Food characteristics and territory habitat selection in Lapland longspurs *Calcarius lapponicus* in the early part of the breeding season at Hardangervidda, southern Norway

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Front page:

A male Lapland longspur *Calcarius lapponicus* at Hardangervidda. Photo: Vegard Finset
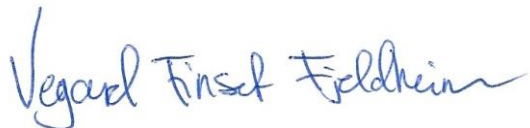Fjeldheim

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Abstract

Climate change currently affects the whole globe. Especially tundra and alpine areas are expected to change in the coming decades, affecting the species which today inhabits these areas. The Lapland longspur *Calcarius lapponicus* is a common passerine bird breeding in such habitats. It has shown a considerable population decline all over Fennoscandia during the last decades. The reason for this decline is suggested to be caused by habitat changes at the breeding ground. Since little is known about the Lapland longspur's diet in the declining populations, I analyzed the stomach content of 39 individuals sampled in early June at Hardangervidda, southern Norway. Seeds dominated the diet, and from this I predicted that the birds would establish their territories in areas rich in seed producing plants as found in the stomach analysis. I also predicted that the longspur did not establish territories in areas dominated by lichens, but that they were found in areas influenced by shrubs. I compared the vegetation within 17 Lapland longspur territories at Hardangervidda in the early part of the breeding season and compared it with vegetation samples in areas with no territories. Contrary to expected, I found that the Lapland longspurs did not establish their territory in a specific plant community. Furthermore, I found no support for the hypothesis that the longspurs avoided lichen dominated areas, but the birds did favor the presence of shrubs like *Salix* sp. and/or *Betula nana*. My results might suggest that the territories do not serve as an exclusive food reservoir in terms of seeds for the Lapland longspurs.

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Introduction

Alpine and tundra biomes around the world are among the most vulnerable ecosystems to climate change (Gonzalez *et al.* 2010). Several studies have shown a poleward and uphill range shift of species as a response to a changing climate (Hickling *et al.* 2006; Lenoir *et al.* 2008; Chen *et al.* 2011; Myers-Smith *et al.* 2011; Pauli *et al.* 2012; Tingley *et al.* 2012), heavily altering the alpine and tundra habitats. The changes in alpine and tundra environments are not only caused by the appearance of new species, but also by changes in the composition of species already present in such areas. Field experiments in alpine environments have shown that increased temperature and higher nutrient availability increases the cover of graminoids, while lichens and mosses are outcompeted (Cornelissen *et al.* 2001; Klanderud & Totland 2005; Jägerbrand *et al.* 2009). However, even if this is the case on a continental scale, individual mountain areas may deviate from this general trend (Gottfried *et al.* 2012), and responses differ among taxonomic groups (Chen *et al.* 2011).

If species do not adapt to the changes taking place, or shift their geographic range accordingly, they might face an increased risk of extinction (Sekercioglu *et al.* 2008), and recent studies show an increased decline in both alpine and tundra bird species. For instance, in a study on rock ptarmigan *Lagopus muta* in the Pyrenees, climatic conditions were pointed out as one of the factors altering the habitat and hence driving the population decline (Bech *et al.* 2013). In the Fennoscandian mountain range, 9 of 14 common bird species declined during 2002-2012 (Lehikoinen *et al.* 2014). It is believed that the reason for the declines lies within the mountain range itself, as both long-distance migrants and resident birds showed negative population trends (Lehikoinen *et al.* 2014).

Hardangervidda in southern Norway is the largest high mountain plateau in Europe. It covers approximately 8000 km^2 (Thorsnæs 2014), and is inhabited by the largest remaining population of reindeer *Rangifer tarandus* in Europe (Miljødirektoratet 2013). Due to its vast and unique landscape, 3422 km^2 of the plateau is preserved as a national park (Tvedt & Ryvarden 2015). Most of the area at Hardangervidda is found above the tree line, and the vegetation is mostly dominated by different heaths as well as relatively large patches of marshlands. Shrubs like *Salix* spp. are typically found around the many rivers and lakes at the plateau. Hardangervidda is also utilized by many farmers as a summer pasture for their livestock, especially sheep (Rekdal *et al.* 2009).

The vegetation at Hardangervidda has changed during the last decades, and one of the most conspicuous changes is found at the ground layer. Even if it is predicted that lichens will be a "climate loser" (Cornelissen *et al.* 2001; Klanderud & Totland 2005), the lichen cover has increased at Hardangervidda since the 1980's (Jordhøy & Strand 2009). This increase might be linked to the decline in the local reindeer population recorded over the last few decades, which eases the grazing pressure on lichens, especially during winter (Jordhøy & Strand 2009; Odland *et al.* 2014). There has also been a decline in the livestock of sheep utilizing Hardangervidda during summer (Austrheim *et al.* 2008). Less sheep leads to less trampling, which could be positive for the lichens.

Hardangervidda is inhabited by a relatively rich avifauna (Tvedt & Ryvarden 2015). One of the many bird species breeding at Hardangervidda is the Lapland longspur *Calcarius lapponicus*, which has a circumpolar distribution and is closely related to the tundra biome (Haftorn 1971; Cramp & Perrins 1994). Lapland longspurs are in southern Norway only found in montane areas, where Hardangervidda traditionally has been regarded as the most important breeding grounds. The species is otherwise found in montane and tundra areas throughout Norway (Haftorn 1971; Breiehagen 1994). In breeding plumage, males are easily recognizable with brown neck feathers, black head and throat feathers with a yellow-white zigzag line from behind the eye and down to the breast (Fig. 1). The female is less conspicuous, but has the same brownish neck and a greyish-black area on the breast (Cramp & Perrins 1994; Svensson *et al.* 2010). Both sexes have a yellow beak with a black tip (Cramp & Perrins 1994; Svensson *et al.* 2010).

The Lapland longspur is a territorial bird, where territories are established rapidly after spring arrival (Drury 1961, Bjørnsen 1988). It favors mesic areas with tussock tundra, often with a small cover of shrubs like *Betula nana* and *Salix* spp. (Haftorn 1971; Seastedt & MacLean 1979; Cramp & Perrins 1994; Henry & Mico 2002; Boelman *et al.* 2015). In the pre-nesting period, males defend their territory with song duels, flight chases and ground postures (Drury 1961; Cramp & Perrins 1994), but do accept visiting birds as long as they do not exert territorial behavior (Drury 1961). The size of the territories is furthermore found to be related to available food resources. In Alaska, territories containing large proportions of mesic areas had better feeding resources and were smaller than territories with more unfavorable feeding habitats (Seastedt & MacLean 1979). However, territory borders disappear as incubation progresses (Drury 1961; Seastedt & MacLean 1979; Gierow & Gierow 1991).
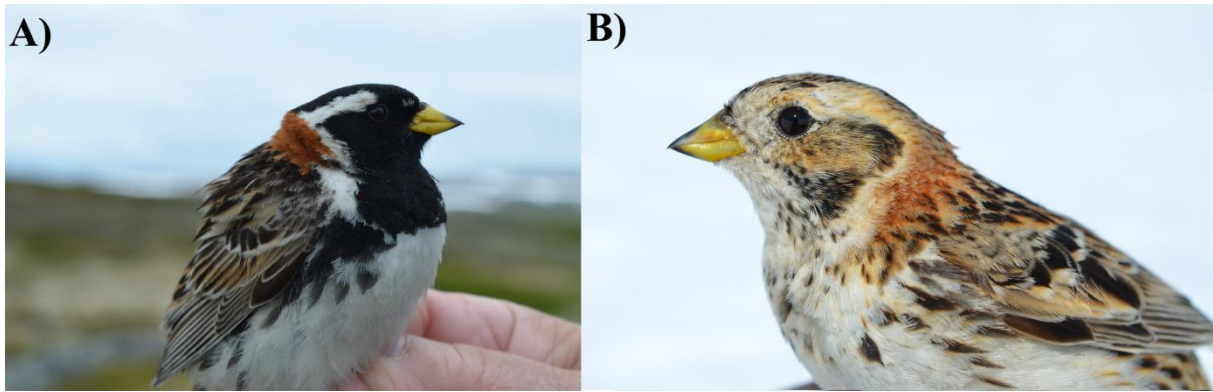
Figure 1. Lapland longspurs in breeding plumage. A) male B) female. Photo: Vegard Finset Fjeldheim

The diet of Lapland longspurs consists of both plant seeds and arthropods. Studies from Alaska and Greenland have shown that seeds account for a major part of the longspurs' diet when birds arrive at their breeding sites in spring (Salomonsen 1950; Custer & Pitelka 1978). At this time insect activity is reduced due to low temperatures and large areas still being covered by snow. Seeds are however relatively low in energy in comparison to arthropods (Custer & Pitelka 1978), and as soon as the arthropod activities increase, the longspurs shift their diet from seeds to larval and adult arthropods (Haftorn 1971; Custer & Pitelka 1978).

Food abundance is also an important factor in timing of the breeding season. Lapland longspurs tend to time their breeding so that food abundance is at a peak when the nestlings leave the nest. By doing this, the nestlings are independent before the end of the insect emergence period (Custer & Pitelka 1977). When the Lapland longspur shifts from seed to arthropods, Coleoptera, Diptera and Hemiptera are important food resources (Custer & Pitelka 1977). As the shrub cover in general becomes more dominant in alpine and tundra areas, the population of Coleoptera is reported to decline (Anthelme *et al.* 2001). However, Boelman *et al.* (2015) predicted that this will not necessarily become a problem for the longspurs as the abundance of Hemiptera and Diptera increases with increasing shrub cover (Rich *et al.* 2013) assuring abundant food resources in the nestling period (Boelman *et al.* 2015).

