Norwegian University of Life Sciences
Faculty of Environmental Science and Technology
Department of Ecology and Natural Resource Management

Master Thesis 2014
30 credits

Spatial and Temporal Patterns in Habitat Selection by Rock Ptarmigan (*Lagopus muta muta*) in mainland Norway

Gøran Bolme & Thomas Rohde

Acknowledgments

This master thesis is written in collaboration with the Norvegian Institute for Nature Research (NINA) and their rock ptarmigan project. The thesis, which is 30 credits, is part of a MSc degree in Management of Natural Resources, at the Department of Ecology and Natural Resource Management (INA), at the Norwegian University of Life Sciences (NMBU).

We wish to thank our external supervisor Erlend B. Nilsen for exceptional help during the entire process regarding our master thesis. We also wish to thank our supervisor Vidar Selås for good help during the writing of our master thesis.

Additional thanks goes to Hans Ole Ørka for advises regarding our GIS-analysis, Lierne Fjellstyre for free rent of Rauberghytta during our field period and all involved in TOV-E and the rock ptarmigan project which has contributed to help of recieved observations.

Department of Ecology and Natural Resource Management
Norwegain University of Life Sciences
Ås, 15th May 2014

Gøran Bolme
Thomas Rohde

Abstract

1. Predictions based on several reports and harvest statistics during the last decades have proven a worrying decrease in density and abundance of the rock ptarmigan (*Lagopus muta*) in the entire distribution area.
2. In this thesis, we applied high quality observation data of rock ptarmigans to examine habitat selection at two scales, across seasons and between different regions.
3. We extracted habitat and terrain variables from a GIS, and modelled habitat selection of rock ptarmigans. We also followed three broods for a total of 36 hours to retrieve some information of their usage of area and habitat.
4. At the regional scale some different patterns emerged across regions. Terrain heterogeneity had a strong influence of occurrence in all regions with positive curve linearity in region West and East, and negative for region Central. Altitude had a positive curvlinear influence in region West (1000 m a.s.l) and East (1550 m a.s.l). Low hillshade values influenced occurrence positively in region East and Central. The vegetation variables Forest/mire, Mooreland, Snow/glacier and Heath with lichen, had all a negative influence in region Central.
5. At a local scale, slope at low to middle steepness had a positive influence of occurrence in both winter and summer. In addition we found that high hillshade values and altitude around the tree-line had a positive influence, whereas the vegetation variable Snow-covered area had a negative impact. Snow-beds seemed to have a positive influence on occurrence in the summer season.
6. Results from our brood analysis indicate that the broods are relatively stationary during day time, spending much of their time in moist and open areas with dominance of vascular plants like different heath species (*Calluna* spp.), alpine bistort (*Polygonum viviparu*), snow-bed willow (*Salix herbacea*) and goldenrod (*Solidago virgaurea*), while moving at greater distances in the night hours.
7. This thesis is the first analysis of habitat selection by rock ptarmigans in mainland Norway. In addition, it is the first of its kind in Fennoscandia to compare habitat selection between seasons for this species. To prevent further decline in Norwegian rock ptarmigan populations, these results may be indicative in harvest management and conservation to preserve the rock ptarmigans core areas and separate the management from its forest dwelling relative, the willow ptarmigan (*Lagopus lagopus*).

Sammendrag

1. Rapporter og jaktstatistikk fra de siste tiår viser en negativ bestandsutvikling for fjellrypa (*Lagopus muta*) i hele dens utbredelsesområde.
2. I denne oppgaven har vi innhentet kvalitetssikrede observasjoner av fjellrype fra hele landet for å innbringe kunnskap om artens habitatseleksjon på to skalaer, mellom sesonger og ulike regioner.
3. Verdiene til våre prediktive variabler er hentet ut fra et digitalt vegetasjonskart og en digital terrengmodell for å kunne analysere fjellrypas habitatvalg. Vi har også fulgt tre kull i totalt 36 timer for å innhente informasjon om deres områdebruk og habitatvalg.
4. På regional skala fant vi forskjellige mønstre på tvers av regioner. Felles for alle var at Terrengheterogenitet hadde en klar innvirkning på tilstedeværelsen, med en positiv kurve for regionene Vest og Øst, samt negativ for den Sentrale regionen. Høyde hadde en positiv kurvlineær innvirkning i regionene Vest (1000 moh) og Øst (1550 moh). Lave Hillshade-verdier påvirket tilstedeværelsen positivt i region Øst og i den Sentrale regionen. Vegetasjonsvariablene Skog/myr, Snø/isbre, Rishei og Lavhei, hadde alle en negativ innflytelse i den Sentrale regionen.
5. I analysene fra lokal skala hadde lav til middels Helningsgrad en positiv påvirkning av tilstedeværelse, både i vinter- og sommerhalvåret. I tillegg til Helningsgrad fant vi at høye Hillshade-verdier og høyder rundt tregrensa hadde en positiv påvirkning mens vegetasjonsvariabelen Snødekt areal hadde en negativ påvirkning. Snøleier hadde en positiv innflytelse på tilstedeværelse i sommerhalvåret.
6. Resultater fra våre kullanalyser indikerer at kullene er relativt stasjonære på dagtid. De tilbrakte mye av sin tid i fuktige og åpne områder med dominans av karplanter som forskjellige lyngarter (*Calluna* spp.), harerug (*Polygonum viviparu*), musøre (*Salix herbacea*) og gullris (*Solidago virgaurea*), mens de flyttet seg over større områder i den mørke delen av døgnet.
7. Denne oppgaven er den første analysen av habitatvalg for fjellrype på det norske fastlandet. I tillegg er det den første av sitt slag i Fennoskandia til å sammenligne habitatvalg mellom ulike årstider for fjellrypa. Disse resultatene kan være veiledende for fremtidig høstingsmodeller og for å bevare fjellrypas kjerneområder. Vi håper også at dette vil kunne føre til en mer spesifikk målrettet forvaltning av fjellrypa, som i dag ikke skilles forvaltningsmessig fra sin nære slektning lirypa (*Lagopus lagopus*), til tross for sine store forskjeller.

Table of Contents

1 Introduction

Alpine and arctic ecosystems are now in a challenging era. Biological interactions, adapted over thousands of years, are undergoing rapid changes. Habitat degradation, fragmentation and disturbance activities in addition to shrub encroachment and the fact that the tree-line has climbed 25-90 meters during the last century due to climate changes are all major threats that may affect the abundance and distribution of alpine and arctic species (Serreze et al. 2000; Hinzman et al. 2005; Myers-Smith et al. 2011; Hofgaard et al. 2012; Revermann et al. 2012; Bech et al. 2013). Observed changes in rodent cycles in many alpine and arctic ecosystems the last decades additionally affect the predator-prey interactions (Kausrud et al. 2008). Lower densities and less cyclic activity for rodents influence the density and reproductive outcome of other species in the ecosystems (Schmidt et al. 2012; Ims et al. 2013; Nolet et al. 2013). To develop a targeted and sustainable management of these concerned species, it is necessary to determine habitat preferences and distribution over wide ranges of the species' distribution area (Boyce & McDonald 1999; Luoto et al. 2002; Blaschke 2010).

Large-scale multi-species data on population changes of alpine and arctic bird species in northern Fennoscandia showed that the Norwegian ptarmigans (*Lagopus* spp.) were two of the species experiencing the most severe decline (Kålås et al. 2014; Lehikoinen et al. 2014). Future predictions suggests further decline in density and abundance of rock ptarmigans (*Lagopus muta*) in several other parts of the distribution area (Huntley et al. 2007; Virkkala et al. 2008; Borecha 2011; Jiguet et al. 2013).

Although the rock ptarmigan belongs to one of the world's most studied taxa (*Tetraonidaes*), this primeval and more unavailable species has been overshadowed by its close relative, the willow ptarmigan (*Lagopus lagopus*) (Moss et al. 2010). Habitat preferences of the rock ptarmigan are poorly investigated in Norway as well as in other northern parts of Europe, both within seasons and especially between seasons, where the literature is highly deficient. Nilsen et al. (2012) emphasized the need for such studies for predicting the potential responses of rock ptarmigans to climate driven changes in habitat distributions.

The rock ptarmigan is one of few bird species that is present in alpine and arctic regions throughout the year (Storch 2007; Nilsen et al. 2012). Previous studies have reported that altitude, slope, aspect, vegetation cover, moisture, presence of rock, food availability and potentially interactions between these variables affect the species niche (Unander & Steen 1985; Sandercock et al. 2005; Favaron et al. 2006; Zohmann & Wöss 2008; Wilson & Martin 2008; Pedersen et al. 2011; Schweiger et al. 2012; Nelli et al. 2013; Zohmann et al. 2013; Pedersen et al. 2014). Occurrence of the rock ptarmigan varies throughout the distribution area due to differences in vegetation cover and terrain features. Moreover, the distribution will also vary between seasons, and at different life stages (Sandercock et al. 2005; Pedersen & Karlsen 2007).

In the end of April male rock ptarmigans establish territories. Males select their territory based on certain preferences such as big rocks that serves as lookout-points, often with a snow-bed nearby in a generally heterogeneous area which they defend until the brood is hatched (Fig. 1) (Unander & Steen 1985; Pedersen & Karlsen 2007; Nopp-Mayr & Zohmann 2008; Pedersen et al. 2014). The brood will stay in or nearby the territory for some weeks after hatching, while the males often gather in small groups separated from females and juveniles (Nilsen et al. 2012).

Some days after hatching, the hen will lead the brood to areas with high quality and availability of food, often at lower altitudes than the nest site (Moss & Hanssen 1980; Steen & Unander 1985). Different hens with different broods seem to prefer the same environment, leading to the conclusion that there are some strong preferences regarding habitat (Steen & Unander 1985). Subsequently, in late autumn and winter, rock ptarmigans form larger groups, across gender and age (Nilsen et al. 2012), in habitats that meet their needs for survival during the extreme winter months.

Based on current literature, the rock ptarmigan is generally assumed to be a relatively stationary bird. Between seasons, however, there will be some movements between different altitudes (Favaron et al. 2006; Pedersen & Karlsen 2007). These seasonal movements are most likely triggered by food availability and abundance. Weather conditions and snow accumulation will also affect the seasonal movement (Giesen & Braun 1992). Research conducted by Unander and Steen (1985) at Svalbard reported that the rock ptarmigan migrated between their winter habitat and the breeding areas.

Development of new GIS-tools (geographic information systems) and statistical techniques such as predictive habitat models has become important tools in management and ecological research (Scott et al. 2002). Such models are useful because they statistically show the relationship between ecological features and the distribution of the species (Boyce & McDonald 1999;

Guisan & Zimmermann 2000; Austin 2002; Boyce 2006; Stokland et al. 2008; Long et al. 2009). The mapping and maintenance of high-quality habitats of wildlife in alpine ecosystems are key issues in conserving these species (Zohmann et al. 2013). Predictive habitat models have been developed for many bird species and *Tetraonidaes* are well represented (e.g. Pedersen et al. 2007; Muller et al. 2009; Pedersen et al. 2012; Zohmann et al. 2013; Pedersen et al. 2014). To promote sustainable and targeted management for the rock ptarmigan, quantified ecological features must be charted. This will make it possible to follow trends and developments over time, which is a prerequisite for a provident adaptive management (Williams 2011).

Our purpose in this thesis is to detect correlations between ecological features and the probability of rock ptarmigan occurrence in different parts of the country and between seasons at two different spatial scales. In addition we have obtained some data on brood movement and habitat characteristics used by broods. The results will be discussed in relation to the goal of establishing a more targeted and adapted management for the rock ptarmigan in Norway.

Figure 1. A male rock ptarmigan in a typically preferred territory habitat with high heterogeneity, snow-bed and big rocks which serves as look-out points.

1.1 Aims and objectives

The overall aim of this thesis is to evaluate rock ptarmigans habitat preferances using predictive habitat models. Obtained information might be applied in future conservation and management of the species. The specific objectives adressed in our paper are:

1. Which terrain and vegetation characteristics represent the rock ptarmigan’s fundamental niche?
2. Are there differences in these characteristics across regions?
3. Will these characteristics differ between seasons and affect the abundance?
4. What characterizes the area, used by rock ptarmigan broods during the first weeks after hatching?

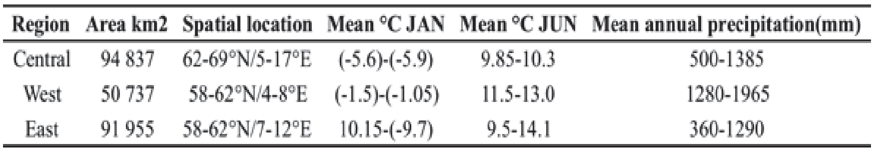
2 Methods

2.1 Study area

2.1.1. Regional scale

Data for our regional scale study was obtained from all of Norway through the TOV-E project (see 2.2.1). To facilitate modelling and interpretation, we divided the country into 4 regions: North, Central, West and East (Fig. 2), defined on the basis of similarities in precipitation rates between counties (Table 1) (see Kvasnes et al. 2010 for a justification). The Northern region, including Troms and Finnmark counties, was excluded from the modelling. The potential niche for rock ptarmigans in these two counties are widely distributed regarding terrain and vegetation features which is primary affected by altitude. This lead to rough and incoherent analyses beacause the rock ptarmigans are present from the pebbles up to 1000 m a.s.l. (Pedersen & Karlsen 2007).

Table 1. Mean temperatures and precipitation (www.met.no) for the three regions included in this study. The calculations are rough means based on historical data from four different weather stations in each region. These weather stations are situated in North, Central, East and West in each region. Data obtained from met.no concerns mean January and June temperature in addition to mean annual precipitation and spatial location.



