26 dens where the cavity openings were measurable 8 faced west, 7 south, 6 east and 5 faced north. The Wilcoxon test did not indicate that the cover around the den would affect the bearing of the cavity opening (W: 280, p: 0.2922).

4. Discussion

Three sets of models regarding the micro-habitat den site selection of brown bear males in Hedmark County suggested that the three general factors; concealment, food availability and insulation may all be important on some level: Visibility (my proxy for concealment), presence of branch above the location (a proxy for the potential snowfall and hence insulating properties of the snow cover) and presence of ant mounds were the factors associated with the presence of a den. Den type was associated with visibility and canopy cover (my second proxy for potential snow cover). Presence of ant mounds, which I studied using the field data collected for the den site selection analyses, was associated with the dominant berry species and whether an edge habitat was present within 50 meters.

Bears seemed to select to den in places with less visibility, which means shorter distances to surrounding vegetation. This provides greater concealment cover for the wintering bear and it has been suggested in previous studies as a way to reduce the probability of disturbance and predation (Hayes & Pelton 1994; Weaver & Pelton 1994; Hightower, Wagner & Pace III 2002; Ciarniello *et al.* 2005; Pigeon, Côté & Stenhouse 2016). Consistent with Linnell et al. (2000), majority of the dens were dug into ant mounds. The bears that denned in open dens, had more concealment from the surrounding trees than the ones that denned in ant mounds, offering further evidence that the bears indeed look for horizontal concealment. On the contrary, the direction from where the bear chooses to dig into the ant mound, according to my results, did not seem to be affected by the cover around the den despite it creates some openness to the closed ant mound den. The branch -variable directly above den assumed to present a limitation of snowfall. A deeper snow cover provides better insulation to minimize heat loss, which is essential for the wintering bear (Schoen *et al.* 1987). My results suggesting that brown bear males prefer a branch above their den, was contrary to my initial prediction and what previous study from Elfström et al. (2008) have reported, which is that bears in Scandinavia select for open canopy (Elfström, Swenson & Ball 2008). However, my result suggesting bears to select for increased canopy cover when denning in open dens, is consistent with the same studies, and suggests that the insulating snow cover is more important in open dens than in ant mound dens that offer some insulation even without the snow. The effect of a branch can still indicate similar properties as the horizontal concealment, since the measurement was done from 1 m above the ground, so also quite low branches were regarded. Therefore, this may be attributed to bears’ preference to avoid disturbance. Presence of ant mounds was the third factor that was favoured by the bear when selecting its denning site. In order to den in an ant mound, the presence of ants is essential, but this outcome can also reflect foraging behaviour, since brown bears practice myrmecophagy (Swenson *et al.* 1999).

What kind of disturbance and predation the bears seek cover from has not been clarified. Various human-related disturbance causes have been reported to cause den abandonment, such as: hunting, skiing, recreation, forestry survey activity, excavation machines and general human presence (Swenson *et al.* 1997). These activities make noise and often involve human activity. Horizontal cover from surrounding trees or in form of an ant mound, can be the bears' adaptation towards these previously mentioned disturbance factors. As for predation, brown bears and other large carnivores have been hunted by humans ~40,000 years in Europe (Olson 2003). Bears have been suggested to have antipredator adaptations to hunting by humans, since they have been reported to change their movement patterns in Sweden (where brown bear is a game species) during the hunting season (Ordiz *et al.* 2012). Furthermore, bears have been reported to be killed by wolves (Rogers & Mech 1981; Ballard 1982) and by other bears (Ross, Hornbeck & Horejsi 1988; Mattson, Knight & Blanchard 1992). Wolves and bears are likely to detect bears from other senses than visual and acoustic, such as smell. Hence, the security acquired from the horizontal cover, such as surrounding vegetation or enclosed den, is mainly an adaptation towards human disturbance and -hunting. Whether the bears' preference for horizontal cover during denning is an adaptation to hide from predators other than humans is unclear.

Many of the previous den site selection studies cited in this thesis were conducted in different populations, areas or even on distinct species. For example brown bears in central and northern Sweden have been found to select for open canopy and rich vegetation (Manchi & Swenson 2005), whereas my results show, that dens tend to have cover compared to the near control points and they do not seem to select between different vegetation types. This apparent contradiction may be due to different methods, since the studies of habitat selection typically use data from remote sensing and aerial photographs (Glenn & Ripple 2004; McDermid *et al.* 2009). Such data may capture variation at a larger spatial scale, but lack the accuracy of the data gathered in the field (Glenn & Ripple 2004). Differences with previous findings may also be due to different habitat or because bears at the population's expansion front, with low bear densities and male-skewed sex ratio, behave differently from bears in the population core (Swenson, Sandegren & SO-Derberg 1998). Nevertheless, this leaves me with a question, whether my scale was even too small. I could also have selected the scale in accordance to other factors than scale, such as within certain number of ant mounds, since my results suggest that the brown bears prefer to den in sites where ant mounds are present.