The Norwegian breeding population of Lapland longspurs is currently estimated to 100 000-225 000 pairs (Shimmings & Øien 2015). Even though the International Union for Conservation of Nature (IUCN) reports an increase in the population trend worldwide (IUCN 2015), the Lapland longspur showed a mean annual decrease by 5% from 2002 to 2012 in Fennoscandia (Lehikoinen *et al.* 2014). At Hardangervidda, where the Lapland longspur previously was considered as one of the most numerous passerine species together with the meadow pipit *Anthus pratensis* (Haftorn 1971), Byrkjedal and Kålås (2012) found that the

number of breeding Lapland longspur pairs had declined by as much as 85% between 1980 and 2010-2011. The Lapland longspur is therefore classified as vulnerable (VU) on the Norwegian red list for threatened species (Kålås *et al.* 2015). It has been suggested that the decline in Lapland longspur populations could be due to habitat changes at the breeding grounds (Byrkjedal & Kålås 2012; Lehikoinen *et al.* 2014). One hypothesis is that the increased lichen cover in recent years has resulted in a reduction in seed producing plants that are utilized as food sources by the longspurs, especially in early spring (Byrkjedal & Kålås 2012). When the birds arrive in spring, it can be challenging to find food as most of the ground is still covered by snow. At the same time, it is an energy demanding period for the longspurs. Spring temperatures at Hardangervidda are often low (Skartveit *et al.* 1975), and the birds need sufficient energy to maintain their body temperature (Dawson *et al.* 1983). Females also require enough energy to produce eggs (Martin 1987). Therefore, the pre-nesting period might constitute as a bottleneck for the population if the birds do not find sufficient food. However, little is generally known about the food choice of Lapland longspurs in Fennoscandia, and to my knowledge there is limited data available on the habitat preference in Lapland longspurs from this part of the world. Such information is vital for the conservation of Lapland longspurs and for enhancing our understanding of basic breeding ecology in this species.

In this thesis I focus on food characteristics and territory habitat selection in Lapland longspurs at Hardangervidda. To see what the diet of Lapland longspurs breeding at Hardangervidda consists of early in the breeding season, I examined the stomach content of 39 Lapland longspurs collected in early June 1974. Based on information from other parts of the species' distribution, I predicted that seeds should account for a major part of the diet. Moreover, I recorded plant characteristics within and outside longspur territories to see if the birds had any habitat preferences in establishing their territories. I hypothesized that the territories were established in areas rich with seed producing plants similar to the seeds found in the stomach analysis, and that they avoid lichen dominated areas. Finally, as other studies of the Lapland longspurs breeding biology have reported that the territories often have small proportions of shrubs, I predicted the territories to be located in areas on the tundra with an occurrence of *Salix* spp. or *Betula nana*.

Materials and Methods

Study area

The study area is situated around Bjoreidalshøgda and in Stigstudalen on the western part of the Hardangervidda mountain plateau (approximately 1250 m a.s.l, 60°21´ N, 7°33´ E; Fig. 2), and lies mostly within the low- and middle-alpine zone. This study area was selected due to observations of Lapland longspurs early in the field season, and because previous field recordings showed a minimum of 30 males present around Bjoreidalshøgda and the surrounding areas in 2011 (T. Lislevand, pers. comm.). Prevailing warm and moisture-bearing westerlies from the North-Atlantic make the area relatively wet, with temperatures much higher than other places at the same altitude and latitude, especially during the winter months (Østbye *et al.* 1975). Due to a thick snow cover during the long winters, there is no permafrost even if the study area is classified as tundra (Østbye *et al.* 1975). The soil layer is regarded as relatively nutrient poor, and most of the heath communities are oligotrophic (Østbye *et al.* 1975; Tvedt & Ryvarden 2015).
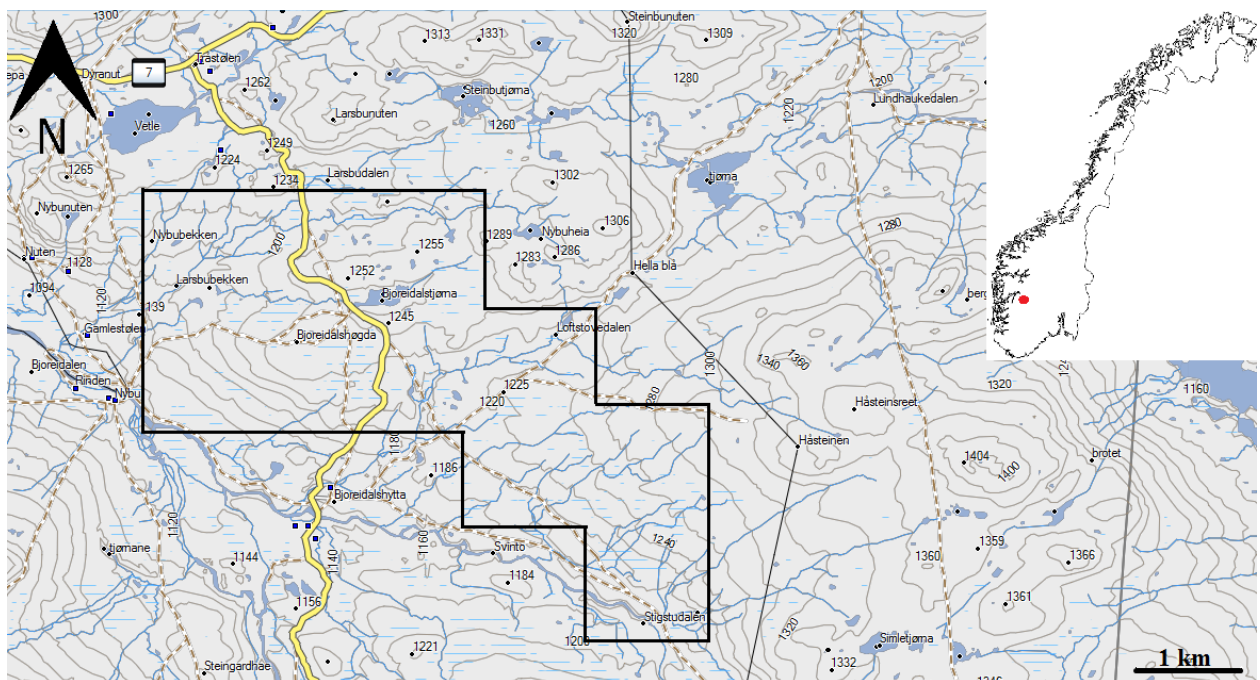

Figure 2. Map showing a section of Hardangervidda, with the study area within the black polygon. The map is taken from N50-Hardangervidda in MapSource (Garmin Ltd. 2010). Map of Norway inserted to the top right shows the location of the study area (Kartverket 2016).

Stomach samples

I examined the stomach contents of 39 Lapland longspurs collected at Hardangervidda during 5th-12th June 1974. The samples were stored at the University Museum of Bergen, Norway, where the stomachs were removed from the collected birds and preserved in 70% ethanol shortly after they were collected. The birds were shot at Halne (60°25′ N, 7°41′ E) and Dyranut (60°22′ N, 7°31′ E). Dyranut lies close to my study area, whereas Halne is located around 11 km to the northeast, both areas at the same altitudinal range as my study area. I opened the stomachs with a scalpel and flushed them with 70% ethanol onto a petri dish before analyzing the content using a dissection microscope. For each stomach, the number of different seeds was counted and classified (L. Halvorsen, pers. comm.). Arthropods were identified based on fragments and quantified from a minimum number of equivalent legs, wings, mouthparts, head capsules, cithinized spiracle openings and similar morphological descriptions. In order to identify adult Coleoptera, remains were compared with a reference collection of the most common Coleoptera species present at Hardangervidda (I. Byrkjedal, pers. comm.). The dry weight of seeds and arthropods were not measured, but estimated from Byrkjedal (1980) and Custer and Pitelka (1978; Appendix A)

Territorial mapping

I searched the study area for Lapland longspur territories between 21st May and 23rd June 2016. In areas where singing males were either seen or heard a GPS plot was marked and categorized as a potential territory. Plots were transferred from the GPS onto the map "N50-Hardangervidda" using MapSource (version 6.16.3; Garmin Ltd. 2010). Maps with 200 m scales for each possible territory were then printed and brought into the field.

Territorial mapping (Sutherland *et al.* 2004) was performed in the following way. Within each presumable territory, I followed the male by sight for 10 minutes from the spot where I first discovered the bird. The number of times the territories were mapped is given in Appendix B. The males' position was plotted on the printed map with a pencil every minute, giving me 11 observation points for each territorial mapping sequence (including the start point). In some occasions it was necessary to change my position after the bird was spotted to have a better view of the territory and hence make it possible to perform the territory mapping sequence. In such cases, the movements were done as gentle as possible not to affect the activity or behavior of the observed bird. As it is possible that my presence could disturb the birds, I tried to approach each territory from different angles for every mapping sequence. By doing so, I did not press the bird into the same area of the territory for each visit, which could lead to

wrong estimates of the territory borders. Individual territories could be mapped two times per day, but between each mapping sequence, I left the area for a minimum of one hour to minimize the possibility that my presence affected the mapping results. However, due to the size of the study area, all territories were not visited every day.