Region	Area km2	Spatial location	Mean °C JAN	Mean °C JUN	Mean annual precipitation(mm)
Central	94 837	62-69°N/5-17°E	(-5.6)-(-5.9)	9.85-10.3	500-1385
West	50 737	58-62°N/4-8°E	(-1.5)-(-1.05)	11.5-13.0	1280-1965
East	91 955	58-62°N/7-12°E	10.15-(-9.7)	9.5-14.1	360-1290

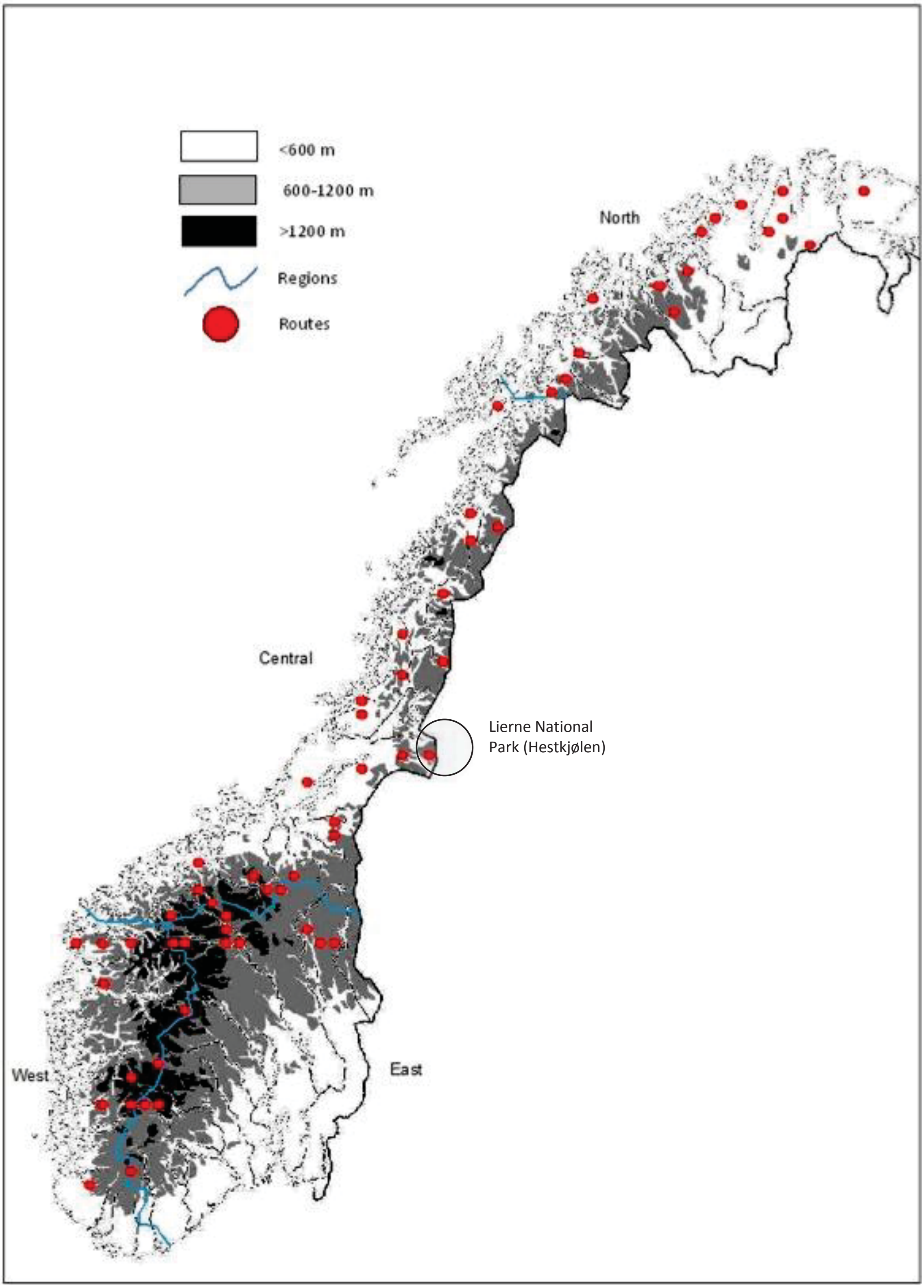


Figure 2. Illustration of the analyzed TOV-E routes, regions with elevation, in addition to a overwiev where Lierne National Park (Hestkjølen) is located.

2.1.2 Local scale (Hestkjølen/Lierne national park)

Lierne national park (64°N-13°E), where our field surveys were carried out, is a significant contiguous area where technical interventions are humble. The national park covers 333 km^2 and is situated in the slightly oceanic section (O1) characterized by alpine ridges, lee sides and snow patches (Moen 1998; Nasjonalparkrådet 2007). The area has a mean annual precipitation of 690 mm and mean June and January temperatures of 9.9° C and -10.0° C, respectively (met.no). The central areas has a rich alpine flora characterized by a mosaic of bilberry heath (*Vaccinium myrtillus*), juniper (*Juniperus communis*), dwarf birch (*Betula nana*), screes and willow communities (*Salix* spp.). The floor of the valleys consists of sub-alpine birchwoods and minerothrophic mires (Haugan 2013).

Potential rock ptarmigan predators in the study area are stoat (*Mustela erminea*), weasel (*Mustela nivalis*), red fox (*Vulpes vulpes*), golden eagle (*Aquila chrysaetos*), gyrfalcon (*Falco rusticolus*), common kestrel (*Falco tinnunculus*), long tailed skua (*Stercorarius longicaudus*), hooded crow (*Corvus cornix*) and raven (*Corvus corax*) (Krogh 1954; Nasjonalparkrådet 2007; Bergerud & Gratson 1988; Cotter & Boag 1992; Watson et al. 1998; Pedrini & Sergio 2002; Nystrøm et al. 2006).

2.2 Rock ptarmigan dataset

2.2.1 Study design

TOV-E (Extensive monitoring of breeding bird)

Our region scale data is obtained by the TOV-E project initiated by the Norwegian Institute for Nature Research (NINA), the Norwegian Ornithological Society (NOF) and the Norwegian Environment Agency. In the monitoring project, persons with high qualification in bird identification appraise assigned square routes (1.5x1.5 km^2) in all parts of Norway (Fig. 2). Each route consists of 20 points with a 300-meter distance between each point (some routs consist of fewer points due to lack of accessibility). Each point, which has an exact GPS-position, is registered for 5 minutes sharp between 4 and 10 a.m. in a specific time period each year. The number of pairs of each bird species is registered within and outside 50 meters from the registration point. One pair of a bird species is defined as 1) one male heard or observed, 2) one couple observed, 3) one female observed, 4) one litter able to fly or a nest of the year observed (Kålås & Husby 2002). After the routes have been appraised, the results are reported electronically through a web-portal.

Hestkjølen – Radio monitoring of rock ptarmigan

In February 2012, NINA in cooperation with Nord-Trøndelag University College (HINT) and Lierne Fjellstyre initiated “Fjellrypeprosjektet” (The rock ptarmigan project). The objective of the project was to increase the knowledge about the rock ptarmigan’s basic biology and to better understand how climate, predation and harvest influence the species. Central parts of the project were to study the bird’s movements through different seasons monitored by radio transmitters. In February 2012 and 2013, NINA captured 51 and 29 rock ptarmigans respectively, and equipped them with radio transmitters.

We received NINA’s data from air- and field bearings from 2012/2013, which were used in addition to our own data obtained by homing equipment. We also included spatial information of unmarked ptarmigans that we observed randomly during the survey from June–August 2013. All spatial positions of the observed ptarmigans (388 presence-points) were manually recorded in an excel-format.

Intensive monitoring of rock ptarmigan broods

During our field survey in Hestkjølen in June–August 2013, we observed three different broods for a total time of 36 hours. This was one radiolabeled female with brood monitored over three days and two randomly sighted unmarked females with brood, observed for one day each. We took their exact position every half an hour and when the broods were out of sight we obtained vegetation and terrain data within a circle of 2.5 m radius around each position. Using these positions we obtained some rough vegetation analyses, movement of the brood (meter/30min), angle of the movement, and applied area for each day (n=5).

2.2.2 Quality assurance of data

TOV-E

We received 203 routes with bird census from NINA, but we applied only those 61 routes where rock ptarmigans had been observed minimum one of the years the route had been assessed. For these routes, we compared points with rock ptarmigans observations to those without. By adding the number of assessed years for each route we got 110 routes, which consisted of 2200 points. We ommited 159 because they gave different biases in the GIS-analysis. Hence, 2041 points were used in our analyses, 180 presence points and 1861 absence points, i.e. with and without ptarmigan observations (Appendix 1).

Hestkjølen

The data we received from NINA in addition to our own surveys represents 388 observations of rock ptarmigans, i.e. presence points. From these 388 presence points we generated 19 random absence points per single presence point within a buffer (radius 500 m). Some of these random absence points were deleted due to errors in the GIS-analyses. In total we ended up with 7503 points that we included in our statistical analysis.

Classification of data

The spatial accuracy regarding data obtained from Hestkjølen will vary due to different collection methods. We divided these data into three groups of accuracy. The least accurate, accuracy III, was obtained using homing equipment from an airplane, and other cases where the position was inaccurate. Accuracy II consists of data that are obtained using triangular bearing in the field. The most accurate, accuracy I, includes data from direct observations of rock ptarmigans in the field. Based on preliminary modelling, we decided to include only the most accurate data (accuracy I) in our analyses.

To examine potential differences in habitat preferences between seasons, we divided our data into winter (16. September–14. April) and summer (15. April–15. September). We conducted separate analysis for the winter- and summer season.

2.3 Landscape variables

All landscape variables referred to in our habitat model were calculated from digital maps in a geographic information system (GIS). We used ArcMap10.1 and ArcScene10.1 with ‘spatial analyst’, ‘3D analyst’ and ‘analysis tools’ (ESRI 2009). We examined all landscape variables at two different spatial scales. The buffers surrounding a presence point with its associated random points had a spatial range of 1 km^2 in Hestkjølen and 1.4 km^2 in TOV-E, which represents a large rock ptarmigan territory (Pedersen & Karlsen 2007). Habitat features from these points were generalized to explain the rock ptarmigans probability of occurence in a resource type x, based on the available distribution of the same resource type in a local (Hestkjølen) and a regional (TOV-E) scale (Lele et al. 2013).

2.3.1 Vegetation variables

Information about the vegetation was retrieved using a digital vegetation map based on LANDSAT (scenes from 1988-2006) with a spatial resolution of 30x30 meters (Johansen 2009). This vegetation layer consists of 25 different habitat types, which we re-classified into eight habitat classes during summer (Table 2) and four habitat classes during winter (Table 3). These classes were based on the rock ptarmigans habitat requirements within different seasons consistent with previous studies (Favaron et al. 2006; Zohmann et al. 2013; Pedersen et al. 2014). The amount of the different vegetation classes was calculated within a buffer of 50 meter in radius around each presence and absence point and was used as an explanatory variable in our habitat models.

Table 2. Re-classification of vegetation classes possessing summer observation (15. April–15. September) at a regional scale (Central, West and East) for TOV-E and a local scale (Hestkjølen).

			% of analyzed area			
Original veg. class	**Veg. class**	**Vegetation name**	**Central**	**West**	**East**	**Hestkjølen**
1,2,3,4,5,6,7,8,9,10,11	1	Forest and mires	10.5	7.3	5.6	19.6
12,13,14	2	Ridges	30.7	30.5	39.6	12.7
15	3	Heaths with lichen	0.6	0	4.6	0
16	4	Lee with rich heather	6.1	11.4	7.4	10.2
17,18	5	Mooreland	28.7	13.8	18.7	33.2
19,20	6	Snow-bed	19.5	32.7	19.8	14.1
21	7	Snow/glacier	2.2	0.5	1.6	2.8
22,23,24,25,0	8	Shadow areas/north facing hillside	1.7	3.8	2.7	7.4

Table 3. Re-classification of vegetation classes possessing winter observation (16. September–14. April) at a local scale in Hestkjølen.

Original veg. class	Veg. class	Vegetation name	% of analyzed area
1,2,3	1	Coniferous	13.4
4,5,6,7,8	2	Deciduous	29.4
12,13,14	3	Ridges	5.7
9,10,11,15,16,17,18,19,20,21,22,23,24,25,0	4	Snow covered areas	51.5

2.3.2 Terrain variables

We applied a national digital elevation model (DEM) for Norway to obtain information about altitude, aspect, slope, shading and the topographic variation of the landscape. The DEM had a spatial resolution at 50x50 meter (Statens Kartverk). Explanatory variables linked to terrain were chosen based on previous developed ptarmigan habitat models (e.g. Pedersen et al. 2007; 2012; 2014). We calculated values for the following variables: Slope, Aspect, Altitude, Hillshade and Terrain ruggedness. Values of terrain variables were calculated as mean values of all cells in the 50 meter buffer (radius) around each presence and absence points, except altitude where the exact value at the observation point was used. Terrain ruggedness is a way to capture variability in slope and aspect into a single measure; this was calculated using ‘vector ruggedness measure’ (VRM). VRM indicates high values in a special heterogeneous terrain and low values in a flat, homogeneous terrain (Sappington et al. 2007). The hillshade tool obtains the hypothetical illumination of a surface by determining illumination values for each cell in a raster, by setting angle and azimuth for a hypothetical sun and thereby calculate the illumination values of each cell in relation to neighbouring cells. A high value indicates high solar radiation and lower values indicating lower solar radiation (Burrough & McDonell 1998). The hillshade tool will give information about shading but also indirectly some information about moisture. For more information about hillshade see Appendix 2.

2.4 Statistical analyses

In our analysis we used two different approaches of design which is common in wildllife habitat studies (Boyce 2006). The TOV-E data are based on a used/unused (presence/absence) design with comparisons between three different areas at a regional scale. The data from Hestkjølen has a use/avalibility (presence/pseudo-absence) design (Pearce & Boyce 2006), with comparisons between two different temporal scales.

To predict the probability of rock ptarmigan occurrence we used generalized mixed models (GLM's), in R (Version 3.0.2 (2013–09–25)) to decide the most descriptive habitat variables in each region (TOV-E) and accuracy in addition to season (Hestkjølen) (Manly et al. 2002; Hirzel & Le Lay 2006). Five terrain- and eight vegetation predictor variables could potentially be included in our candidate lists for TOV-E and summer observations in Hestkjølen. Winter observations in Hestkjølen had five terrain- and four vegetation predictor variables (see Table 2 and 3 for classification). Four of the predictor variables Altitude, Slope, Hillshade and VRM were also described using a second-order polynomial since we expected a nonlinear effect. Based on these variables, we constructed a set of biological relevant candidate models (Johnson et al. 2006; Phillips & Elith 2013). No interactions were tested in our analysis to keep the models as simple as possible. Selection of models was based on Aikake information criterion corrected for small sample size (AICc), with differences in AICc values (ΔAICc) and AICc weights (w_i) (Anderson et al. 2001; Burnham & Anderson 2002) in library 'AICcmodavg' for R (Mazerolle 2013) with the functions 'AICcmodavg' and 'confset'. We checked for correlations between variables using Pearson product-moment correlation coefficient (Pearsons's r). If two variables gave ($|r_S| > 0.7$) we excluded the variable with least individual effect on AIC. As a post hoc test of our model selection routines, we compared these models against the result from a fully automated model selection procedure (using the '*dredge'* function in add-on library MuMIn (Bartoń 2013)). The comparisons between the two approaches were very similar and we chose our manually created models based on Burnham & Anderson (2002) quote:

"Let the computer find out is a poor strategy and usually reflects the fact that the researcher did not bother to think clearly about the problem of interest and its scientific setting."

We applied the ‘mod.avg’ function (Burnham & Anderson 2002) in library MuMIn (Bartoń 2013) to obtain averaged parameter estimates and standard deviations in addition to variable importance. Finally we tested each model’s performance by calculating the area under curve by using the function AUC (Fawcett 2006) in library ‘PresenceAbsence’ (Freeman 2012). An AUC value below 0.5 will be useless because it cannot discriminate between presence and absence of rock ptarmigans. An AUC-value between 0.6-0.9 indicates a low to fair discrimination while values between 0.9-1.0 indicate excellent discrimination (Fawcett 2006).

We plotted the most important variables based on the model averaging, with their standard errors, for the six best models in different seasons and regions with the remaining variables set to their mean values. Since TOV-E and Hestkjølen have two different approches of design we got two different values on the y-axis. In TOV-E we plotted the real scale of probability for the use of the specific feature. This will not be the appropriate value for Heskjølen since we here deal with use/availability (Manly et al. 2002). The y-axis in plots from Hestkjølen shows an estimate of the selection coefficient = w(i), which are proportional to the probability of use (Boyce 2006). Defferences between the model avaraging and the best model for different regions and seasons are shown in the tables.