In all the tree analyses, tree models were within $\Delta AIC < 2$. My decision was to choose the simplest one, but I also could have chosen the one with $\Delta AIC = 0$ or the one describing most of the variance within the $\Delta AIC < 2$. In the den selection analyses, the model with presence of the skirt spruces and the quadratic effect of visibility could have been selected. The big spruces offer both horizontal and canopy cover, which are the effects that my final model suggested. The difference with the cover from the close-to-ground branches of a skirt spruce is that they can increase the thermal insulation instead of decreasing it by preventing the snow to land as an insulating factor. In the den type analyses the presence of ant mounds and the branch above the den were variables that could have been included in the model. The branch variable was used as a measure for the obstruction of snow fall, as an alternative to the percentage of canopy cover, which maybe was better measure in this analysis. In the analysis of the presence of ant mounds tree age and a linear effect of visibility were the variables that could have been included in the final model. They can indicate the same as the edge habitat, which is the increased sun-exposure, assuming that older forest and less cover imply more open habitat.

There was one variable that did not stay within any of the best fit models, in any of the analyses. This variable was vegetation type, which I had grouped into five different categories. The reason for the apparent low fit of this variable can be that the vegetation type does not vary a lot on such a small scale (only 50 m between the dens and the respective control sites), or that it simply does not have much of an impact on brown bear males' selection of a den, den type, or ants' habitat selection. It can also be that the grouping of the variable could have been done in a way that would describe better the possible selection preferences.

In building the candidate models interactions were not added due to the small dataset. With a bigger sample size, other than additive correlations could have been evaluated. My results are also conditional on the set of variables I chose to include. I did, for example not include factors describing the soil or measure the snow depth for a better indication of the insulating properties of the snow cover. Also, the model selection was done according to the principle of parsimony, which leaves the question whether some variables that got excluded did actually affect the den site selection.

The year that the dens were used varied from 2001 to 2014, which means that in the oldest sites, 15 years had passed from the bear used the den to the field work was carried out for this study. There is a possibility that the surroundings have changed enough within that time to make a difference in the studied variables. One of the dens was in a logging site and was therefore excluded from the data set. Smaller changes might have occurred in the other dens as well, such as edge habitat if there has been logging within 50 meters from some den or control sites. Other variables are less likely to have changed, since e.g. the tree age is categorised so widely that it is not very likely for a data point to have moved from one category to another. Differences in visibility could have changed as well, but since the conditional analyses compares the den to its near surroundings, the development within the same site has most probably been in the same direction within the same site which is always within 100 m.

The presence of ant mounds was studied post-hoc using the data that were collected for the den site selection models, which were clustered in groups of five data points, and limited to the close surroundings of the brown bear winter dens. The results from these analyses can be interpreted only to the habitats within 50 meters from brown bear dens, since the results in other areas may have been different. Including the random factor to the model, which was the cluster ID, the conditional R^2 was 0.18 explaining 18% of the variance, compared to only 0.11 which was the value of marginal R^2 explaining only the fixed effects. The density of ant mounds in the close surroundings of bear dens was higher when edge effect was present and when the dominant berry species was bilberry rather than other species. Presence of edge habitat can have an effect by altering both biotic and abiotic conditions (Murcia 1995). Sun-exposure has been shown to be favourable to small ant colonies (Punttila & Kilpelainen 2009), and is likely to be higher in edge effect. The occurrence of ant mounds in the sites with bilberry as the dominant berry species can be attributed to the indirect effect of ants on bilberries through predation, which has been shown to protect the blueberries from herbivory close to an ant mound (Atlegrim 2005). Still, the cross-validation indicated a poor predictive power..Thus, my analyses are not suitable to give good predictions for where ants select to build their mounds. Nevertheless, the difference between the factors included in the models for den site selection and ant mound occurrence indicate that the brown bears' selection preferences from the conditional logistic regressions were not an artefact of what the habitat selection of ants.

To conclude, the brown bear males seemed to seek for concealment by selecting for cover around the close surroundings of the den, either from the surrounding trees or from an ant mound. The presence of concealment from surrounding vegetation and little cover from the tree canopy branches seemed to be particularly important for open dens. To understand this effect better, a study should be carried out by using a more direct measurement of the insulating properties of the snow cover, by i.e. measuring the snow cover over the den and compare it to selected control points. Finally, the factors associated with the location of den sites on the microhabitat scale were not identical to the factors associated with the distribution of ant mounds. This suggests that my conclusions about the den site preferences of brown bear males are unlikely to be merely an artefact of the habitat selection of ants.

In the management and conservation of brown bear populations the results of this study can be implemented in combination with large scale studies.

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