At the end of each day all position plots from the territorial mapping were manually transferred into MapSource, generating clusters of observations for each territory. New maps without the clusters of observation were printed for the following day. However, to make the territorial mapping as precise as possible, reference points (such as rocks or high *Salix* spp.) at which the longspurs often were seen, were recorded within each territory with a GPS and added to the territory in MapSource, making the printed maps more detailed.

Vegetation sampling

From the clusters of observations that helped define the territories in MapSource, the center of each territory was found by arranging the observation points in north-south and east-west gradients, and calculating the median of each gradient. The center of each territory was chosen as a point for recording vegetation, referred to as an examination point. To better account for the variation of vegetation within each territory, four additional examination points making a square around the center of the territory were selected (Fig. 3). These points were arranged parallel to the UTM grid system in north-south and east-west directions and had an equal distance to the center of the territory, with sides of the square measuring 50 m each. The distance of 50 m was chosen at random, but it was assumed, based on the territorial mapping, that all examination points would then lie within the territory.

To map the extent of available vegetation in the study area, examination points were based on the UTM grid system with 1 x 1 km square grids. Each UTM square grid was divided in four with additional lines, making squares of 500 x 500 meters. Every intersection point between UTM lines or additional lines were treated as a central examination point, with four additional examination points around in the same way as described above for the territories (Fig. 3). This gave 295 examination points for recording of vegetation in the study area.
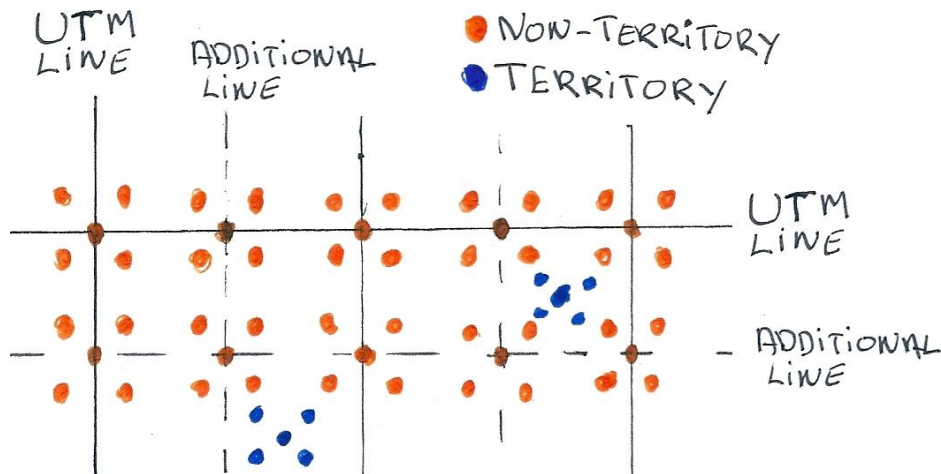
Figure 3. An illustration of examination points in the study area. Both territorial and non-territorial examination points have a central examination point with four examination points making a square around the central examination point. All four examination points had equal distance to the central examination point. In the territories, the central examination point is calculated from the territorial mapping. For the non-territorial central examination point, it was placed in the intersection points between UTM lines or the additional lines which divide the UTM squares in four. In this illustration two territories are included. The sides of each square measure 50 m, but the illustration is not scaled.

All examination points, both within and outside territories, were transferred to a GPS via MapSource after the territorial mapping was completed, making it easier to conduct the vegetation sampling in the field. If some of the examination points occurred on streams, small ponds or snow, this was classified as an irrelevant surface and the points were moved directly northwards until the first possible examination surface.

For each examination point, a 1 m^2 frame square was used to find the cover in percent of different plant species present at the ground layer (Bullock 1997). *Salix herbacea* was treated as a species, whereas *Salix* higher than 20 cm were marked as *Salix* sp. Lichens, bryophytes, forbs and grasses were only treated as vegetation groups and not identified to species level. To make the estimation of plant cover as easy and precise as possible, the frame square was divided into 100 equal-sized squares with a string of wire. Each of the 100 squares accounted then for one percent of the total frame square area.

In areas where *Salix* sp. was present, I pushed it aside to make it possible to place the square frame on the ground. In this way I could measure the cover of species at the ground level as precise as possible. However, the bottom of the *Salix* sp. trunk, which could cover a considerable proportion of the ground layer, was estimated and included. *Betula nana* could also reach some height in some areas, but was normally prostrate and nevertheless treated as part of the ground layer.

Statistical analysis

Statistical analyses were performed in R (version 3.3.2; R Core Team 2016). In addition to the packages included in R, I also used the 'vegan' package (Oksanen 2015). To avoid strong influence from skewed distributions of small numbers, I decided that species, genera or vegetation groups needed to occur in at least 20 examination points in order to be included in the statistical analysis. A list with the number of times species, genera or vegetation groups occurred in the examination points is given in Appendix C.

Ordination was performed to see whether the Lapland longspurs preferred specific plant communities when choosing their territory. In an ordination, the response variables are distributed on different axes representing the variation in the data set. Species that have much in common occur close to each other in the ordination, and can be treated as a community. As I did not measure any abiotic environmental variables, the gradients in my dataset are underlying, unknown gradients, for which I used an indirect ordination to explore the data (Ter Braak & Prentice 1988). In order to determine whether to use a linear or unimodal response model, the axis length was calculated. As the axis length exceeded 4, I used a detrended correspondence analysis (DCA; Ter Braak & Prentice 1988). Only data on plant cover in percent from each examination point were included in the ordination. To see if the longspurs tend to prefer certain communities, the probability of finding a territory was calculated using the 'ordisurf'-function. An ANOVA was run on the 'ordisurf'-function to see if the function was significant. As the data included in the ordination were plant cover in percentages, the data was square root transformed to dampen the effect of dominant species or vegetation groups such as *Empetrum nigrum* and lichens.

In order to see which plant characteristics were important in establishing territories for Lapland longspurs, I used a generalized linear regression model (GLM). The presence of territories were treated as the predictor variable, hence a binomial distribution. The plant cover data was treated as the response variables in this model, in addition to *Luzula* sp. which I only had presence/absence data available (Table 1). *Carex bigelowii* was also analyzed as a presence/absence factor since it was dominant in the stomach analysis and it is possible that the presence of *Carex bigelowii* are more important than its cover (Table 1). I also controlled the influence of shrubs, here consisting of *Salix* sp. and/or *Betula nana* both as cover data in percent and as a presence/absence factor. As I had more than four variables in the model selection, I used forward selection approach to select the best model. In the first step I compared models including different single variables to the null model which contained only

the intercept. Model selection was performed by using the Akaike Information Criterion (AIC), where the model with lowest AIC was regarded as the best model as long as the improvement was significant ($p < 0.05$). The variable that improved the model most was kept, and the described process was repeated until there was no further improvement of the model. Variables on vegetation cover were tested both as a linear regression and a second-order polynomial regression.

My study design has examination points that could be considered clustered. One of the problems with clustered data points are pseudoreplication (Hurlbert 1984). The GLM-model I used to examine the territory characteristics does not cope with a potential clustering effect. In order to overcome this problem, both the GLMER-function from the 'lme4'-package (Bates *et al.* 2015) and GLMMPQL-function from the 'MASS'-package (Venables & Ripley 2002) were considered. However, the GLMER-function cannot include data as a second-order polynomial regression, whereas the GLMMPQL-function has to my knowledge no possibility to be used in model selection. Hence, I ended up with the GLM-function and disregarded the possibility of a clustering effect. However, during the vegetation sampling I noticed that the vegetation structure changed drastically on short distances. This mosaic in the vegetation indicates that the clustering effect is negligible, and that GLM-modelling should be precise.

Table 1. The different variables included in the GLM-model. In addition to plant cover measured in percent, some were also tested as a presence/absence factor.

Variable	Type of variable
Lichens	Cover
Bryophytes	Cover
Salix sp.	Cover + presence/absence
Carex bigelowii	Cover + presence/absence
Eriophorum sp.	Cover
Empetrum nigrum	Cover
Betula nana	Cover + presence/absence
Salix herbacea	Cover
Nardus stricta	Cover
Forbs	Cover
Grasses	Cover
Luzula sp.	Presence/absence
Carex bigelowii + *Luzula* sp.	Presence/absence
Salix sp. + *Betula nana*	Cover + Presence/absence
Altitude	---

Results

Stomach samples

In the stomach analysis (n=39), a total of 2469 food items were identified. Seeds accounted for 2202 (89%) items, followed by 176 (7%) adult Coleoptera, 93 (4%) different arthropod larvae and 8 (<1%) adult Arachinda. The seeds came from 27 different plant species and 15 different genera, as well as 30 seeds from the family Ranunculace (Fig. 4, 5). Of adult Coleoptera, *Otiorrhynchus dubius* was most dominant with 83 (49%) individuals and was present in 28 longspur stomachs, whereas Tipulidae was the most abundant arthropod larva with 78 (84%) individuals in 24 of the analyzed stomachs (Table 2). In dry weight, the arthropods accounted for approximately 40% of the diet (Fig. 6)

Of the total amount of seeds, most of them came from the genera *Potentilla* and *Luzula.* Also sporangia from *Selaginella selaginoides*, which I have treated as seeds in this thesis, were also found in a large quantity (Fig. 4). *Empetrum nigrum*, *Omalotheca* sp. and *Carex* spp. were also present in rather large quantities, with 103 (5%), 130 (5%) and 244 (12%) seeds respectively. The rest of the species, genera and the family Ranunculace had a relatively little fraction of the total amount of seeds found, with less than 50 items per species or genera.