3 Results

3.1 TOV-E

None of the variables were highly correlated ($|r_s|<0.7$), indicating that all could be included in the models simultaneously. In region Central, two continuous terrain variables were included in the selected models, VRM and Hillshade, in addition to the numerical vegetation variabels: Mooreland, Forest/mire, Snow/glacier and Heath with lichen (Table 4). In region West the continuous terrain variables Altitude, VRM and Slope were included in the selected models (Table 4). The selected models for region East included the numerical terrain variable Altitude, VRM and Hillshade (Table 4).

AUC values for the models in the different regions were fairly similar, and ranged between 0.67 and 0.72 (Table 4).

Table 4. Variables included in the six best models for each TOVE-region. Selection of the best predictive habitat model was based on ΔAICc and w_i from the averaging of the 6 best models. The predictive strength of the models is presented as AUC values. VRM = vector ruggedness measure.

Region	Model	Alt+Alt^2	VRM+VRM^2	Hills+Hills^2	Slope+Slope^2	Aspect	Forest/mires	Mooreland	Ridges	Heath w/lichen	Lee w/heather	Snowbed	Snow/glacier	Shadow/north	*df*	AIC_c	ΔAIC_c	w_i	AUC
Central	1		x	x			x	x		x			x		9	495.51	0.00	0.45	0.71
	2	x	x	x			x	x		x			x		11	496.87	1.37	0.22	0.71
	3	x	x	x			x	x					x		10	497.73	2.21	0.14	0.70
	4	x	x	x			x	x	x				x		12	498.90	3.38	0.08	0.71
	5	x		x			x	x		x			x		9	500.04	4.52	0.04	0.70
	6	x		x			x	x					x		8	500.44	4.92	0.03	0.69
	Intercept														1	523.64	28.12	0	
West	1	x	x		x										7	171.90	0.00	0.27	0.70
	2		x		x		x								6	172.34	0.44	0.21	0.69
	3		x		x		x					x			7	172.72	0.82	0.18	0.71
	4	x	x		x		x								8	173.37	1.47	0.13	0.70
	5		x		x				x			x			7	173.94	2.04	0.10	0.70
	6	x	x		x			x				x			9	174.30	2.40	0.08	0.72
	Intercept														1	175.50	3.60	0.04	
East	1	x	x	x											7	284.80	0.00	0.42	0.70
	2	x	x	x			x								8	285.90	1.11	0.24	0.70
	3	x	x	x	x										9	286.72	1.92	0.16	0.71
	4	x	x	x	x		x								10	287.77	2.97	0.10	0.72
	5	x	x									x			6	289.40	4.60	0.04	0.67
	6	x	x	x	x		x	x							11	289.74	4.95	0.04	0.72
	Intercept														1	298.59	13.79	0.00	

Variables included in the models had different importance in predicting the presence of rock ptarmigans. In general, terrain variables had a higher importance than different vegetation variables.

For region Central, increased proportions of the habitat variables Forest/mires, Mooreland, Snow/glacier and Heath w/lichens had all a negative predictive effect for the probability of rock ptarmigans being present (Fig. 3). Increased VRM and decreased Hillshade gave a positive effect of rock ptarmigans being present (Fig. 3). All these variables showed a great importance in the models for the region (Table 5).

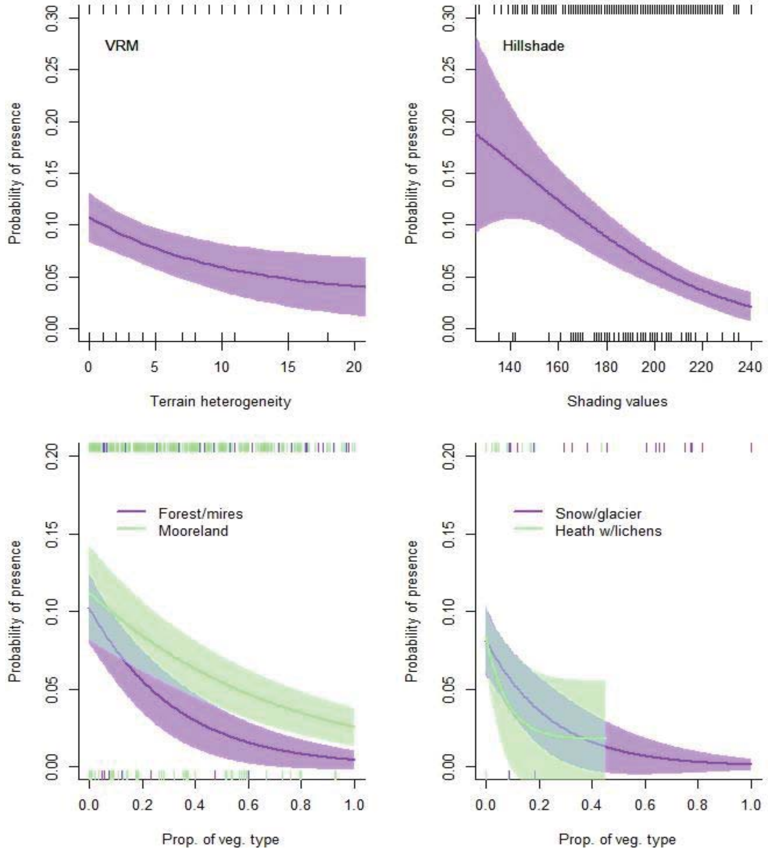


Figure 3. Plots with their standard errors (shaded areas), presenting the most important variables from the model averaging for the six best models in region Central. The figure shows the probability of rock ptarmigans being present. Presence points are marked with rugs on the bottom of the y-axis and the absence points at the top. VRM = vector ruggedness measure.

For region West, the probability of rock ptarmigans being present was positively influenced by higher VRM values and Altitude (peak between 800-1200 m a.s.l) (Fig. 4). Increasing proportion of the vegetation variable Forest/mires had a negative influence on the probability of presence. When Slope increased above 20 degrees, the probability of rock ptarmigans being present decreased (Fig. 4). Variables mentioned above showed a variable importance >0.47 (Table 5).

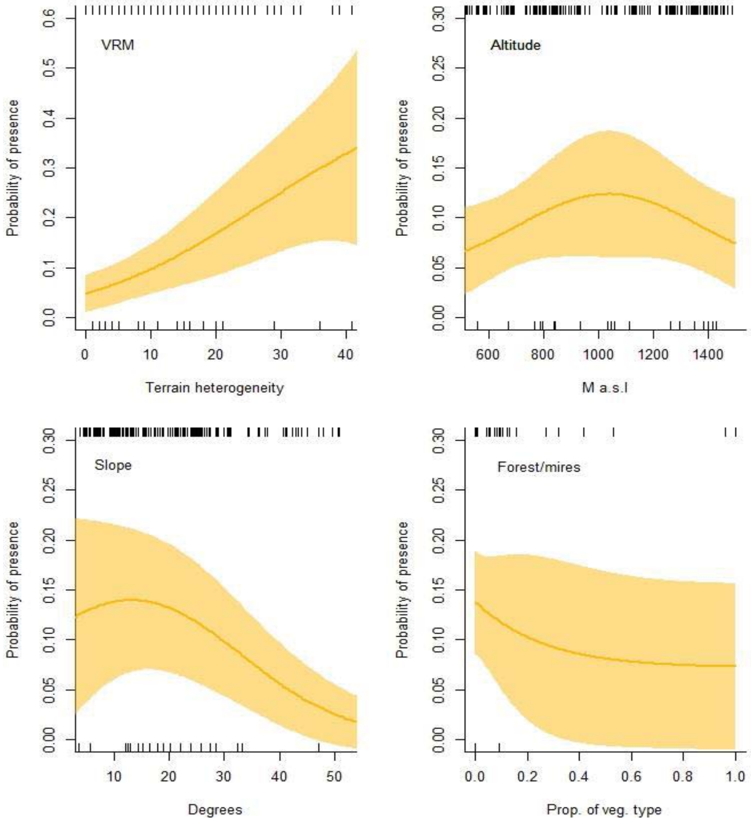
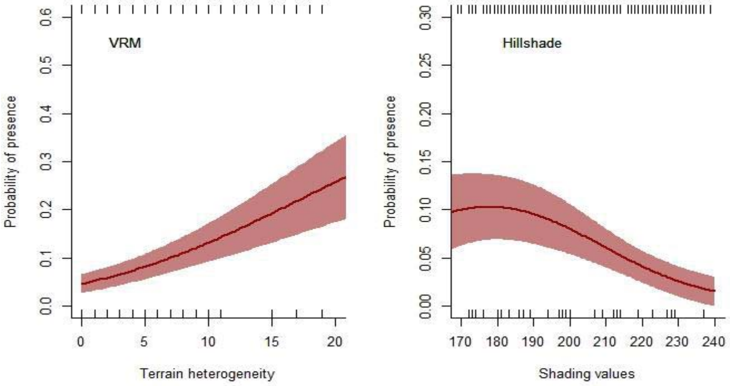


Figure 4. Plots with their standard errors (shaded areas), presenting the most important variables from the model averaging for the six best models in region West. The figure shows the probability of rock ptarmigans being present. Presence points are marked with rugs on the bottom of the y-axis and the absence points at the top. VRM = vector ruggedness measure.

In region East, higher altitudes increased the probability of rock ptarmigans being present with a peak between 1500-1600 m a.s.l (Fig. 5). In general the VRM in region East was low, but increasing values had a positive effect for presence probability. Hillshade showed the opposite effect, with highest presence probability at low Hillshade values (Fig. 5). Altitude, VRM and Hillshade had all a variable importance closely to 1 (Table 5).



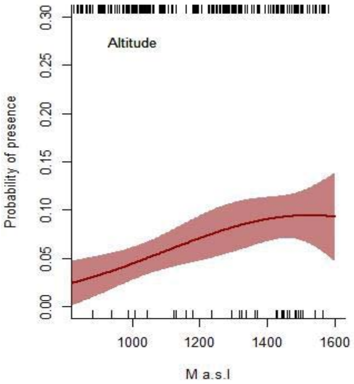


Figure 5. Plots with their standard errors (shaded areas), presenting the most important variables from the model averaging for the six best models in region East. The figure shows the probability of rock ptarmigan being present. Presence points are marked with rugs on the bottom of the y-axis and the absence points at the top. VRM = vector ruggedness measure.

Table 5. Parameter estimates, standard errors and variable importance for the different variables included in the six best models and intercept for each region. Parameter estimates and standard errors for the best models in each region are also included. VRM = vector ruggedness measure.

	Averaged estimates for the 6 best models and intercept				Estimates for the best model	
Region	**Parameter**	**Estimates**	**SE**	**Variable importance**	**Estimates**	**SE**
Central	Intercept	-1.180e+00	6.534e+00		5.622e-01	6.266e+00
	Altitude	5.988e-03	3.523e-03	0.55		
	Altitude^2	-3.628e-06	2.122e-06	0.55		
	VRM	-8.629e-02	4.102e-02	0.91	-9.524e-02	3.909e-02
	VRM^2	1.277e-03	5.269e-04	0.91	1.365e-03	5.140e-04
	Hillshade	7.918e-03	6.764e-02	1.0	3.309e-03	6.783e-02
	Hillshade^2	-7.844e-05	1.849e-04	1.0	-6.616e-05	1.852e-04
	Forest/mires	-3.353e+00	1.321e+00	1.0	-3.653e+00	1.297e+00
	Mooreland	-1.584e+00	4.775e-01	1.0	-1.606e+00	4.690e-01
	Snow/glacier	-4.240e+00	2.967e+00	1.0	-3.979e+00	2.875e+00
	Heath w/lichens	-1.337e+01	1.161e+01	0.81	-1.393e+01	1.155e+01
	Ridges	7.941e-02	4.638e-01	0.08		
West	Intercept	-5.887e+00	3.504e+00		-8.876e+00	3.050e+00
	Altitude	1.141e-02	6.336e-03	0.47	1.178e-02	6.191e-03
	Altitude^2	-5.501e-06	3.120e-06	0.47	-5.650e-06	3.064e-06
	VRM	8.527e-02	6.972e-02	0.96	9.623e-02	6.962e-02
	VRM^2	-6.479e-04	1.551e-03	0.96	-9.480e-04	1.527e-03
	Slope	4.018e-02	7.085e-02	0.96	3.507e-02	7.138e-02
	Slope^2	-1.492e-03	1.319e-03	0.96	-1.404e-03	1.328e-03
	Forest/mires	-4.212e+00	6.613e+00	0.52		
	Snowbed	1.003e+00	7.489e-01	0.35		
	Ridges	3.282e-01	9.859e-01	0.08		
	Mooreland	8.690e-01	1.128e+00	0.10		
East	Intercept	-2.693e+01	1.810e+01		-2.384e+01	1.509e+01
	Ruggedness	1.287e-01	4.639e-02	1.0	1.329e-01	4.491e-02
	Ruggedness^2	-1.539e-03	1.186e-03	1.0	-1.648e-03	1.158e-03
	Altitude	8.823e-03	1.393e-02	1.0	1.099e-02	1.337e-02
	Altitude^2	-2.886e-06	5.544e-06	1.0	-3.675e-06	5.347e-06
	Hillshade	2.082e-01	1.570e-01	0.96	1.540e-01	1.202e-01
	Hillshade^2	-5.845e-04	4.009e-04	0.96	-4.476e-04	3.095e-04
	Forest/mires	-2.063e+00	2.511e+00	0.37		
	Slope	-3.088e-02	7.377e-02	0.29		
	Slope^2	1.793e-03	1.867e-03	0.29		
	Snowbed	7.500e-01	5.148e-01	0.04		
	Mooreland	-2.360e-01	7.368e-01	0.04		

3.2 Hestkjølen

We found some differences between seasons regarding which variables to include in the six best models. Our results indicate some spatial differences in habitat selection during the year. In the summer analysis we incorporated eight numerical vegetation variables, whereas in winter we used four (Table 2 & 3). We also tested differences between diverse observation accuracies as earlier mentioned in section 2.2.2. For further reading about these results see Appendix 3.

All variabless could be used in the same models, as there were no strong internal correlations between explanatory variables ($|r_s| < 0.7$). Variables included in the selected models of summer observation in Hestkjølen consisted of the continuous terrain variable Slope and the numerical vegetation variable Snow-bed (Table 6).

Table 6. Variables included in the six best models possessing summer observation (15. April–15. September) in Hestkjølen. Selection of the best predictive habitat model was based on ΔAICc and w_i. The predictive strength of the models is presented as AUC values. VRM = vector ruggedness measure.

Summer	Model	Alt+Alt^2	VRM+VRM^2	Hills+Hills^2	Slope+Slope^2	Aspect	Forest/mires	Mooreland	Ridges	Heath w/lichen	Lee w/heather	Snowbed	Snow/glacier	Shadow/northe	*df*	AIC_c	ΔAIC_c	w_i	AUC
Accuracy I	1				x							x			4	563.05	0.00	0.25	0.63
	2				x							x	x		5	563.25	0.20	0.22	0.63
	3		x		x							x	x		7	563.47	0.42	0.20	0.66
	4		x		x							x			6	563.78	0.72	0.17	0.65
	5	x	x		x							x	x		8	565.63	2.57	0.07	0.66
	6	x	x		x							x			9	565.99	2.94	0.05	0.65
	Intercept														1	570.61	7.55	0.00	

Both these variables had an importance of 0.99 in the models (Table 8). Slope had a slightly positive predictive response at middle steepness from 20–40 degrees. The categorical vegetation variable Snow-bed had a strong positive influence of rock ptarmigan presence (Fig. 6). The best model for summer observations had an AUC-value of 0.66 indicating relatively poor discrimination by predicting the probability of rock ptarmigans being present.