Carex was the genus which occurred in the highest number of stomachs, as it was present in 85% of the stomachs (Fig. 5). *Potentilla* and *Luzula*, the two genera with most seed items, occurred in 79% and 69% of the stomachs respectively. *Empetrum nigrum* were also relatively often represented, occurring in 44% of the examined stomachs. The other species, genera and the family Ranunculace were found in less than 15% of the analyzed stomachs.

Table 2. The total number of items and the number of stomachs the different arthropod items were found in the Lapland longspur stomachs (n=39).

Arthropod item	Number of items	Number of stomachs
Insecta (adults)	167	37
Coleoptera		
Carabidae		
Calathus melanocephalus	6	5
Notaphilus aquaticus	1	1
Amara praetermissa	1	1
Patrobus septentrionis	3	3
Patrobus assimilaris	8	6
Patrobus sp.	39	18
Curculionodae		
Otiorhynchus dubius	86	28
Heliophoridae		
Helophorus glacialis	13	8
Scarabidaeidae		
Aphodius lapponum	1	1
Staphylinidae		
Tachinus elongates	1	1
Arpedium sp.	4	3
Chrysomelidae		
Gonioctena pallida	1	1
Unidentified	11	9
Insecta (larvae)	89	29
Diptera		
Tipulidae	78	24
Muscidae	1	1
Lepidoptera	3	2
Hymenoptera	1	1
Coleoptera	5	3
Unidentified	3	3
Arachinda (adults)	7	6
Araneae	5	5
Opiliones		
Mitopus morio	2	2

Figure 4. The total number of seeds found in Lapland longspur stomachs (n=39) from Hardangervidda. Numbers in brackets represent the number of different species within each genus.
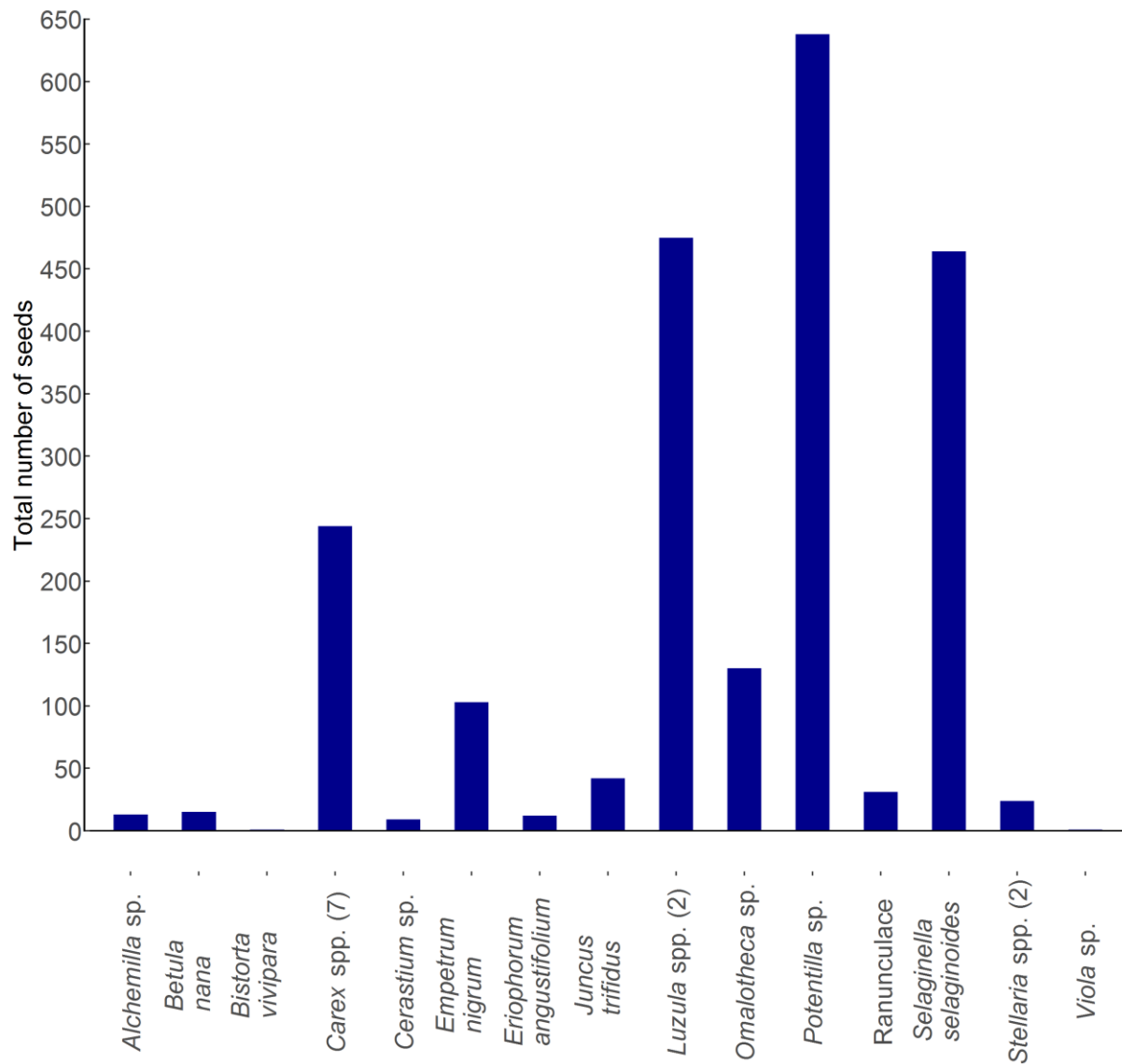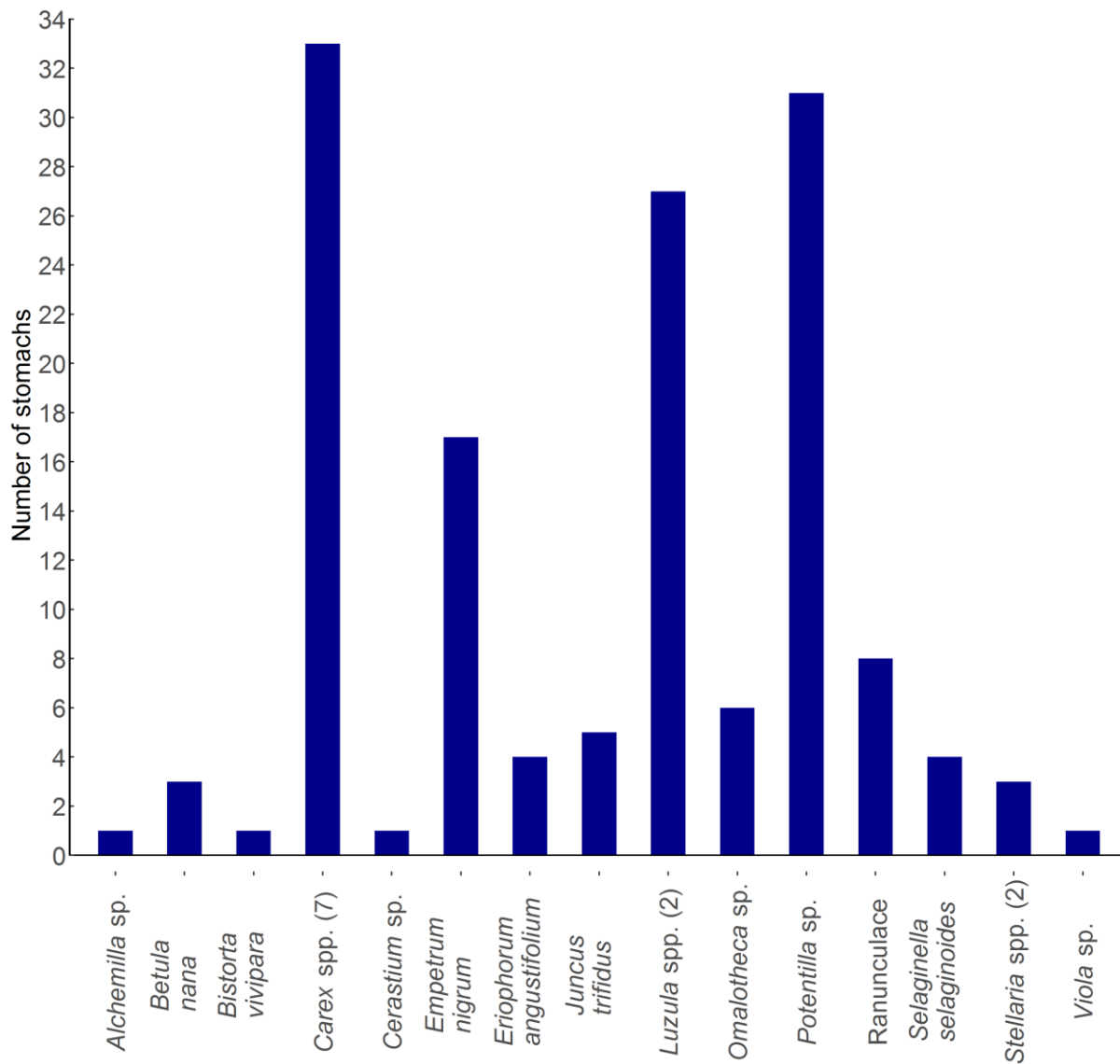
Figure 5. The number of stomachs in which the different seeds were found in Lapland longspur stomachs (n=39) from Hardangervidda. The numbers in brackets represent the number of different species within each genus.
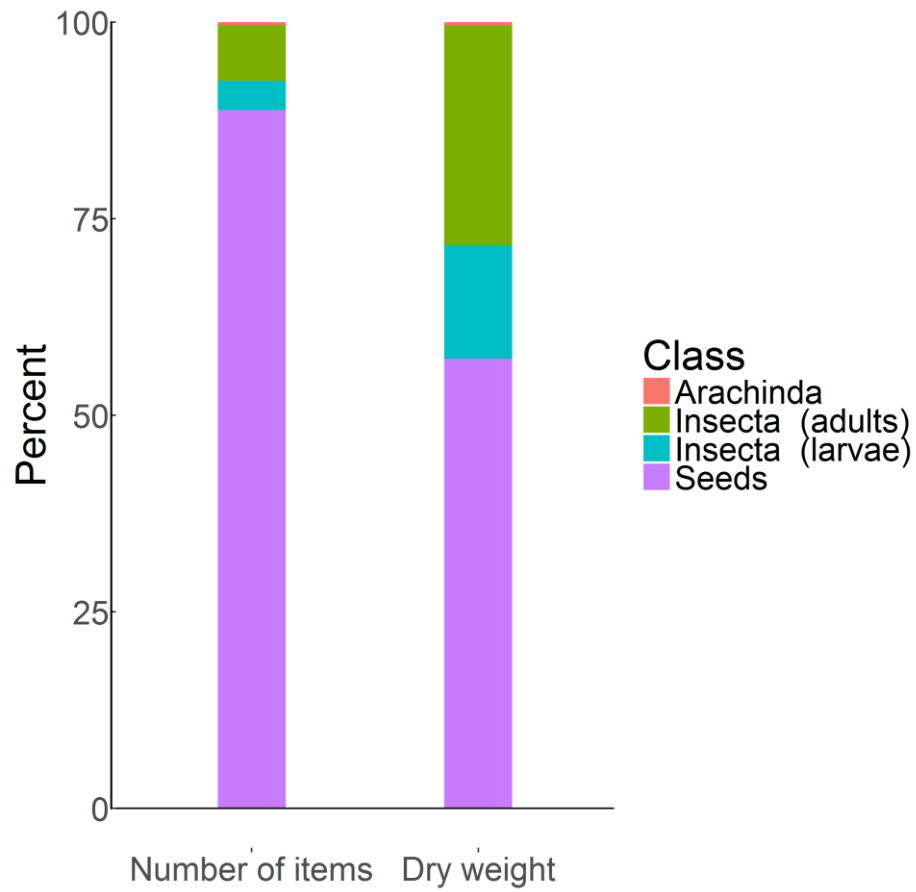
Figure 6. The composition in percent of the content found in the Lapland longspur stomachs (n=39), represented as the total number of items and dry weight.