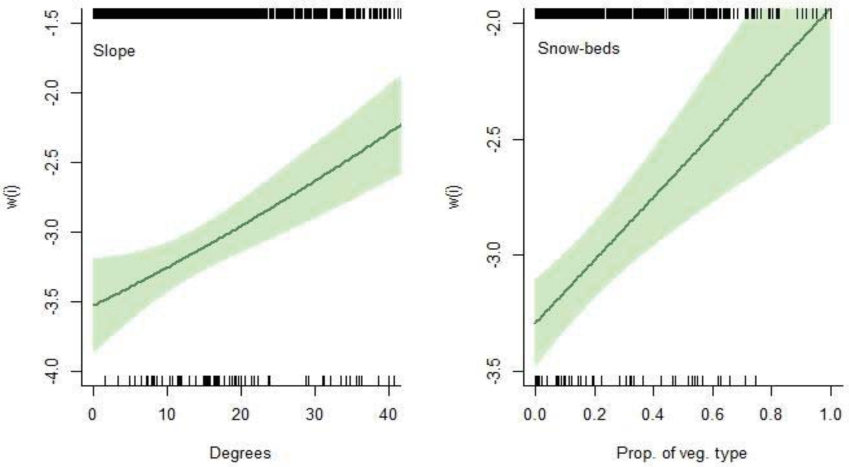


Figure 6. Plots with their standard errors (shaded areas), presenting the most important variables from the model averaging for the six best models during summer in Hestkjølen. The figure shows the estimate of the selection coefficient= w(i) which are proportional to the probability of use. Presence points are marked with rugs on the bottom of the y-axis and the absence points at the top.

In winter we found a significant correlation between the two categorical vegetation variables Snow covered areas and Deciduous forest, and we therefor excluded the latter one from further analyses due to less importance in our models.

The three continuous terrain variables Slope, Altitude and Hillshade in addition to the numerical vegetation variabel Snow covered areas influenced the presence of rock ptarmigan (Table 7). The terrain variable Altitude had a positive influence of rock ptarmigans being present, with a peak from 500-800 m a.s.l. (Fig. 7). Increased values of Hillshade also influenced the rock ptarmigan positively.

Table 7. Variables included in the six best models possesing winter observations (16. September–14. April) in Hestkjølen. Selection of the best predictive habitat model was based on ΔAICc and w_i. The predictive strength of the models is presented as AUC values. VRM = vector ruggedness measure.

Winter	Model	Alt+Alt^2	Hills+Hills^2	VRM+VRM^2	Slope+Slope^2	Aspect	Deciduous	Coniferous	Ridges	Snowcovered	*df*	AIC$_c$	ΔAIC$_c$	w_i	AUC
Accuracy I	1	x	x		x					x	8	539.55	0.00	0.41	0.84
	2	x	x		x			x		x	9	540.96	1.41	0.20	0.84
	3	x	x		x				x	x	9	541.52	1.96	0.15	0.84
	4	x	x		x	x				x	9	541.57	2.02	0.15	0.84
	5	x	x		x			x	x	x	10	542.90	3.35	0.08	0.84
	6	x	x		x	x		x		x	8	557.33	17.77	0.00	0.84
	Intercept										1	796.06	256.51	0.00	

Increased Slope had a negative impact contrary to the result from the summer analyses. In winter we got a peak at low steepness (0–10 degrees) (Fig. 7). In addition, the categorical vegetation variabel Snow covered areas had a negative impact of rock ptarmigans being present.

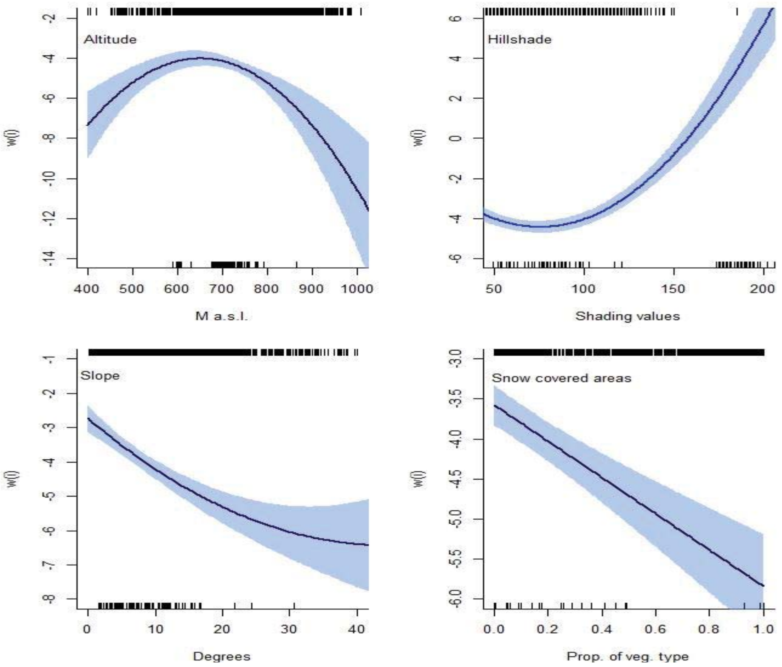


Figure 7. Plots with their standard errors (shaded areas), presenting the most important variables from the model averaging for the six best models during winter in Hestkjølen. The figure shows the estimate of the selection coefficient= w(i) which are proportional to the probability of use. Presence points are marked with rugs on the bottom of the y-axis and the absence points at the top.

All of the mentioned variables in winter had an importance of 1.0 in our models (Table 8). The best model had an AUC-value of 0.84 indicating a good discrimination by predicting the probability of rock ptarmigans being present (Table 7).

Table 8. Averaged parameter estimates, standard errors and variable importance for the six best models and intercept for summer and winter in Hestkjølen, in addition to the parameter estimates and standard errors for the best model for the two seasons. VRM = vector ruggedness measure.

Averaged estimates for the 6 best models and intercept					Estimates for the best model	
Season	**Parameter**	**Estimates**	**SE**	**Variable importance**	**Estimates**	**SE**
Summer	Intercept	-4.627e+00	4.016e+00		-3.5110039	0.3137637
	Slope	2.630e-02	2.601e-02	0.99	0.0184988	0.0246496
	Slope^2	1.190e-04	3.725e-04	0.99	0.0001377	0.0003732
	Snowbed	1.360e+00	5.580e-01	0.99	1.2561413	0.5406495
	Snow/glacier	-1.833e+00	1.522e+00	0.49		
	VRM	-8.441e-02	4.644e-02	0.51		
	VRM^2	1.854e-03	1.091e-03	0.51		
	Altitude	2.073e-02	1.727e-02	0.12		
	Altitude^2	-1.194e-05	9.796e-06	0.12		
Winter	Intercept	-2.852e+01	1.095e+01		-2.805e+01	1.078e+01
	Altitude	9.666e-02	3.266e-02	1.00	9.574e-02	3.236e-02
	Altitude^2	-7.654e-05	2.463e-05	1.00	-7.605e-05	2.446e-05
	Hillshade	-9.318e-02	2.304e-02	1.00	-9.383e-02	2.277e-02
	Hillshade^2	6.325e-04	1.236e-04	1.00	6.348e-04	1.228e-04
	Slope	-1.552e-01	5.530e-02	1.00	-1.553e-01	5.461e-02
	Slope^2	1.666e-03	1.867e-03	1.00	1.687e-03	1.827e-03
	Snowcovered	-5.073e-01	4.070e-01	1.00	-5.380e-01	3.944e-01
	Coniferous	4.655e-01	5.881e-01	0.28		
	Exposed ridges	3.626e-01	1.435e+00	0.23		
	Aspect	-2.242e-03	4.832e-02	0.18		

3.3 Brood movement

Our data consisted of three individual broods, where brood one and two were observed for seven and five and a half hour, respectively, while a third brood was followed over three days (Table 9). In a total observation time of 36 hours, these broods made 65 movements. The mean movement distance pr. 0.5 hour was 4.39 meters (SD = 35.1, range 0–186 m), and 83.1% of all movements were shorter than 30 meters pr. 0.5 hours (Appendix 4).

The broods stayed in relatively moist and open areas. The chicks were rarely more than 10 meters away from the hen when browsing. The mean area used by broods during observation was 30 000 m^2 with a range between 1296 m^2 for the smallest chicks (brood 2), up to 79 643 m^2 for brood 3c. The mean angle of movement was in a northwest direction (Table 9).

Table 9. Sum up table of the broods and their movements.

Brood	Num. Chicks	Est. age (Days)	Obs. time (Hours)	Mean speed (m pr. 1/2 h)	Mean angle	Altitude (m a.s.l.)	Used area (m2)
1	4	14	7.5	11.5	NV	913-925	2284
2	9	7	5.5	10.3	S	927-961	1296
3a	3	21	7.5	13.1	N	844-851	1926
3b	3	21	10.0	26.5	NV	963-976	63 625
3c	3	21	5.5	54.2	NV	959-988	79 643

We failed to re-locate the two unmarked broods (brood 1 & 2) from one day to another. Brood 3, however, was easy to re-locate because the hen was radiocollared, which made it possible to follow it during three days. Data based on these three days showed that the brood moved at a mean distance of 804 meters between the last points of observation at late evening to the first observation point the next day (range 590–1080 m). The total area used by brood 3 during the three days of observation was 0.5 km^2 (Appendix 4).

The sites used by broods had a high amount of vascular plants species consisting of important foraging plants such as alpine bistort (*Polygonum viviparu*), snow-bed willow (*Salix herbacea*) and different species of sedges (*Carex* spp.) and heath (*Calluna* spp.) (Fig. 8).

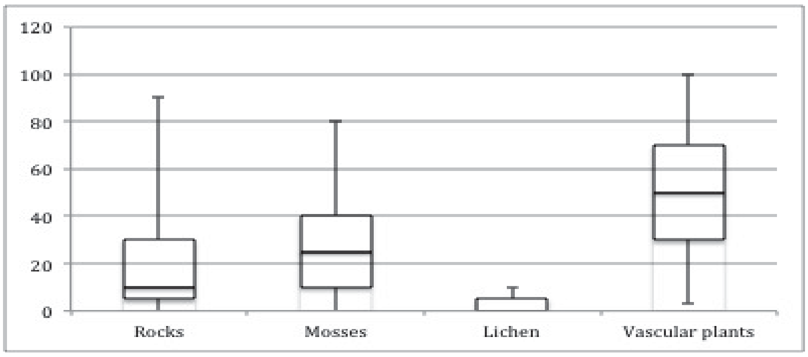


Figure 8. Proportion of different environmental features on sites, used by rock ptarmigan broods.

4 Discussion

4.1 TOV-E

To our knowledge, this is the first study that uses predictive habitat models to reveal habitat selections by rock ptarmigans in mainland Norway. Beacuse our study covers much of the total area of the country, both the terrain and vegetation variables are likely to differ greatly within and between the regions, making it difficult to compare the results from the different regions. However, it is highly interesting to obtain information about these differences and to understand them.

In region East the rock ptarmigan appeared to be present at a higher altitude than in region West, which coincide with the generally higher mountain peaks in this region and the tree-line at higher elevations (Moen 1998; Larsson 2004). Larger differences or similarities between regions could have been found if the TOV-E routes used in the present analysis had covered the entire range of altitude.

Increased VRM increased the probability of rock ptarmigans being present for region West and East, meaning that the rock ptarmigan selected heterogeneous areas rather than homogenous. This is consistent with other studies on rock ptarmigan habitat selection (Pedersen et al. 2007; 2014). Areas with high heterogeneity include many microhabitats with differences in vegetation cover, moisture and solar radiation within a restricted area, compared to more homogenous (Kudo 1991; Jobbágy et al. 1996; Zelený 2008). Additionally, heterogeneous areas have a higher occurrence of the vegetation type Snow-bed, which previous studies have indicated to be important for the presence of rock ptarmigans (Pedersen et al. 2014). Differences in moisture and solar radiation will lead to different germination time for important feeding plants with high nutritional contents throughout the season for the rock ptarmigan (Kudo & Hirao 2006). In region Central, however, the results showed an opposite pattern, where decreased VRM increased the probability of presence, although they appeared to use the same range regarding VRM values as in the other regions.

Hillshade proved to be an important variable to explain habitat selection for rock ptarmigans in region Central and East. Increased Hillshade values, meaning higher solar radiation, had a negative effect on the occurence of rock ptarmigans. In both regions, the rock ptarmigan showed a clear selection towards lowest possible solar radiation. During summer the solar radiation would be linked closely to the moisture gradient and soil temperature (Bliss 1962). Moisture, soil temperature and solar radiation together will determine germination time for different important browsing plants to adult rock ptarmigans and the amount of insects for chicks the first few weeks after hatching (Bliss 1962; Kudo & Hirao 2006; Kaler et al. 2010). Nutrients and fresh food will be available during the entire season in more moist areas than in dry areas with high solar radiation, where the vegetation will be less nutritious through the season (Kudo & Hirao 2006). Hillshade is strongly affected by aspect and slope (Revermann et al. 2012). One could therefore indirectly consider selection for low Hillshade values as a selection for north facing areas, which is supported by a survey on rock ptarmigan habitat selection in northern parts of Sweden (Pedersen et al. 2014). Selection for north facing areas are probably also a result of presence of snow-beds because snow tend to accumulate in these areas, hence providing high quality food for a long period of time (Novoa et al. 2008; Pedersen et al. 2014).

Slope was only included in the models for region West. The rock ptarmigan seemed to prefer slopes around 15 degrees, while flat terrain were higher preferred than steep terrain. This result is in accordance with other surveys that report a selection towards medium to low slopes (Favaron et al. 2006; Zohman et al. 2013). Flat homogenous terrains contain few lookout-points for the rock ptarmigan, and such lookout-point have been described as an important variable, especially for male rock ptarmigans when they settle in a territory or when defending the territory against intruders (Unander & Steen 1985). One could also speculate that steeper terrain provides a better opportunity to detect predators at an earlier stage than in a flat area, which in some cases may be crucial for both the adult birds, but especially for the broods (Pedersen & Karlsen 2007).

Vegetation types did not seem to influence the habitat selection for rock ptarmigans to a great extend other than in region Central, were four vegetation types were included in the models and in region West where the vegetation type Forest/mires were included. Rock ptarmigans tended to avoid the vegetation types Forest/mires, Mooreland, Snow/glacier and Heath w/ lichens, wich is normally not described as suitable rock ptarmigan habitats (e.g. Favaron et al. 2006; Pedersen et al. 2014). We expected to find a positive selection towards some vegetation types such as snow-bed, which has been reported earlier (Favaron et al. 2006), but we were not able to locate any strong preference for the remaining vegetation types. The lack of strong positive preference for specific vegetation types might be explained by a more opportunistic feeding pattern on a wide range of plant species during a long summer period as Weeden (1969) argued for in a survey from Alaska.