Territory characteristics

I found a total of 17 territories in the surveyed area, giving 85 territorial examination points in addition to the 295 non-territorial examination points (Fig. 7). In the vegetation recordings, I found 11 different plant species and three different genera in additions to lichens, bryophytes, forbs and grasses. A full list of the species found is given in Appendix C.

Figure 7. Vegetation examination points within the study area. Blue represent territorial examination points (n=85), with five points within each territory, while orange are non-territorial examination points (n=295). The black polygon shows the study area.

In the ordination, the different species, genera or vegetation groups are distributed in a two-dimensional space along the two axes representing most of the variation in my dataset (outputs from the indirect ordination is given in Appendix D). Species, ge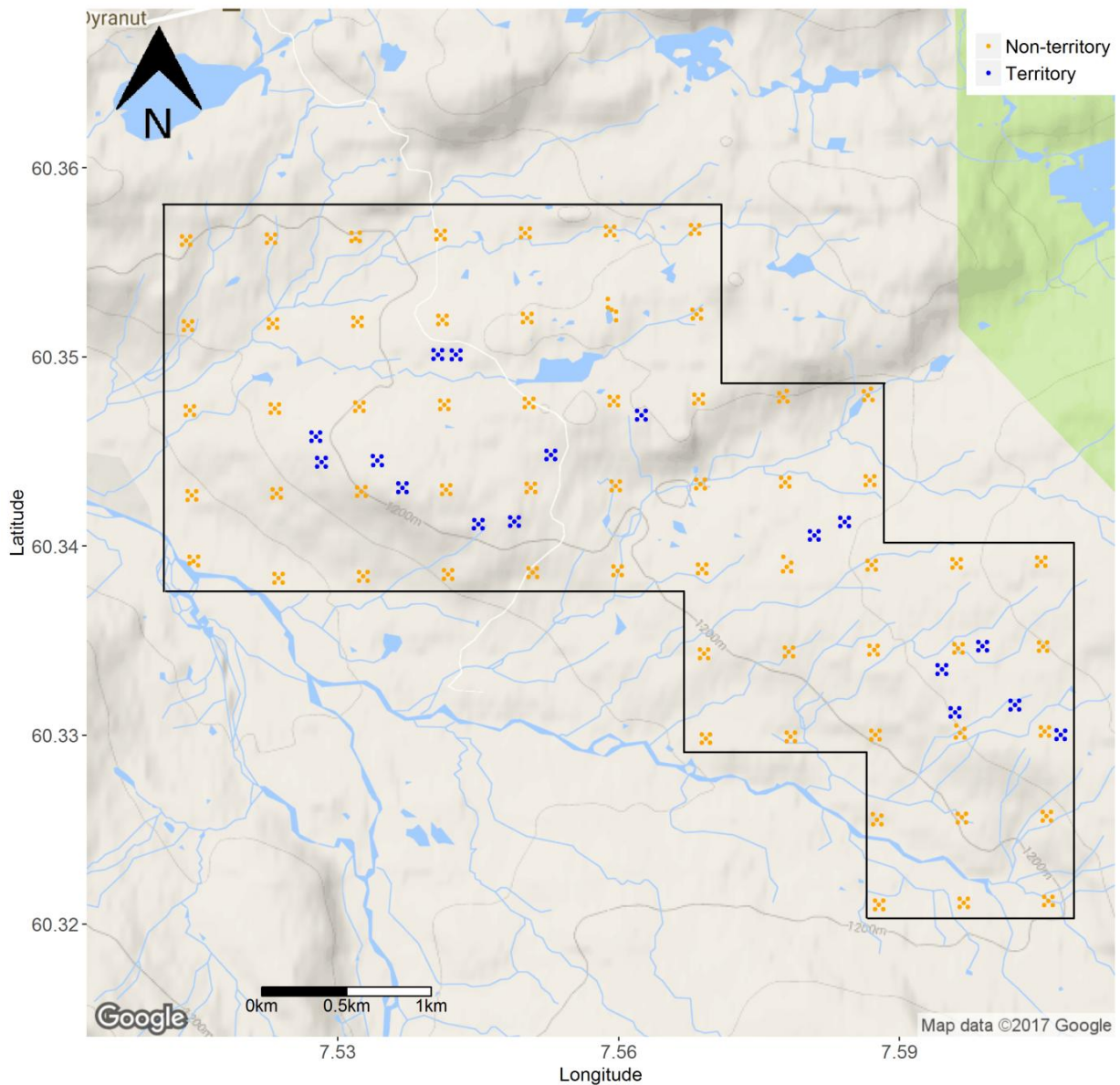nera or vegetation groups that have much in common are found close to each other, while vegetation types with less in common are further away (Fig. 8, 9). This means that *Empetrum nigrum* and lichens have much in common whereas both of them have little in common with *Eriophorum* sp. Species, genera or vegetation groups located close to each other could further be regarded as communities. In my dataset, lichens, *Empetrum nigrum* and *Betula nana* would form one community (hereafter LEB-community), whereas forbs, grasses and *Salix* sp. another (Fig. 8, 9). The other species, genera or vegetation groups are treated as communities on their own.

The distribution of the 85 territorial and 295 non-territorial vegetation examination points is shown in Figure 8. Points close to origo is either a mean of the species, genera and vegetation groups represented here, or explained by some of the axis not shown in the figure. A large amount of the vegetation points are found close the LEB-community (Fig. 8). Several examination points are also found around the *Carex bigelowii* community, influenced by both by the *Nardus stricta* community and the LEB-community. Many examination points are also found in the forbs-grasses-*Salix* sp. community.

The "ordisurf"-function was found to be significant (df=8.3, Chi.sq=195.1, p<0.001). One peak is found around 1.5 on the DCA1-axis, with a probability of finding a territory at around 40% (Fig. 9). As the curves in the figure become darker, the probability of finding a territory decreases. Thus, the forbs-grasses community has a 25% chance of hosting a territory, the same chance as the *Carex bigelowii* community. Between the LEB-community and *Carex bigelowii* community the probability again increased up to 40%, but the probability decreases with increasing *Betula nana* cover.