4.2 Hestkjølen

In summer (15. April–15. September), we found that the terrain variable Slope with low to medium (20–40 degrees) steepness influenced the probability of occurrence for rock ptarmigans slightly positively. Our results are in accordance with results from the Alps where rock ptarmigans were most often situated in medium steepness <50 degrees (Favaron et al. 2006; Zohmann et al. 2013). The reason for this result might concern the fact that when a male rock ptarmigan arrives his territory from the middle of April until the first half of May, each male pick out some specific rocks that acts as lookout-points. These lookout-points are often situated at medium slopes in heterogeneous terrain where the ptarmigans get an overview of their territory and can easily spot potentially intruders or attract females (Frederick & Gutierrez 1992; Zohmann & Wöss 2008; Schweiger et al. 2012). The males also use these lookout-points while the female incubates or browse, in order to spot predators so he could alert the female (Pedersen & Karlsen 2007).

Our results showed that snow-beds had a positive effect on rock ptarmigan occurrence in accordance with earlier habitat surveys (Favaron et al. 2006). As snowdrift melts, new plants will germinate and offer a continuous fresh and nutritious pantry through a crucial period for chick's survival (Hannon & Martin 2006). To hold a snow-bed in a territory would be advantageous for a male because such traits would be appreciated by the females (Bart & Earnst 1999). Having access to a stable source of high nutritious food can also reduce the broods` foraging time and limit the risk of being discovered by predators (Yoder et al. 2004). Pedersen et al. (2014) found that snow patches seemed to be positive for the occurence of rock ptarmigans in a territory and landscape scale. They also believed, in accordance with earlier studies (Frederick & Gutierrez 1992; Martin & Wilson 2011), that it was not the snow patches themselves that were important, but the habitat features in their vicinity, which we describe as snow-beds. As the chicks grow and becomes more mobile they migrate to higher elevation to utilize fresh vegetation (Pedersen & Karlsen 2007). Together with the exploitation of snow-beds, this is a parallel to the phenomen of ungulates "following the spring" from lower to higher altitudes, but on a smaller scale.

Our winter analyses indicates that the rock ptarmigan prefers lower altitudes in winter (16. September–14. April) than in summer (Pedersen & Karlsen 2007). The second-order polynomial term showed a peak at 500-800 m a.s.l. with few observations above 800 m a.s.l. In addition, we demonstrated that snow covered areas had a slightly negative impact of occurrence. This will indirectly mean a weak positive selection for the ridges and the deciduous forest. Such ridges could provide the rock ptarmigans with food if they are not covered by snow or ice (Pedersen & Karlsen 2007). Surveys conducted by Haugan (2013) showed that the tree line is situated at 700-750 m a.s.l. in Hestkjølen, meaning that the rock ptarmigan are residing in mountain birch forests to a greater extent than in summer. The main reason for rock ptarmigans to move to lower altitudes during winter is most likely food availability, but also poor snow condition for snow burrows and fewer opportunities to hide may be of importance (Giesen & Braun 1992). The fact that rock ptarmigans move down to lower altitudes in the winter season is also known from Svalbard and the Alps (Unander & Steen 1985; Favaron et al. 2006), and may explain why there are preferences for more gentle slopes than in summer time.

The result for hillshade showed a strong preference for high values, i.e. high solar radiation. Hillshade is strongly influenced by aspect and slope. Keating et al. (2007) claimed that hillshade is a problematic surrogate for solar radiation. However, hillshade values will give an idea about how sunlight affects the predictive probability of rock ptarmigan occurence. Hillshade have also been used in other habitat selection surveys and have been interpreted to have a positive effect (Ciarnello et al. 2005; Nelli et al. 2013). To give a biological explanation for the hillshade values, we would assume that the correlation between high solar radiation and earlier date of snowmelt would have a positive effect (Ecosystem Classification Group 2012). Rock ptarmigans will most likely be attracted to those sites were food plants are first available, such as exposed ridges (Weeden 1969).

4.3 Brood movement

Our analysis revealed that broods in general used areas with a high amount of vascular plant species. The utilized areas generally consisted of heterogeneous terrain with elements of screes and moist areas. All these features provide the rock ptarmigan feeding opportunities and also some shelter from predators, which is consistent with previous surveys (Weeden 1969; Hannon & Martin 2006). The broods were often exposed during browsing, the only protection being the heterogeneity of the terrain, like rocks and ravines.

The absence of denser vegetation was in contrast to other studies (Hannon & Martin 2006; Sawa et al. 2011). However, at two occasions, we observed how the ptarmigans used the terrain to their advantage in the presence of a raven. At one occation, the hen used a rock to avoid being exposed. She always kept the rock between herself and the raven. The chicks went to a freezing position, or crouched to the ground (Steen & Unander 1985; Ausmus & Clarke 2013). At a second occation, the hen reacted immediately to the sound of a raven by raising her neck and giving an alarm call to the chicks. The chicks responded as observed in white-tailed ptarmigan chicks by Ausmus & Clarke (2013) by instantaneously assuming an upright and alert position. After a few seconds the whole brood was running towards a bush of fern, in which they staid for almost an hour (Fig. 9).

Figure 9. Chicks seeking shelter in a fern after an alarm call from their mother.

The broods tended to move upwards in the terrain, which is also reported for chicks of willow ptarmigans (Hjeljord 2008). The reason could be that the brood tend to follow the greenness and seek optimal foraging patches. One possible bias is that we usually stayed lower in the terrain than the brood, which may have led to movement away from us. The age of the chicks might have affected the mobility, as younger chicks were stationary (brood 1 & 2) while the older chicks (brood 3), used larger areas. Brood 3, which we followed over three days, was also quite stationary during daytime but moved to a greater extent during night. This could be a result of decreased chance of being detected by predators that hunt by sight (Cotter & Boag 1992; Reif et al. 2004; Steen & Haugvold 2009; Sandercock et al. 2011). For further results of brood movement, see Appendix 4.

4.4 Alternative factors affecting the realized niche of rock ptarmigans

Because predation is the main mortality factor for the rock ptarmigan (Wilson & Martin 2008; Novoa et al. 2011), predators are likely to affect not only population dynamics but also the distribution of individuals. In their habitat choise, rock ptarmigans have to perform a trade-off between availability of high quality food and risk of predation (Hannon & Martin 2006; Cresswell & Quinn 2013). This might also be a factor when the rock ptarmigan has to choose an optimal nest location. Mönkkönen et al. (2007) showed that some small passerines, but also larger birds such as the hazel grouse (*Bonasa bonasia*), often localized their nest closer to a predator than expected from a free ideal distribution, probably to provide protection against other predators. This means that rock ptarmigans could balance the threat and usefulness of nesting predators, such as smaller raptors, to decide optimal nest sites to be protected against corvids.

Common for both ptarmigan species in Fennoscandia is that they are likely to be affected by future reduction of alpine habitats. Fragmentation, disturbance activities, shrub encroachment and tree-line expansion associated with climate changes, are all major threats that may affect the abundance and distribution of alpine and arctic species (Serreze et al. 2000; Hinzman et al. 2005; Myers-Smith et al. 2011; Hofgaard et al. 2012; Bech et al. 2013). Increased temperatures had a strong negative impact on the abundance of rock ptarmigans in the Alps (Revermann et al. 2012). Booms et al. (2011) found evidence for a decrease of the rock ptarmigans fundamental niche with 40% in a 200-year interval in Alaska. This might lead to more interspecific competition between willow- and rock ptarmigans. This specific interaction is poorly understood, but since the willow ptarmigan prefers to breed in areas with higher lateral cover, one could expect more interactions as a result of an expanded treeline (Pedersen & Karlsen 2007; Wilson & Martin 2008). Since there is also observed changes in intervals of pronounced rodent peaks in arctic and alpine regions, we would expect predators to switch from rodents to other food sources, leading to a higher egg loss for the rock ptarmigans (Schmidt et al. 2012; Ims et al. 2013). On the other hand, this could also lead to a general decrease in density of predators with high proportions of rodents in their diet, leading to a generally lower mortality for rock ptarmigans (Hjeljord 2008; Kausrud et al. 2008).

4.4 Use of scales and possible biases

Boyce et al. (2003) claim that "*There is no one best scale for habitat studies. Instead, the appropriate scale depends on the question at hand".* Our results from the regional scale can not be seen as a final answer to optimal habitat choise, because this only reflects that the rock ptarmigan selects the optimal features based on the availability in that specific area at the specific scale. This is particularly important for such a large country as Norway, with large differences in habitat and landscape features. Future research on habitat preferences by rock ptarmigans in Norway should do this at a smaller and more appropriate scale to better understand the ecological patterns and processes (Graf et al. 2005).

TOV-E was based on a presence/absence approach at a regional scale where 20 points in a route being assessed as either observation of ptarmigans or not. The temporal scale is good since these routes are appraised at the most optimal time of year and in the most active part of the day (Kålås & Husby 2002). Biases regarding this method is that we selected routes where we knew that rock ptarmigans were observed, meaning that both the absence and presence points will be situated in a fairly good rock ptarmigan area, thus bringing out the best of the best when it comes to preferences within a territory. This could give lower AUC-values than if we had compared these routes against those without observations of rock ptarmigan. The scale of the survey could also disguise a stronger effect of vegetation, because terrain variables will influence the results greater than vegetation on a large scale (Bailey et al. 1996; Boyce 2006). Since we used highly accurately collected data in our survey, we did not delete any “questionable” observations, as one must consider when using a more opportunistic data set (Pedersen et al. 2014). Some possible biases by use of the TOV-E data set must however be mentioned. There is a risk of double counting individuals if rock ptarmigans were observed by sound recognition. Since some of the observations were made by sound recognition, we would not get a completely accurate position for each individual.

At our local scale in Hestkjølen we had a more opportunistic method that is a fair alternative to systematic surveys (e.g. Sardà-Palomera et al. 2012), but the persons involved in the obtained observations are educated in species recognition. Biases associated with the method in Hestkjølen could be connected to less activity in steep areas or areas not considered as suitable rock ptarmigan habitat (Yoccoz et al. 2004).

Favaron et al. (2006) found large differences in habitat preferences within the different stages in summer. Our summer time period from Hestkjølen is fairly long (15. April–15. September), which could make it difficult to detect strong preferences due to differences within the season. Nor have we taken temporal aspects such as the time of the day (Beyer & Haufler 1994; Nielsen et al. 2004), or disimilarities between different years (Pettorelli et al. 2005) into account.

Studies that examine use-availability factors and resource selection functions (RSF’s) are most commonly based on presence only. Then, one must generate absence points to cover the availability concept (Chefaoui & Lobo 2008). The results of use-availability data might contain asymmetry of errors due to generated absence points with random selection (MacKenzie 2005), because random absence points may be used if monitored more intensively or for a longer period of time (Johnson et al. 2006; Stokland et al. 2011). Additionally, the number of these absence points relative to the presence points and the distribution of them might give biases in the AUC-model (VanDerWal et al. 2009). This might be the case in our local study in Hestkjølen, where few environmental variables explained the rock ptarmigan occurrence. Another biological bias concerning estimates of availability emerges when generalizing all individual observations as one “group” in the analysis. This will potentially lead to loss of individual variations in sex, age and metapopulations (Gillingham & Parker 2008). The data-set available did however not allow us to investigate individual heterogeneity in habitat selection.

4.5 Conclusion

Our results indicates that patterns in habitat selection for the rock ptarmigan is mainly driven by terrain features such as altitude, terrain heterogeneity, hillshade, slope and some vegetation variables, but this will vary between different spatial and temporal scales. Thus it becomes difficult to establish a general answer to the everlasting question *where are the rock ptarmigan?*

However, we hope that this thesis could provide some information concerning the rock ptarmigan habitat preferences, leading to improved knowledge about this species. To achieve a more targeted management of the rock ptarmigan, mapping and maintenance of high-quality habitats are key issues in conserving this species. Additionally, we need more precise estimates of the population size in different parts of the country and knowledge about how the populations respond to todays management. Knowledge about how hunting affects the rock ptarmigan and how the populations respond to future predicted climatic changes should especially receive increased attention in future research. Such information should be implemented to achieve a more adaptive management improving the conditions to the goddess of the mountain, the rock ptarmigan (Fig. 10).

Figure 10. What will the future bring for the rock ptarmigans?

5 References

Anderson, D.R., Link, W.A., Johnson, D.H. & Burnham, K.P. (2001). Suggestions for presenting the results of data analysis. – *The Journal of Wildlife Management,* 65:373-378.

Ausmus, D.M. & Clarke, J.A. (2013). Mother knows best: functionally referential alarm calling in white-tailed ptarmigan. – *Animal Cognition,* 17(**3**):671-679

Austin, M.P. (2002). Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. – *Ecological Modelling,* 157:101-118.

Bailey, D.W., Gross, J.E., Laca, E.A., Rittenhouse, L.R., Coughenour, M.B., Swift, D..M. & Sims, P.L. (1996). Mechanisms that result in large herbivour grazing distribution patterns. – *Journal of Range Management,* 49:386-400.

Bart, J. & Earnst, S.L. (1999). Relative importance of male and territory in pairing success of male rock ptarmigan (*Lagopus mutus*). – *Behaviour Ecology Sociobiology,* 45:355-359.

Bartoń, K. (2013). MuMIn: Multi-model inference. R package version 1.9.0. Available: http://CRAN.R-project.org/package = MuMIn. Accessed 2013 May 4.

Bech, N., Barbu, C.M., Quéméré, E., Novoa, C., Alienne, J.F. & Boissier, J. (2013). Pyrenean ptarmigan decline under climatic and human influences through the Holocene. – *Heredety,* 111:402-209

Bergerud, A.T. & Gratson, M.W. (1988). Adaptive strategies and population ecology of northern grouse. – *University of Minnesota Press*, Minneapolis. 809 pp.

Beyer, D.E. & Haufler, J.B. (1994). Diurnal versus 24-hour sampling of habitat use. – *Journal of Wildlife Management*, 58:178-180.

Blaschke, T. (2010). Object based image analysis for remote sensing. – *Journal of Photogrammetry and Remote Sensing,* 65:2-16.

Bliss, L.C. (1962). Adaptions of arctic and alpine plants to environmental conditions. – *Arctic Institute of North America,* 15:117-144.

Booms, T.M., Lindgren, M. & Huettmann, T. (2011). Linking Alaska's predicted climate, gyrfalcon and ptarmigan distributions in space and time: a unique 200-year perspective. In: Watson, R.T., Cade, T.J., Fuller, M., Hunt, G. & Potapov, E. (eds) Gyrfalcons and Ptarmigan in changing World. – *The Peregrine Fund,* Boise pp. 1-14.

Borecha, D.E. (2011). Population viability analyses of Swedish and Norwegian rock ptarmigan *Lagopus muta* populations. – *Faculty and Forestry and Wildlife Management,* Hedmark University College, Evenstad. 33 pp.

Boyce, M.S. (2006). Scale for resource selection functions. – *Diversity and Distributions,* 12:269-276.

Boyce, M.S. & McDonald L.L. (1999). Relating populations to habitats using resource selection functions. – *Tree* ,14:268-272.

Boyce, M.S., Mao, J.S., Merrill, E.H., Fortin, D., Turner, M.G., Fryxell, J. & Turchin, P. (2003). Scale and heterogeneity in habitat selection by elk in Yellowstone National park. –*Écoscience,* 10:421-431.

Burnham, K.P. & Anderson, D.R. (2002). Model Selection and Multimodel Inference: a practical information-theoretic approach. Second edition. – *Springer,* New York. 488 pp.

Burrough, P.A. & McDonell, R.A. (1998). Principles of Geographical Information Systems. – *Oxford University Press*, New York. 352 pp.

Chefaoui, R.M. & Lobo, J.M. (2008). Assessing the effects of pseudo-absences on predictive distribution model performance. – *Ecological Modelling*, 210:478–486.

Ciarniello, L.M., Boyce, M.S., Heard, D.C. & Seip, D.R. (2005). Denning behaviour and den sites of grizzly bears along the Parsnip River, British Columbia, Canada. – *Ursus,* 16:47-58.

Cotter, R. & Boag, D.A. (1992). Raptor predation on rock ptarmigan (*Lagopus mutus*) in the central Canadian Arctic. – *Journal of Raptor Research*, 26:146-151.

Cresswell, W. & Quinn, J.L. (2013). Contrasting risks from different predators change the overall nonlethal effects of predation risk. – *Behavioral Ecology,* 24:871-876

Ecosystem Classification Group. (2012). Ecological Regions of the Northwest Territories. – Southern Arctic Department of Environment and Natural Resources, Government of the Northwest Territories, Yellowknife, NT, Canada. 170 pp.

Favaron, M., Scherini, G.C., Preatoni, D., Tosi, G. & Wauters, L.A. (2006). Spacing behaviour and habitat use of rock ptarmigan *(Lagopus mutus)* at low density in the Italian Alps. – *Journal of Ornithology,* 147:618-628.

Fawcett, E. (2006). An introduction to ROC analysis. – *Pattern Recognition Letters,* 27:861-874.

Frederick, G.P. & Gutierrez, R.J. (1992). Habitat use and population characteristics of the white-tailed ptarmigan in Sierra-Nevada California. – *Condor,* 94:889-902.

Freeman, E. (2012). Presence- Absence Model Evaluation. R package version 1.1.9. Available http://cran.r-project.org/web/packages/PresenceAbsence/PresenceAbsence.pdf. Accessed 2012 August 17.

Giesen, K.M. & Braun, C.E. (1992). Winter home range and habitat characteristics of white-tailed ptarmigan in Colorado. – *The Wilson Bulletin,* 104:263-272

Gillingham, M.P. & Parker, K.L. (2008). The importance of individual variation in defining habitat selection by moose in northern British Columbia. – *Alces,* 44:7-20.

Graf, R.E., Bollmann, K., Suter, W. & Bugmann, H. (2005). The importance of spatial scale inhabitat models: capercaillie in the Swiss Alps. – *Landscape ecology*, 20:703-717.

Guisan, A. & Zimerman, N.E. (2000). Predictive habitat distribution models in ecology. – *Ecological Modelling,* 135:174-186.

Hannon, S.J. & Martin, K. (2006). Ecology of juvenile grouse during the transition to adulthood. – *Journal of Zoology,* 269:422-433.

Haugan, K. (2013). Botaniske undersøkelser I Lierne nasjonalpark. *HINT Utredning 155.* 19 pp.

Hinzman, L.D., Bettez, N.D., Bolton, W.R., Chapin, F.S., Dyergerov, M.B., Fastie, C.L., Griffith, B., Hollister, R.D., Hope, A., Huntington, H.P., Jensen, A.M., Gensuo, J.J., Jorgensen, T., Kane, D.L., Klein, D.R., Kofinas, G., Lynch, A.H., Lloyd, A.H., McGuire, A.D., Nelson, F.E., Oechel, W.C., Osterkamp, T.E., Racine, C.H., Romanovsky, V.E., Stone, R.S., Stow, D.A., Sturm, M., Tweedie, C.E., Vourlitis, G.L., Walker, M.D., Walker, D.A., Webber, P.T., Welker, J.M., Winker, K.S. & Yoshikawa, K. (2005). Evidence and implications of recent climate change in northern Alaska and other arctic regions. – *Climate Change,* 72:251-298

Hirzel, A.H. & Le Lay, G. (2006). Resource selection functions and niche theory: a review. – *Journal of Wildlife Management,* 45:1372-1381.

Hjeljord, O. (2008). Viltet – biologi og forvaltning. – Tun forlag/Landbruksforlaget. 352 pp.

Hofgaard, A., Harper, K.A. & Golubeva, E. (2012). The role of circum-arctic forest-tundra ecotone for arctic biodiversity. – *Biodiversity,* 13:174-181.

Huntley, B., Green, R.E., Collingham, Y.C. & Willis, S.G. (2007). A climatic atlas of European breeding birds. – Durham Univ., The RSPB and Lynx Edicions, Barcelona. 521 pp.

Ims, R., Henden, J.A., Thingnes, A-V. & Killengreen, S.T. (2013). Indirect food web interactions mediated by predator-rodent dynamics: relative role of lemmings and voles. - *Biology letters,* 9.

Jobbágy, E.G., Paruelo, J.N. & León, R.J.C. (1996). Vegetation heterogeneity and diversity in flat and mountain landscapes of Patagonia (Argentina). – *Journal of Vegetation Science,* 7:599-608.

Jiguet, F., Barbet-Massin, M., Devictor, V., Jonzen, N. & Lindström, A. (2013). Current population trends mirror forecasted changes in climatic suitability for Swedish breeding birds. – *Bird Study,* 60:60-66.

Johansen, B.E. (2009). Vegetasjonskart for Norge basert på Landsat TM/ETM+ data. – *Norut Rapport* 4:1-87. Tromsø, Norway, Norut Northern Research Institute.

Johnson, C.J., Nielsen, S.E., Merill, E.H., McDondald, T.L. & Boyce, M.S. (2006). Resource Selection Functions Based on Use- Availability Data: Theoretical Motivation and Evaluation Methods. – *Journal of Wildlife Management,* 70:347-357.

Kaler, R.S.A., Ebbert, S.A., Braun, C.E. & Sandercock, B.K. (2010). Demography of a reintroduced population of Evermann's rock ptarmigan in the Aleutian islands. – *The Wilson Journal of Onithology,* 122:1-14.

Kausrud, K.L., Mysterud, A., Steen, H., Vik, J.O., Østbye, E., Cazelles, B., Framstad, E., Eikeset, A.M., Mysterud, I., Solhøy, T. & Stenseth, N.C. (2008). Linking climate changes to lemming cycles – *Nature*, 456:93-98.

Keating, K.A., Gogan, P.J.P., Vore, J.M. & Irby, L.R. (2007). A simple solar radiation index for wildlife habitat studies. – *Journal of Wildlife Management,* 71:1344-1348.

Krogh, K. (1954). Fugleliv I et grenseområde. In: Haave, M., Jørgensen, R. & Kierulf, E. (red.) *Årbok 1954- Trondhjems turistforening pp. 73-80.* Arkitekttrykkeriet I Trondhjem.

Kudo, G. (1991) Effects of snow-free period on the phenology of alpine plants inhabiting snow patches. – *Arctic Alpine Research,* 23:436-443.

Kudo, G. & Hirao, A.S. (2006). Habitat-specific responses in the flowering phenology and seed set of alpine plants to climate variation: implications for global-change impacts. – *Population Ecology,* 48:49-58.

Kvasnes, M.A.J., Storaas, T., Pedersen, H.C., Bjørk, S. & Nilsen E.B. (2010). Spatial dynamics of Norwegian tetraonid populations. –*Ecological Research,* 25:367-374

Kålås, J.A. & Husby, M. (2002). Terrestrisk naturovervåking. Ekstensiv overvåking av terrestre fugl i Norge. – *NINA Oppdragsmelding* 740:1-25.

Kålås, J.A., Husby, M., Nilsen, E.B. & Vang, R. (2014). Bestandsvariasjoner for terrestriske fugler I Norge 1996-2013. – *NOF Rapport* 4. 36 pp.

Larsson, J.Y. (2004). Skoggrensa i Norge – indikator på endringer i klima og arealbruk? – *NIJOS dokument 03/04,* 47 pp.

Lehikoinen, A., Green, M., Husby, M., Kålås, J.A. & Lindström, Å. (2014). Common montane birds are declining in northern Europe. – *Journal of Avian Biology,* 45:3-14.

Lele, S.R., Merrill, E.H., Keim, J. & Boyse, M.S. (2013). Selection, use, choice and occupancy: clarifying concepts in resource selection studies. – *Journal of Animal Ecology,* 82:1183-1191.

Long, R.A., Muir, J.D., Rachlow, J.L. & Kie, J.G. (2009). A Comparison of Two Modeling Approaches for Evaluating Wildlife-Habitat Relationships. – *Journal of Wildlife Management,* 73:294-302.

Luoto, M., Kuussaari, M. & Toivonen, T. (2002). Modelling butterfly distribution based on remote sensing data. – *Journal of Biogeography*, 29:1027-1037

MacKenzie, D.I. (2005). What are the issues with presence-absence data for wildlife managers? – *Journal of Wildlife Management*, 69:849-860.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002). Resource selection by animals, 2nd edn. – *Kluwer Akademic Publishers*, Dord recht, the Netherlands. 221 pp.

Martin, K. & Wilson, S. (2011). Ptarmigan in North America: influence of life history and environmental conditions on population persistence. In: Watson, R.T., Cade, T.J., Fuller, M., Hunt, G., & Potapov, E. (eds) Gyrfalcon and ptarmigan in a changing world. – *The Peregrine Fund,* Boise, pp. 45-54.

Mazerolle, M.J. (2013). AICcmodavg: Model selection and multimodel inference based on (Q) AIC. R package version 1.35. Available at: http://cran.r-project.org/web/packages/AICcmodavg/AICcmodavg.pdf. Accessed 2013 November 11.

Met.no
< http://sharki.oslo.dnmi.no/portal/page?_pageid=73,39035,73_39049&_dad=portal&_schema=PORTAL>
[Reading date 23.01.2014]

Moen, A. (1998). National Atlas of Norway: Vegetation. – Norwegian Mapping Authority, Hønefoss. 200 pp.

Moss, R. & Hanssen, I. (1980). Grouse nutrition. – *Nutrition Abstracts and Rewievs Series B,* 50:555-567.

Moss, R., Storch, I. & Müller, M. (2010). Trends in grouse research. – *Wildlife Biology,* 16:1-11.

Muller, D., Schroder, B. & Muller, J. (2009). Modelling habitat selection of the cryptic Hazel Grouse, *Bonasa bonasia* in a montane forest. – *Journal of Ornithology,* 150:717-732.

Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., Macias-Fauria, M., Sass-Klaasen, U., Levesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L.S., Weijers, S., Rozema, J., Rayback, Elmendorf, S., Ravoiainen, V., Welker, J., Grogan, P., Epstein, H.E. & Hik, D.S. (2011). Shrub expansion in tundra ecosystems: dynamics impacts and research priorities. – *Environment Research Letters,* 6:1-15.

Mönkkönen, M., Husby, M., Tornberg, R., Helle, P. & Thompson, R.L. (2007). Predation as a landscape effect: trading off by prey species between predation risks and protection benefits. – *Journal of Animal Ecology,* 76:619-629.

Nasjonalparkrådet. (2007). Forvaltningsplan for Lierne/Lijre nasjonalpark. Nordli 08.05.2009.

Nelli, L., Meriggi, A. & Franoi, A. (2013). Habitat selection by breeding rock ptarmigan (*Lagopu muta helvetica*) males in the western Italian Alps. – *Wildlife Biology,* 19:382-389.

Nielsen, S.E., Boyce, M.S. & Stenhouse, G.B. (2004). Grizzly bears and forestry I. :selection of clearcuts by grizzly bears in west-central Alberta, Canada. – *Forest Ecology and Management,* 199:51-65.

Nilsen, E.B., Pedersen, S., Brøseth, H. & Pedersen, H.C. (2012). Fjellryper - En kunnskapsoversikt. – *NINA Rapport,* 869, 38 pp.

Nopp-Mayr, U. & Zohmann, M. (2008). Spring densities and calling activities of Rock Ptarmigan (*Lagopus muta helvetica*) In the Austrian Alps. - *Journal of Ornithology,* 149:135-139.

Novoa, C., Besnard, A., Brenot, J.F. & Ellison, L.N. (2008). Effect of weather on the reproductive rate of rock ptarmigan *Lagopus muta* in the eastern Pyrenees. – *Ibis,* 150:270-278.

Novoa, C., Desmet, J.F., Brenot, J.F., Muffat-Joly, B., Arvin Bérod, M., Resseguir, J. & Tran, B. (2011). Demographic traits of two alpine populations of rock ptarmigan. – In: Sandercock, B.K., Martin, K. & Segelbacher, G. (red). – *Ecology, Conservation and Management of Grouse,* University of California Press. pp. 267-280.

Nolet, B.A., Bauer, S., Feige, N., Kokorev, Y.I., Popov, I.Y. & Ebbings, B.S. (2013). Faltering lemming cycles reduce productivity and population size of migratory Arctic goose species. – *Journal of Animal Ecology,* 82:145-152.

Nyström, J., Ekenstedt, J., Angerbjörn, A., Thulin, L., Hellström, P. & Dalén, L. (2006). Golden Eagles on the Swedish mountain tundra - diet and breeding success in relation to prey fluctuation. – *Ornis Fennica,* 83:145-152.

Reif, V., Tornberg, R. & Huhtala, K. (2004). Juvenile grouse in the diet of some raptors. – *Journal of Raptor Research,* 38:243-249.

Pearce, J.L. & Boyce, M.S. (2006). Modelling distribution and abundance with presence-only data. – *Journal of Applied Ecology,* 43 (**3**):405-412.

Pedersen, H.C. & Karlsen, D.H. (2007). Alt om rypa - biologi · jakt ·forvaltning. – Tun forlag, Oslo. pp 259.

Pedersen, H.C., Steen, H., Kastdalen, L., Svendsen, W. & Brøseth, H. (1999). Betydningen av jakt på lirypebestander. Framdriftsrapport 1996-1998. – *NINA Oppdragsmelding* 578:1-43.

Pedersen, Å.Ø., Jepsen, J.U., Yoccoz, N.G & Fuglei, E. (2007). Ecological correlates of the distribution of territorial Svalbard rock ptarmigan (Lagopus muta hyperborea). – *Canadian Journal of Zoology-Revue Canadienne De Zoologie,* 85:122-132.

Pedersen, Å.Ø., Jepsen, J.U. & Fuglei, E. (2011). Habitatmodell for svalbardrype – en storskala GIS-studie som viser fordeling av egnede hekkehabitater på Spitsbergen. – Rapport til Svalbards Miljøvernfond, 31 pp.

Pedersen, Å.Ø., Jepsen, J.U., Biuw, M. & Johansen, B. (2012). Habitatmodell for lirype i Finnmark. – *NINA Rapport* 845, 36 pp.

Pedersen, Å.Ø., Blanchet, M.-A., Hörnell-Willebrand, M., Jepsen, J.U., Biuw, M. & Fuglei, E. (2014). Rock Ptarmigan (*Lagopus muta*) breeding habitat use in northern Sweden. – *Journal of Ornithology,* 155:195-209

Pedrini, P. & Sergio, F. (2002). Regional conservation priorities for a large predator: golden eagle (*Aquila chrysaetos*) in the Alpine range. – *Biological Conservation,* 103:163-172.

Pettorelli, N., Gaillard, J.-M., Yoccoz, N.G., Duncan, P., Maillard, D., Dellorme, D., Van Laere, G. & Toigo, C. (2005). The response of fawn survival to changes in habitat quality varies according to cohort quality and spatial scale. – *Journal of Animal Ecology,* 74:972-981.