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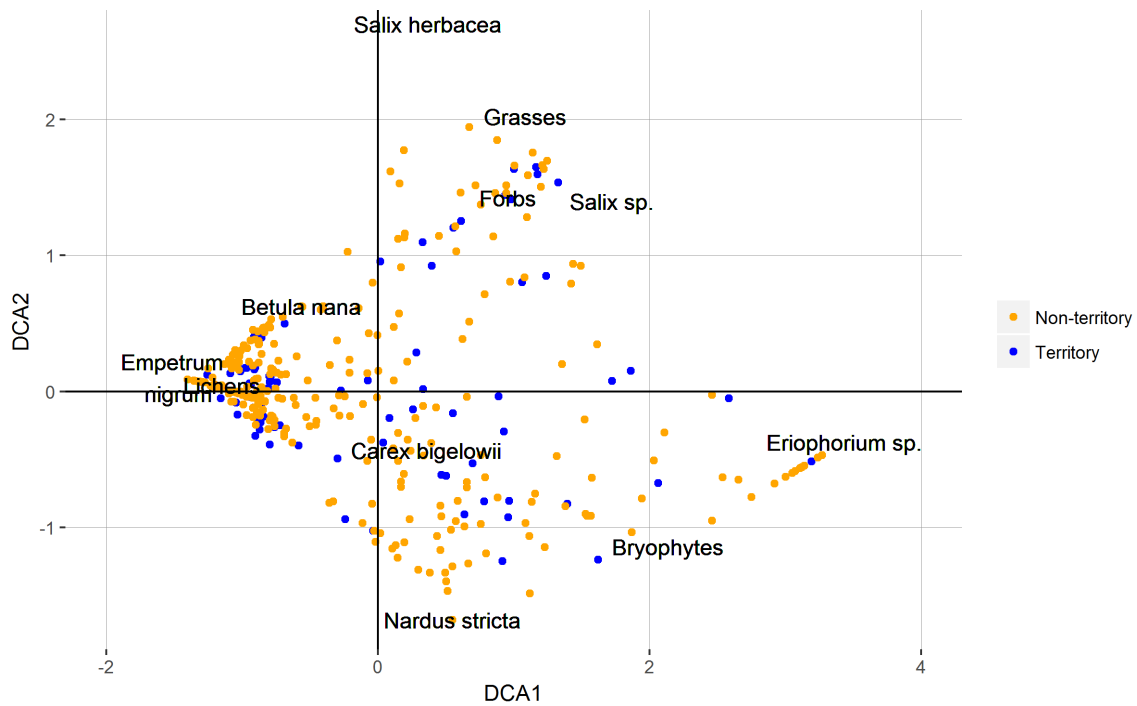
Figure 8. The indirect ordination with all examination points. Blue represents examination points within territories (n=85), whereas the orange are non-territorial (n=295). The distance between examination points, species, genera or vegetation groups say how much they have in common.
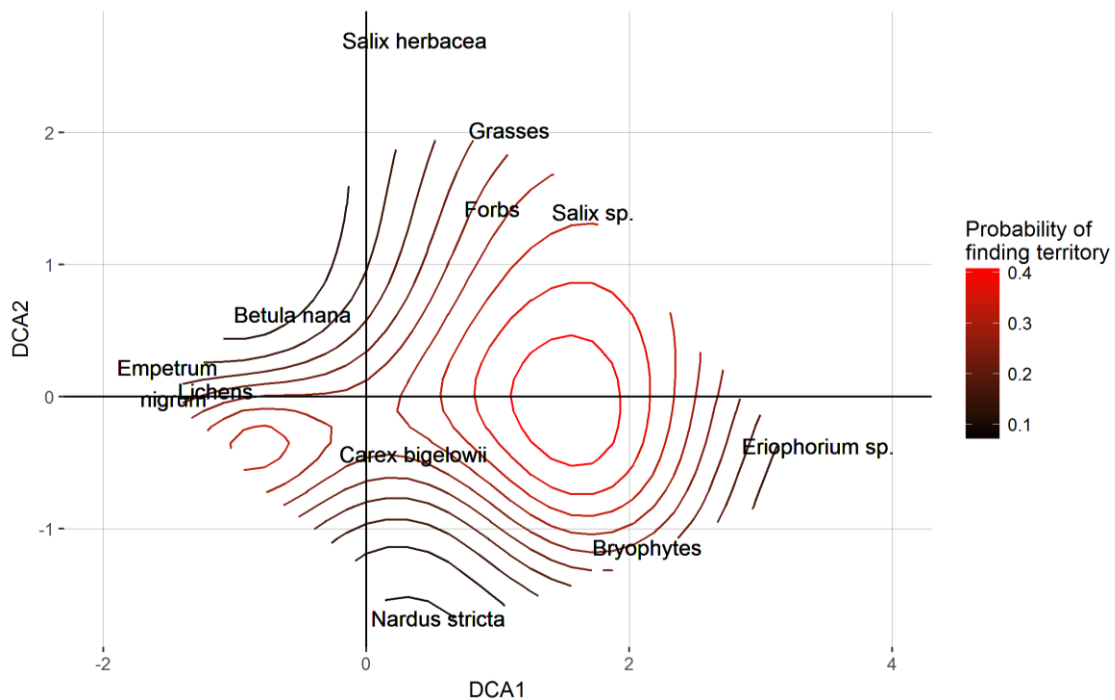
Figure 9. The probability of finding Lapland longspur territories in the different communities based on the examination points shown in Figure 8. The curves placement in relation to the species, genera or vegetation groups says what the vegetation composition is. For instance, the closer a curve is to forbs, the more does the vegetation cover consist of forbs.

There was little difference between the plant cover in territorial and non-territorial examination points, but all territories were found between 1180 and 1270 m a.s.l (Fig. 10). The GLM-model, which tested for plant characteristics within the territories, showed that the second-order polynomial regression of altitude led to a significant improvement of the model (GLM, dev=39.37, df=2, p < 0.001). The presence of shrubs further improved the model significantly (GLM, dev=36.20, df=1, p<0.001), but none of the plant cover data did so. There was no interaction between the altitude and the presence of shrubs, but there was a significant difference in the altitude where shrubs were present (mean ± sd; 1193 ± 40 m a.s.l.) and absent (1225 ± 31 m a.s.l.; t=8.2, df=254.06, p<0.001; Fig.11). Full model output is given in Appendix D
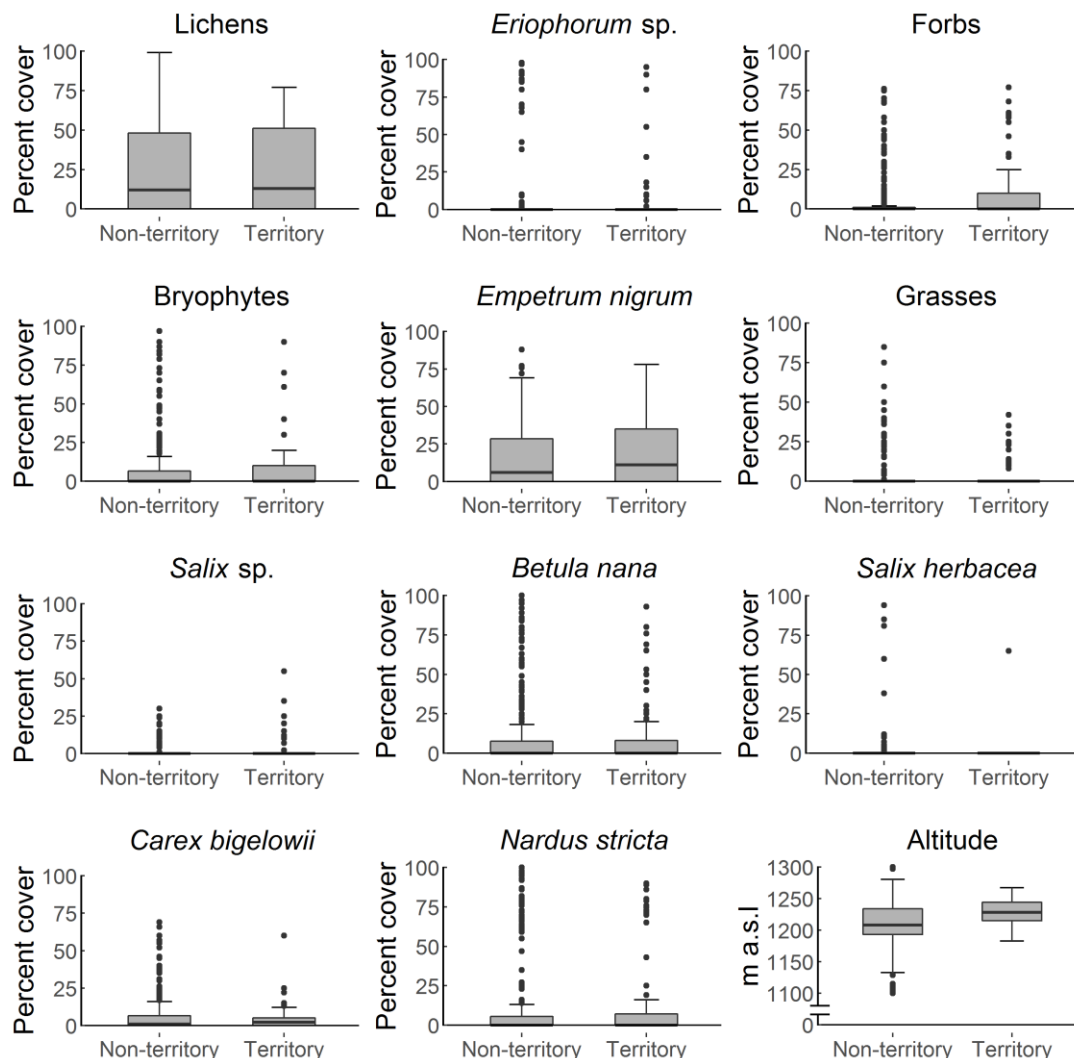
Figure 10. Altitude and cover data in percent for different plant species, genera or vegetation groups for territorial (n=85) and non-territorial (n=295) examination points. The boxes display the 25th and 75th percentile, with the median as the black band within the box. The whiskers represent the 1.5 interquartile range, and outliers as black dots.
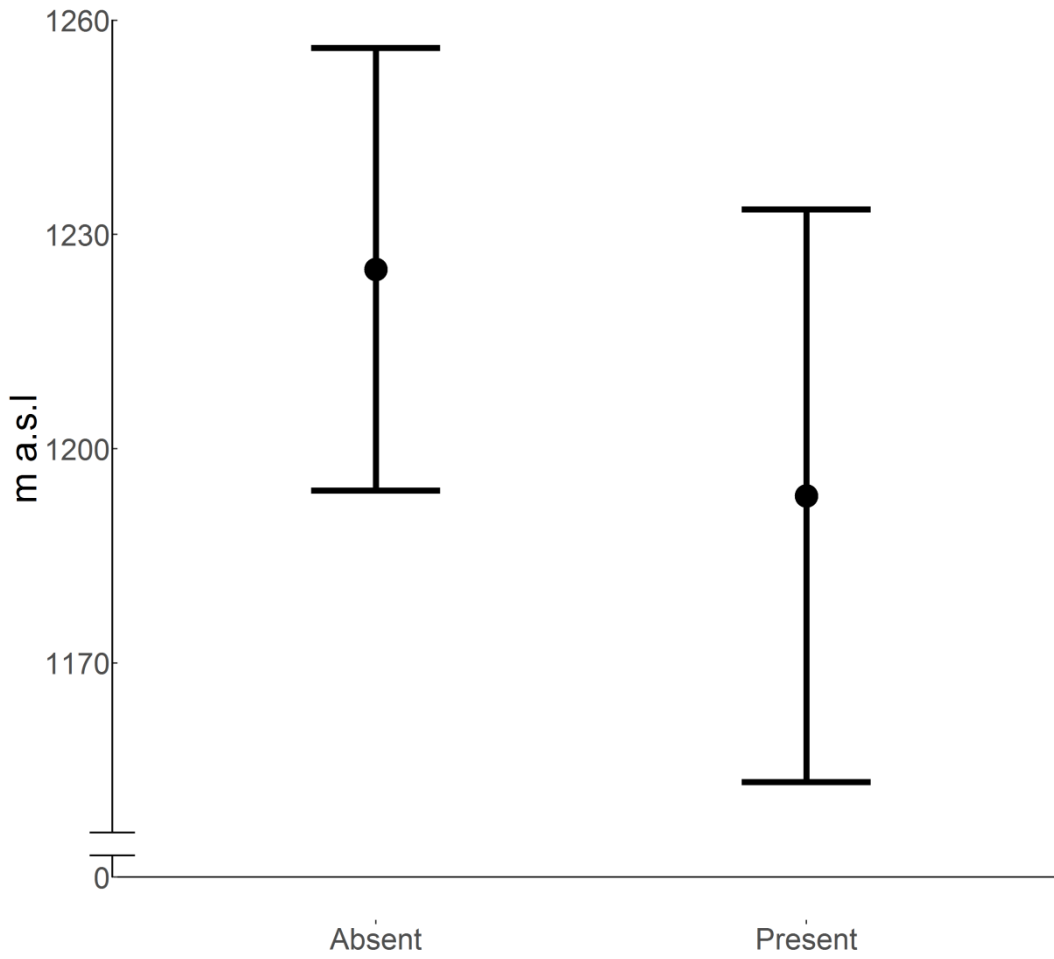
Figure 11. The presence or absences of shrubs like *Salix* sp. and /or *Betula nana* in relation to the altitude. The mean is represented with a black dot, while the whiskers represent the standard deviation of the altitude were the shrubs were represented.

Discussion

Based on stomach samples of Lapland longspurs from Hardangervidda in early June, I have shown a diet dominated by seeds. This is in line with previous studies of the species' diet in Alaska (Custer & Pitelka 1978) and Greenland (Salomonsen 1950). As far as I know, my study is the first to quantify food characteristics in Lapland longspurs in Western Palearctic. Since the longspur population has dramatically declined since the 1980's (Byrkjedal & Kålås 2012), I would assume the remaining population to exploit the most favorable territories available and presumably making vegetative characteristics easier to detect. Despite the dominance of seeds, there were no clear link between plant community and the choice of territory in the Lapland longspurs. The establishment of territories seemed to depend on altitude and the presence of shrubs, as these were found to be the most important factors among those tested in this study.

Most of the seeds found in the stomach analyses are from plants associated with the forbs-grasses-*Salix* sp. community (Påhlsson 1994; Fremstad 1997), except seeds from *Empetrum nigrum, Betula nana* and *Juncus trifidus*, which are all associated with the LEB-community. Also *Carex* seeds can originate from a variety of plant communities (Påhlsson 1994; Fremstad 1997). Since seeds constitute an important part of the longspurs' diet early in the season, one could expect the Lapland longspurs to establish territories in seed rich areas. However, contrary to expected, the longspurs did not show any preference for plant communities rich in seed producing plants. This was also indicated by the GLM-model, as none of the factors including seed producing plants was found to be important habitat characteristics within the territory. This is especially surprising since the stomach samples were collected at a time when the birds should be most strongly territorial (Drury 1961; Bjørnsen 1988). Instead, the highest probability of finding longspur territories was in areas consisting of several different plant communities. As seed producing plants do not seem to affect the placement of territories, but still dominate in the stomach analysis, can indicates that the longspurs are not strictly confined to their territories as the only feeding ground early in the breeding season. Accordingly to Tryon and MacLean (1980), the Lapland longspur utilizes a larger area while searching for food than they actually defend during the pre-nesting period. If the longspurs leave their territory to feed, their territory would not need to be in seed rich areas. During the territorial mapping, I often observed male longspurs clearly marking their territory with song flight before suddenly flying away. Sometimes the males returned shortly after, while at other times they were not seen before a later visit in the territory. The reason why the males exerted

such a behavior is unknown, but it shows that they do not necessarily stick strictly to their territories early in the breeding season.

The dry mass analysis of the stomach contents showed that arthropods accounted for approximately 40% of the diet. If seed availability within the territory is not important for the Lapland longspur, the arthropod abundance might be so. Arthropods have a higher dry mass than seeds (Custer & Pitelka 1978; Byrkjedal 1980), giving them more energy per unit. For instance, one normal sized *Tipula* larva gives the same amount of energy as approximately 35 seeds (Custer & Pitelka 1978). I assume the arthropods to be digested faster than seeds in Lapland longspurs, as was found to be the case in snow buntings *Plectrophenax nivalis* (Custer & Pitelka 1975). My results could therefore be biased towards seeds, making the assumption of seed importance weaker than initially thought. The arthropods I found in the stomach analysis most likely came from different vegetation structures. The species *Otiorrhynchus dubius*, the most dominant adult Coleoptera in my analysis, is previously described as common in dry meadows, wet meadows and lichen heaths at Hardangervidda (Solhøy *et al.* 1975). The most dominant Carabidae *Calathus melanocephalus, Patrobus* spp. and *Notiphilus aquaticus* are mostly associated with dry and wet meadows (Solhøy *et al.* 1975; Eriksen *et al.* 1989). Of the larvae I found, Tipulidae are mostly found in wet meadows whereas the Lepidoptera are more common in dry meadows and lichen heaths (Solhøy *et al.* 1975). As these arthropods are found in a variety of ground characteristics, it might be important for the longspurs to have a mosaic of different vegetation types in the territory to provide the birds with arthropods. This could be the reason for why the highest probability of finding a territory was in areas with different plant communities.

My study of Lapland longspurs was conducted early in the breeding season, and ended at the time when the eggs normally hatch (Bjørnsen 1988). When the longspurs establish their territories, it might be more important for territory selection what happens in the nestling period. In American studies, the Lapland longspur is described to select a territory size in relation to the expected food abundance (Seastedt & MacLean 1979), and stick more strictly to their territory during the nestling period (Tryon & MacLean 1980). As the longspurs feed their nestling almost exclusively with arthropods (Custer & Pitelka 1978; Seastedt 1980), this emphasizes the importance with different vegetation structures that could contribute to a wider range of arthropod species available throughout the summer. This would also save time and energy for the adults when feeding the nestlings (Tryon & MacLean 1980). Moreover, by having several plant communities in their territories, the birds are less dependent on one

single arthropod species, but can rather exploit the arthropod species available at the time. The fact that the longspurs do not rely on only one type of prey is demonstrated in several studies. Custer and Pitelka (1978) reported that *Tipula carinifrons* were the most important prey at Barrow, Alaska, whereas Seastedt (1980) found that *Prionocera* spp. were clearly the most important species in his study at Old Chevak, Alaska. Furthermore did Seastedt (1980) only find a 12% overlap in the diet in dry weight between longspurs at Barrow and Old Chevak. In Greenland, the arthropod diet consisted mostly of the moth caterpillar species *Eurois occulta* (Fox et al. 1986).