Phillips, S.J. & Elith, J. (2013). On estimating probability of presence from use–availability or presence–background data. – *Ecology,* 94:1409-1419.

Revermann, R., Schmid, H., Zbinden, N., Spaar, R. & Schröder, B. (2012). Habitat at the mountain tops: how long can Rock Ptarmigan (*Lagopus muta helvetica*) survive rapid climate change in the Swiss Alps? A multi-scale approach. – *Journal of Ornithology,* 53:891-905.

Sandercock, B., Martin, K. & Hannon, S.J. (2005). Life history strategies in extreme environments: comparative demography of arctic and alpine ptarmigan. – *Ecology,* 86:2176-2186.

Sandercock, B.K., Nilsen, E.B., Brøseth, H. & Pedersen, H.C. (2011). Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. - *Journal of Animal Ecology,* 80:244-258

Sappington, J.M., Longshore, K.M. & Thomson, D.B. (2007). Quantifying LAndscpae Ruggedness for Animal Habitat Analysis: A case Stuy Using Bighorn Sheep in the Mojave Desert. – *Journal of Wildlife Management,* 71:1419-1426.

Sardà-Palomera, F., Brotons, L., Villero, D., Siersema, H., Newson, S.E. & Jiguet, F. (2012). Mapping from heterogeneous biodiversity monitoring data sources. – *Biodiversity Conservation,* 21:2927-2948.

Sawa, Y., Takeuchi, Y. & Nakamura, H. (2011). Nest site selection and nesting biology of rock ptarmigan *Lagopus muta japonicas* in Japan. – *Bird Study,* 58:200-207.

Schmidt, N.M., Ims, R.A., Høye, T.T., Gilg, O., Hansen, L.H., Hansen, J., Lund, M., Fuglei, E., Forchhammer, M.C. & Sittler, B. (2012). Response of an arctic predator guild to collapsing lemming cycles. – *Proceedings of the Royal Society B,* 279:4417-4422.

Schweiger, A.-K., Nopp-Mayr, U. & Zohmann, M. (2012). Small-scale habitat use of black grouse (*Tetrao tetrix* L.) and rock ptarmigan (*Lagopus muta helvetica* Thienemann) in the Austrian Alps. – *European Journal of Wildlife Research,* 58:35-45.

Scott, J.M., Heglund, P.J., Samson, F., Haufler, J., Morrison, M., Raphael, M. & Wall, B. (2002). Predicting Species Occurrences: Issues of Accuracy and Scale. – *Island Press,* Covelo, CA, 868 pp.

Serreze, M.C., Walsh, J.E., Chapin, F.S., Osterkamp, T., Dyurgerov, M., Romanovsky, V., Oechel, W.C., Morison, J., Zhang, T. & Barry, R.G. (2000). Observational evidence of recent change in the northern high-latitude environment. – *Climatic Change,* 46:159-207.

Steen, J.B. & Unander, S. (1985). Breeding biology of the Svalbard Rock Ptarmigan *Lagopus mutus hyperboreus. – Ornis Scandinavica,* 16:191-197

Steen, J.B. & Haugvold, O.A. (2009). Cause of death in willow ptarmigan (*Lagopus L. lagopus*) chicks and the effect of intensive, local predator control on chick production. – *Wildlife Biology,* 15:53-59.

Stokland, J.N., Bakkestuen, V., Bekkby, T., Rinde, E., Skarpaas, O., Sverdrup-Thygeson, A., Yoccoz, N.G. & Halvorsen, R. (2008). Prediksjonsmodeller som verktøy for kartlegging, overvåking og forvaltning av biologisk mangfold – anvendelse, utviklingspotensial og utfordringer. – *Naturhistorisk Museum,* Oslo, Rapport 1, 1-74 pp.

Stokland, J.N., Halvorsen, R. & Støa, B. (2011). Species distribution modelling - Effect of design and sample size of pseudo-absence observations. – *Ecological Modelling,* 222:1800-1809.

Storch, I. (2007). Grouse: Status Surveys and Conservation Action Plan 2006-2010. WBA/Birdlife/SSC/Grouse Specialist Group. – *IUCN, Gland and Cambridge, and the World Pheasant Association,* Reading. 125 pp.

Unander, S. & Steen, J.B. (1985) Behaviour and Social Structure in Svalbard Rock Ptarmigan *Lagopus mutus hyperboreus. – Ornis Scandinavica,* 16:198-204.

VanDerWal, J., Shoo, L.P., Graham, C. & Williams, S.T. (2009). Selecting pseudo-absence data for presence-only distribution modelling: How far should you stray from what you know? – *EcologicalModelling,* 220:589-594.

Virkkala, R., Heikkinen, R.K., Leikola, N. & Luoto, M. (2008). Projected large-scale range reductions of northern-boreal land bird species due to climate change. *–Biological Conservation,* 141:1343-1353.

Watson, A., Moss, R. & Rae, S. (1998). Population dynamics of Scottish rock ptarmigan cycles. – *Ecology,* 79:1174-1192.

Weeden, R.B. (1969). Foods of Rock and Willow Ptarmigan in central Alaska with comments on interspesific competition. – *The Auk,* 86:271-281.

Williams, B.K. (2011). Adaptive management of natural resources - framework and issues. – *Journal of Environmental Management,* 92:1346-1353.

Wilson, S, & Martin, K. (2008). Breeding habitat selection of sympatric White-tailed, Rock and Willow Ptarmigan in the southern Yukon Territory, Canada. – *Journal of Ornithology,* 149:629-637

Yoccoz N., Nickhols, J.D. & Boulinier, T. (2004). Monitoring of biological diversity in space and time. – *Trends in Ecology and Evolution,* 16:446-543

Yoder, J.M., Marschall, E.A. & Swanson, D.A. (2004). The cost of dispersal: predation as a function of movement and site familiarityin ruffed grouse. – *Behavioural Ecology,* 15:469-476.

Zelený, D. (2008). Patterns of vegetation diversity in deep river valleys of the Bohemian Massif. Ph. D. Thesis, in English. – *Faculty of Science, University of South Bohemia*, České Budějovice, Czech Republic. 126 pp.

Zohmann, M. & Wöss, M. (2008). Spring density and summer habitat use of alpine rock ptarmigan *Lagopus muta Helvetica* in the southeastern Alps. – *European Journal of Wildlife Research* 54:379-284.

Zohmann, M., Pennerstorfer, J. & Nopp-Mayr, U. (2013). Modelling habitat suitability for rock ptarmigan (*Lagopus muta helvetica*) combinig object-based classification of IKONOS imagery and Habitat Suitability Index modeling. – *Ecological Modelling,* 254:22-32.

6 Appendices

Appendix 1 TOV-E routes and observations of rock ptarmigans**.**

Route	Area	Year of assessment	Points of observation	Present
	Hedmark			
431	Rendal	06/07/08/09/10/**13**	6,11/4/4,6/4/3/**6**	8
432	Engerdal	09	16	1
435	Alvdal	08	20	1
444	Tynset	**11**	**16**	1
	Totalt			**11**
	Oppland			
526	Skjåk	06/07/09	13/5,13/5,13	5
527	Skjåk	06/08/09	12/12/13^2	3
528	Vågå	08	2	1
529	Dovre	06/07/08/**11**	11(f6),12(f10)/11(f30),16/ 10,13/**10**	7
532	Lesja	09/**11**	12/**13,15**	3
534	Lesja	06	3	1
536	Lesja	09	18	1
	Totalt			**21**
	Telemark			
821	Vinje	09	7	1
822	Vinje	09/**11**/**12**/**13**	3/**7,15**/**5,9**/**2,7**	7
	Totalt			**8**
	Aust-Agder			
911	Valle	08	15^2	1
	Totalt			**1**
	Rogaland			
1106	Gjesdal	10	17	1
	Totalt			**1**
	Hordaland			
1202	Etne	09/**12**/**13**	3,7,12/**8,12**/**12**	6
1204	Odda	10	3	1
1211	Ullensvang	**13**	**10**	1
1215	Eidfjord	**11**	**15**	1
	Totalt			**9**
	Sogn og Fjordane			
1405	Lærdal	**11**/**13**	**1(f5)**/**2,6,13**	4
1410	Høyanger	**12**	**13**	1
1421	Bremanger	**13**	**13^2**	1
1422	Gloppen	09/10/**11**/**12**/**13**	1/19,20/**19**/**1,2,5**/**20**	8
1423	Gloppen	**12**	**11/18**	2
	Totalt			**16**
	Møre og Romsdal			
1504	Norddal	**13**	**20**	1
1509	Nesset	10/**12**	17/**20**	2
1517	Nesset	**11**	**4,8**	2
	Totalt			**5**
	Sør- Trøndelag			
1603	Oppdal	05/06/08/**12**	15/14/12/**1,16**	5
1606	Oppdal	**12**	**6**	1

1607	Midtre Gauldal	06/08	5,6,8,10,13,16^2/15,16	8
1620	Selbu	**13**	**6**	1
	Totalt			**15**
Nord- Trøndelag				
1703	Stjørdal	**12**	**13**	1
1707	Verran	07	11	1
1713	Snåsa	08	1	1
1719	Lierne	08/09/**11**/**12**/**13**	6,7,10^2,11,20/5(f9),11/**2, 11**/**4,7^2,11**/**11**	13
1720	Lierne	07/**11**/**12**	14,15/**8^2**/**10^2,13,15**	6
1731	Fosnes	05/06/09/**11**	9/9/9/**9**	4
1734	Nærøy	10/**11**/**12**/**13**	7/**7,14**/**5**/**4**	5
	Totalt			**31**
Nordland				
1806	Grane	09	3	1
1810	Hattfjelldal	10	3	1
1814	Vefsn	09	8	1
1824	Rana	10/**11**/**12**/**13**	8/**14**/**7,13**/**10**	5
1835	Saltdal	12	1^2,3,4,5,6,8	6
1842	Saltdal	13	16	1
1844	Bodø	10/**11**/**12**/**13**	4,17,18,19/**5,18,19**/**8,12,19**/**17,18**	12
1862	Lødingen	**12**	**10**	1
	Totalt			**28**
Troms				
1903	Gratangen	**12**	**1,4,14,19**	4
1906	Bardu	**12**	**1**	1
1913	Målselv	**12**/**13**	**16**/**17**	2
1926	Nordreisa	**13**	**1,15**	2
1927	Tromsø	**13**	**11**	1
1934	Nordreisa	**13**	**11**	1
	Totalt			**11**
Finnmark				
2027	Alta	**11**	**7**	1
2041	Tana	**12**	**8**	1
2045	Alta	**13**	**3^2**	1
2047	Porsanger	**13**	**6,17**	2
2053	Kvalsund	**11**	**11,14,19**	3
2055	Lebesby	**12**	**1,2**	2
2061	Måsøy	**11**/**13**	**12,16^2,20**/**16^2**	4
2070	Lebesby	**13**	**2^2,9,13,14,16,17,18**	7
2073	Båtsfjord	10/**13**	16/**18**	2
	Totalt			**23**
SUM	**61**	**110**		**180**

Year color code: 2005, 2006, 2007, 2008, 2009, 2010, **2011**, **2012**, **2013**

Other signs:

,	same year
/	different year
X^2	Two observation at one point
(fX)	Number in group

Appendix 2 Hillshade calculations

The hillshade tool obtains the hypothetical illumination of a surface by determining illumination values for each cell in a raster. It does this by setting a position for a hypothetical light source and calculating the illumination values of each cell in relation to neighboring cells. The hillshade values are a index with values between 0-255. A high value indicates low solar radiation and lower values indicating higher solar radiation (Burrough & McDonell 1998).

Our position of the hypothetical light source where calculated as a mean value in each region (TOV-E) and different seasons (Hestkjølen) at the website astronomi.no. In TOV-E we used the maximum altitude and a 180° azimuth at 15. June 2013 to obtain a mean value, since most of the observations is around this date.

Hillshade calculation TOV-E

Region	Location	Date	Altitude	Azimuth
Central	Trondheim	15.06.13	49.9°	180°
West	Bergen	15.06.13	52.9°	180°
East	Oslo	15.06.13	53.4°	180°

In the Hestkjølen we used maximum altitude at 1. July 2013 in summer observations (15. April – 15. September), and maximum altitude at 1. Marc 2013 in winter observations (16. September – 14. April. Both seasons with a 180° azimuth.

Hillshade calculation Hestkjølen

Period	Location	Date	Altitude	Azimuth
Summer	Trondheim	01.07.13	49.7°	180°
Winter	Trondheim	01.03.13	19.2°	180°

References

Astronomi.no
< http://astronomi.no/kart.php>
[Reading date 24.01.2014]

Burrough, P.A. & McDonell, R.A. (1998). Principles of Geographical Information Systems. – Oxford University Press, New York, 190 pp.

Appendix 3

– AICc-models and estimated for observations in Hestkjølen with accuracy II and III.

Averaged parameter estimates and standard errors for the spatial accuracy I+II and I+II+III, in addition to variable importance for the summer season in Hestkjølen. The table also include the parameter estimates and standard errors for the best model for the two different accuracies.

Averaged estimates for the six best summer models and intercept					Estimates for the best model	
Summer	**Parameter**	**Estimates**	**SE**	**Variable importance**	**Estimates**	**SE**
AccuracyI+II	Intercept	-3.3701803	0.3129450		-3.4481717	0.3054944
	Slope	0.0160431	0.0250953	0.99	0.0112459	0.0235402
	Slope^2	0.0002206	0.0003593	0.99	0.0002119	0.0003587
	Snowbed	1.2600213	0.5339051	0.99	1.2019506	0.5243208
	Shadow/north	0.7992627	0.4801166	0.71	0.8146631	0.4804406
	Snow/glacier	-1.9141253	1.5206124	0.37		
	VRM	-0.0861669	0.0455050	0.46		
	VRM^2	0.0018806	0.0010787	0.46		
AccuracyI+II+III	Intercept	-3.3945929	0.2497030		-3.4286226	0.2308234
	Slope	0.0339244	0.0185055	1.0	0.0354871	0.0182534
	Slope^2	-0.0001955	0.0002877	1.0	-0.0002076	0.0002852
	North/shadow	0.9233738	0.3499705	0.91		
	Snow/glacier	-1.7722145	1.1613857	0.83	-1.7385016	1.1439174
	Ridges	0.4749600	0.3632199	0.25		
	Mooreland	-0.3355117	0.2845716	0.25		

Best models based on ΔAICc and w_i for spatial accuracy I+II and I+II+III during summer in Hestkjølen. The predicting ability of the different models is presented in the table as AUC models.

Summer	**Model**	**Alt+Alt^2**	**VRM+VRM^2**	**Hills+Hills^2**	**Slope+Slope^2**	**Aspect**	**Forest/mires**	**Mooreland**	**Ridges**	**Heath w/lichens**	**Lee w/heather**	**Snowbed**	**Snow/glacier**	**Shadow/north**	***df***	**AIC$_c$**	**ΔAIC$_c$**	**w_i**	**AUC**
AccuracyI+II	1				x							x		x	5	634.65	0.00	0.19	0.61
	2				x							x	x	x	6	634.68	0.02	0.18	0.65
	3		x		x							x	x	x	8	634.71	0.05	0.18	0.65
	4				x							x			4	635.15	0.50	0.14	0.60
	5		x		x							x		x	7	635.17	0.52	0.14	0.64
	6		x		x							x			6	635.39	0.74	0.13	0.63
	Intercept														1	640.08	5.43	0.00	
AccuracyI+II+III	1				x								x	x	5	1011.68	0.00	0.29	0.60
	2				x				x				x	x	6	1012.07	0.38	0.24	0.60
	3				x			x					x	x	6	1012.45	0.77	0.20	0.61
	4				x									x	4	1012.84	1.16	0.16	0.58
	5				x			x					x		5	1015.34	3.65	0.04	0.59
	6				x								x		4	1016.03	4.34	0.03	0.57
	Intercept														1	1020.37	8.69	0.00	

Averaged parameter estimates and standard errors for the spatial accuracy I+II and I+II+III, in addition to variable importance for winter in Hestkjølen. The table also include the parameter estimates and standard errors for the best model for the two different accuracies.

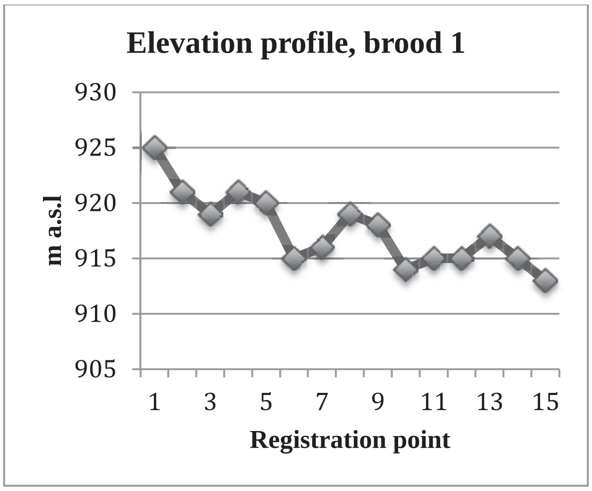
	Averaged estimates for the six best models and intercept				Estimates for the best model	
Winter	**Parameter**	**Estimates**	**SE**	**Variable importance**	**Estimates**	**SE**
AccuracyI+II	Intercept	-3.296e+01	1.127e+01		-3.335e+01	1.122e+01
	Altitude	1.082e-01	3.308e-02	1.00	1.088e-01	3.298e-02
	Altitude^2	-8.539e-05	2.434e-05	1.00	-8.594e-05	2.424e-05
	Hillshade	-9.642e-02	2.197e-02	1.00	-9.329e-02	2.167e-02
	Hillshade^2	7.020e-04	1.234e-04	1.00	6.881e-04	1.227e-04
	Slope	-1.055e-01	5.305e-02	1.00	-9.917e-02	5.215e-02
	Slope^2	7.045e-04	1.860e-03	1.00	6.078e-04	1.863e-03
	Snowcovered	-2.600e-01	3.336e-01	0.57		
	Exposed ridges	1.488e+00	8.436e-01	0.40		
	Ruggedness	-2.089e-02	1.070e-01	0.09		
	Ruggedness^2	-5.477e-03	7.494e-03	0.09		
	Coniferous	2.007e-01	5.407e-01	0.09		
	Aspect	-3.498e-03	4.339e-02	0.08		
AccuracyI+II+III	Intercept	-1.041e+01	4.203e+00		-9.932e+00	4.076e+00
	Altitude	3.406e-02	1.140e-02	1.00	3.320e-02	1.120e-02
	Altitude^2	-2.550e-05	7.865e-06	1.00	-2.479e-05	7.774e-06
	Hillshade	-9.515e-02	1.327e-02	1.00	-9.733e-02	1.301e-02
	Hillshade^2	6.667e-04	7.143e-05	1.00	6.755e-04	7.057e-05
	Slope	-1.164e-01	2.624e-02	1.00	-1.193e-01	2.596e-02
	Slope^2	3.119e-04	4.985e-04	1.00	3.326e-04	5.007e-04
	Snowcovered	-2.872e-01	2.450e-01	0.36	-2.812e-01	2.447e-01
	Coniferous	5.712e-01	4.005e-01	0.17		
	Exposed ridges	-5.958e-01	7.221e-01	0.30		
	Decidous	1.642e-01	2.460e-01	0.15		

Best models based on ΔAICc and w_i for spatial accuracy I+II and I+II+III during summer in Hestkjølen. The predicting ability of the different models is presented in the table as AUC models.

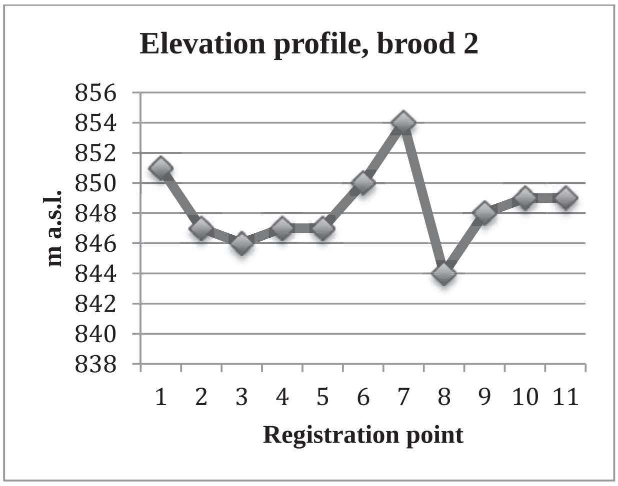
Winter	**Model**	**Alt+Alt^2**	**Hills+Hills^2**	**VRM+VRM^2**	**Slope+Slope^2**	**Aspect**	**Deciduous**	**Coniferous**	**Exposed ridges**	**Snowcovered**	***df***	**AIC_c**	**ΔAIC_c**	**w_i**	**AUC**
AccuracyI+II	1	x	x		x						7	745.78	0.00	0.35	0.85
	2	x	x		x				x	x	9	746.56	0.79	0.24	0.85
	3	x	x		x					x	8	747.19	1.41	0.17	0.85
	4	x	x		x			x	x	x	10	748.44	2.66	0.09	0.85
	6	x	x		x	x			x	x	10	748.57	2.79	0.09	0.85
	5	x	x	x	x						11	749.33	3.56	0.06	0.85
	Intercept										1	1224.86	479.8	0.00	
AccuracyI+II+III	1	x	x		x					x	7	1237.42	0.00	0.26	0.84
	2	x	x		x		x				7	1237.61	0.19	0.24	0.83
	3	x	x		x				x	x	8	1238.02	0.60	0.19	0.84
	4	x	x		x						6	1238.58	1.16	0.14	0.83
	5	x	x		x		x		x		8	1239.19	1.77	0.11	0.83
	6	x	x		x	x					7	1240.25	2.83	0.06	0.83
	Intercept										1	2037.69	800.27	0.00	

Appendix 4

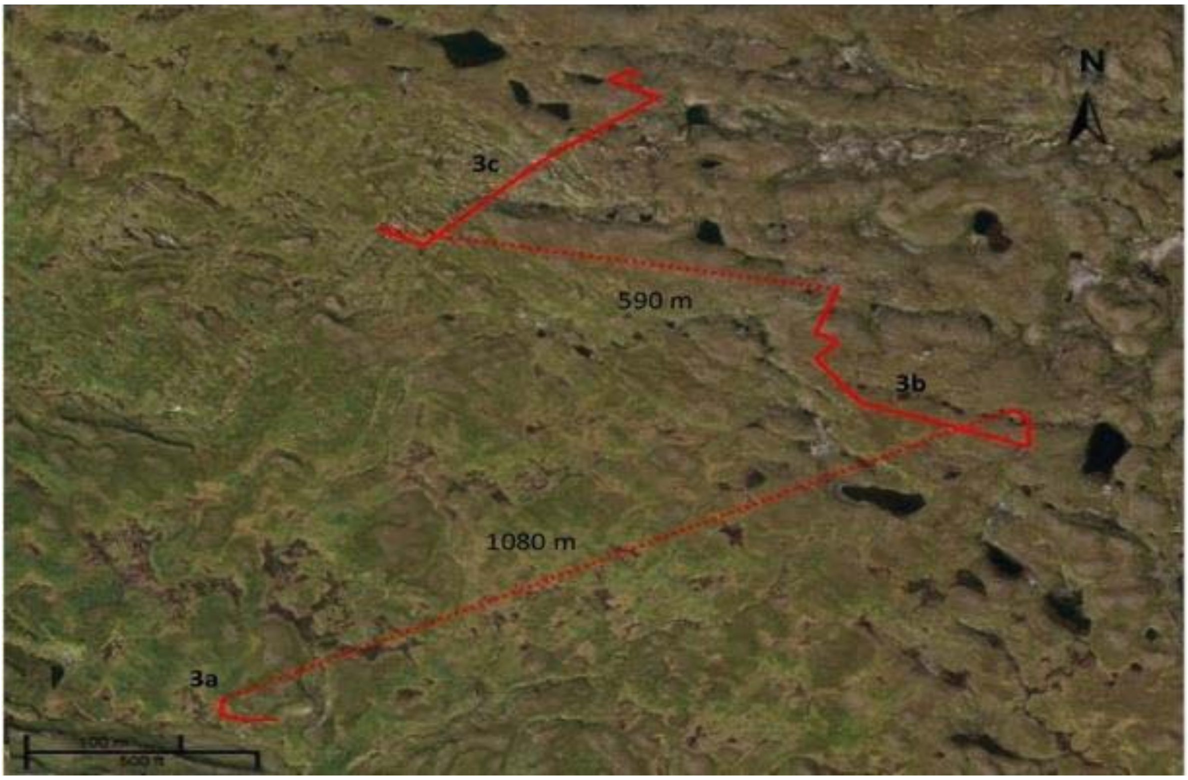
- Movement for different broods in Hestkjølen during the summer 2013



Brood 1
Obs. time: 7.5 h (14 Movement)
≈ Age: 14 days (Four chicks)
Avg. movement: 11.5 m/ ½ h (Range=2.1-19.5)
Tot. distance: 208m.
Mean angle: North West
M a.s.l. : 913-925
Used area: 2284m^2



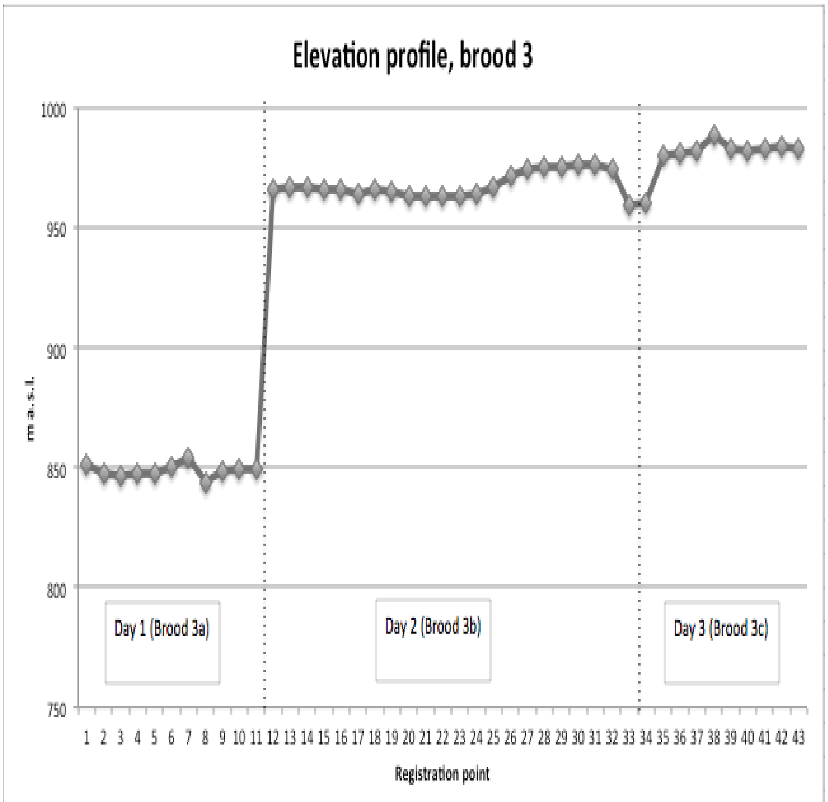
Brood 2
Obs. time: 5.5 h (11 Movement)
≈ Age: 7 days (Nine chicks)
Avg. movement: 10.3 m/ ½ h (Range=0-18.9)
Tot. distance: 113m.
Mean angle: South
M a.s.l. : 927-961
Used area: 1296m^2

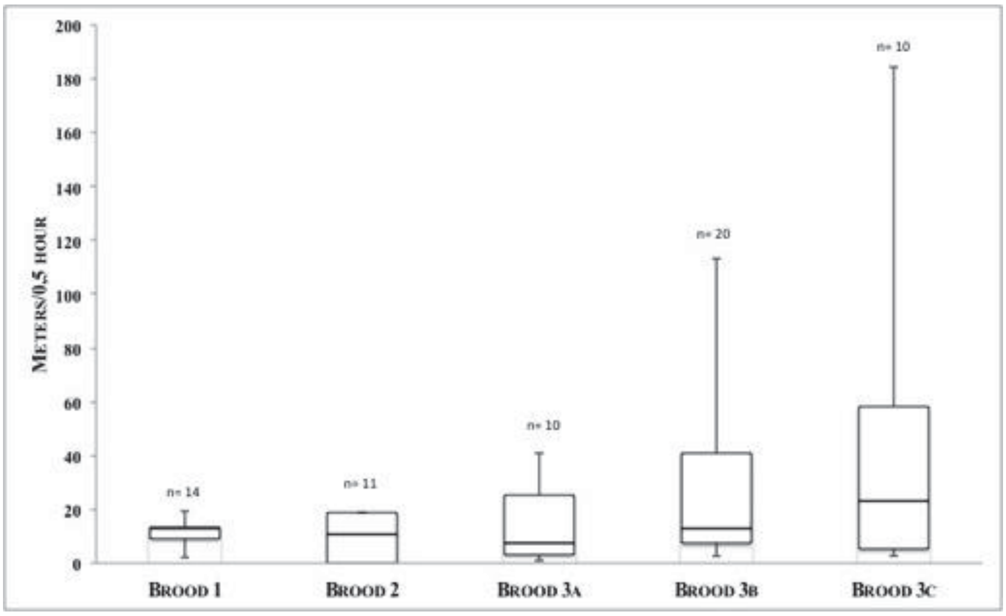


Brood 3a
Obs. time: 7.5 h (10 Movement)
≈ Age: 21 days (Three chicks)
Avg. movement: 13.1 m/ ½ h
(Range=1-41,1)
Tot. distance: 131m.
Mean angle: North
M a.s.l. : 844-851
Used area: 1926m^2

Brood 3b
Obs. time: 10.5 h (20 Movement)
≈ Age: 21 days (Three chicks)
Avg. movement: 26.5 m/ ½ h
(Range=2.5-113)
Tot. distance: 531m.
Mean angle: North West
M a.s.l. : 963-976
Used area: 63 625m^2

Brood 3c
Obs. time: 5.5 h (10 Movement)
≈ Age: 21 days (Three chicks)
Avg. movement: 54.2 m/ ½ h
(Range=2.7-184.5)
Tot. distance: 541.5m.
Mean angle: North West
M a.s.l. : 959-988
Used area: 79 643m^2





Movement in different broods observed in Hestkjølen described as meter/0.5 hour

Norges miljø- og
biovitenskapelige
universitet

Postboks 5003
NO-1432 Ås
67 23 00 00
www.nmbu.no