The altitude and presence of shrubs like *Salix* sp. and/or *Betula nana* were found to be the factors having an impact on the placement of Lapland longspurs territories at Hardangervidda. Since the Lapland longspur is known to breed along the coast in northern Norway (Haftorn 1971; Breiehagen 1994) as well as in Alaska (Drury 1961; Custer & Pitelka 1977), altitude *per se* is unlikely to have an effect on its occurrence. It is more likely that the altitude acts through the shrub cover since there was a significant difference at which altitude the shrub cover was found in my study area. As Lapland longspur is known to avoid areas with dense growth of bushes and shrubs (Gierow & Gierow 1991; Boelman *et al.* 2015), the birds selected the altitude where they have large patches of open tundra, as well as the presence of shrubs. This fits well with my recordings, as most of the territories were found around 1230 m a.s.l and the shrub growth at Hardangervidda reaches 1250 m a.s.l. (Rekdal *et al.* 2009).

There could be several reasons why areas with shrubs should be attractive to the Lapland longspurs. For instance, shrubs might offer a good source of arthropods for the longspurs after the snow has melted. Although Lapland longspurs are known to forage mainly in short vegetation on the ground where it picks seeds and arthropod species off the tundra (Drury 1961; Custer & Pitelka 1978), the canopy of shrubs can be rich in arthropods such as Diptera (Boelman *et al.* 2015). Shrubs might also be attractive for the male longspurs as vantage points and song post from which they both can attract females and protect their territory against other males (Drury 1961; Cramp & Perrins 1994). Having a good view of the territory could also be important for the birds for an early detection of predators. For instance when feeding the nestlings, they may easily reveal the nests position to a predator if they are not careful.

The presence of shrubs could also give important shelter against the weather for the Lapland longspur nests. Even in summertime the weather conditions at Hardangervidda can be harsh.

Low temperatures, especially during the night, can often occur. In combination with strong winds or rain, this can lead to rapid cooling of eggs or newly hatched chicks (Lyon & Montgomerie 1987). Lapland longspurs place their nest on the ground with the opening in a southwesterly direction to increase the exposure of solar radiation (Boal & Andersen 2005) and hence reduce heat loss. Male longspurs are further not known to feed the female while she is incubating (Lyon & Montgomerie 1987), or incubate while the female is foraging (Drury 1961). This emphasizes the importance of reducing the heat loss in the nest when the female is not present. Both Gierow and Gierow (1991) and Boal and Andersen (2005) reported that nests were often covered by shrubs or woody forbs, and out of the four nests I found during the field period, three of them were covered by sprigs from *Salix* sp. or *Betula nana*.

I did not find any support for the hypothesis that the longspurs avoid areas dominated by lichens. The increase in lichen cover is linked to the decline in reindeer population (Jordhøy & Strand 2009; Odland *et al.* 2014), since lichens are an important food source for the reindeers during the winter (Odland *et al.* 2014). There has also been a decline in the stock of grazing sheep at Hardangervidda during the last decades (Austrheim *et al.* 2008), which would lead to less trampling and thus have a positive effect on the lichen cover. However, lichens are mostly found on exposed ridges where few vascular and woody plants are found due to the extremely harsh winter conditions (Fremstad 1997). Moreover, lichens are in general weak competitors in comparison to vascular plants (Cornelissen *et al.* 2001). Hence, although there has been an increase in lichen cover at Hardangervidda during the last decades (Jordhøy & Strand 2009), it does not necessarily mean that the food availability for the longspurs in spring is reduced by this factor.

There might be some methodological issues affecting my results. For instance, seed producing plants might be more abundant than recorded. *Potentilla* was an abundant seed genus in the analyzed stomachs, whereas I did not record a single *Potentilla* species in any of my examination points during the field period. The same can be reported regarding *Luzula*, which was also a dominant genus reported in the stomach analysis but only scarcely observed in field. Although all stomachs came from birds shot at another location, they are close enough that I assume the vegetation to be more or less the same. However, the vegetation may have changed since 1974, with *Potentilla* and *Luzula* perhaps being more abundant genera at that time than now, over 40 years later. Further, the longspurs might be able detect seeds while foraging even when plants are less visible after a long winter and the human eye could be more prone to overlook them. Hence, it would be interesting to re-examine all examination

points in late summer or early autumn, to get a better picture of the vegetation in the area. In areas with dense *Salix* sp. cover, I had to push them aside to make to place my frame square on the ground. In this plots, the leaves cast shadow over the ground and can affect the ground vegetation. It would thus be interesting to calculate the part of the ground not covered with leaves in areas with a dense cover of *Salix* sp., and compare areas with and without leaves.

With climate change, it is hypothesized that shrubs will climb uphill and poleward on a global scale both in tundra and mountain areas (Myers-Smith *et al.* 2011), and graminoids may outcompete lichens and mosses (Cornelissen *et al.* 2001; Klanderud & Totland 2005; Jägerbrand *et al.* 2009). Hardangervidda has however until now had an increase in lichen cover (Jordhøy & Strand 2009) and no drastic changes in the shrub cover. However, the climate in Norway is projected to become warmer and wetter over time (Hanssen-Bauer *et al.* 2009). It is plausible that the vegetation at Hardangervidda will change according to the global assumptions. If so, this will most likely have several implications for the Lapland longspur. If the shrubs in the future start to climb uphill, the Lapland longspur will have to shift upwards to avoid too dense vegetation (Boelman *et al.* 2015; Boelman *et al.* 2016). As most of Hardangervidda is situated at 1100-1400 m a.s.l (Thorsnæs 2014), there are limited opportunities to shift uphill considering the longspurs currently breed between 1150-1250 m a.s.l. Moreover, increased precipitation could make it more challenging to locate arthropods and raise nestlings during the summer (Pérez *et al.* 2016), which could lead to increased mortality.

To conclude, even though seeds make up an important part of the diet of Lapland longspurs at Hardangervidda early in the breeding season, I found no support for the hypothesis that the presence of seed producing plants limits territory choice in this species at Hardangervidda. It would therefore be interesting to gain further knowledge regarding the effects arthropod abundance can have on Lapland longspurs throughout the breeding season. As I also reported that the highest probability of finding Lapland longspur territories were in areas with a mixture of plant communities, it could be interesting to know more about the heterogeneity of vegetation within the longspurs territory. As there are differences in the phenology of plants and arthropods, having a mosaic of vegetation in the territory could hence provide the longspurs with food throughout the whole summer. As I also found that the longspur territories were associated with the presence of shrubs, it could be interesting to gain more knowledge about the connection between shrubs and longspurs, especially as the shrubs are assumed to be more dominant in the future.

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Appendix A – Dry mass of stomach contents

Table A The different dry masses from the items found in the 39 analyzed Lapland longspur stomachs The dry weights are obtained from Byrkjedal (1980) and [b]Custer and Pitelka (1978). All larvae are estimated a length of 15 mm.

Prey item	Dry weight
Empetrum nigrum (ripe)	19
Seeds	1
Calathus melanocephalus	5.9[b]
Notaphilus aquaticus	1.8
Amara praetermissa	7
Patrobus spp.	14
Otiorhynchus dubius	13
Helophorus glacialis	0.8
Aphodius lapponum	5.9[b]
Tachinus elongates	10
Gonioctena pallida	4
Arpedium sp.	0.4
Unidentified adult Coleoptera	5.9[b]
Tipulidae larvae	10.9
Muscidae larvae	1.82[b]
Lepidoptera larvae	10.9
Hymenoptera larvae	10.9
Coleoptera larvae	10.9
Unidentified arthropod larvae	10.9
Araneae	4
Mitopus morio	12

Appendix B – Additional territorial mapping data

Table B. The different territories, the date of first territorial plotting sequence and the number of times the territorial mapping is conducted on each territory in the study area. The codes for territories those I used during the field work.

Territory	Date of first territorial plotting sequence	Total number of territorial plotting sequence
T2	04.06.2016	4
T3	04.06.2016	8
T5	02.06.2016	6
T6	02.06.2016	7
T7	02.06.2016	7
T9	10.06.2016	5
T11	03.06.2016	4
T12	10.06.2016	5
T13	10.06.2016	6
T14	11.06.2016	3
T15	13.06.2016	5
T16	14.06.2016	5
T17	13.06.2016	4
T18	13.06.2016	6
T19	13.06.2016	6
T20	13.06.2016	4
T24	14.06.2016	2

Appendix C – Plant species list

Table C. All species, genera and vegetation groups recorded during the field work, and the number of examination points they were present in.

Species	Number of examination points
Lichens	251
Bryophytes	110
Salix sp.	38
Carex bigelowii	217
Eriophorum sp.	42
Empetrum nigrum	224
Betula nana	116
Nardus stricta	154
Forbs	104
Grasses	54
Hupersia apressa	2
Salix reticulata	1
Salix herbacea	21
Juncus trifidus	16
Diphasiastrum alpinum	2
Vaccinium myrtillus	1
Trichophorum cespitosum	2
Luzula sp.	24

Appendix D – Outputs from R

Outputs from the ordination results in R:

Axis length:

Call:

decorana(veg = sqord.df)

Detrended correspondence analysis with 26 segments.

Rescaling of axes with 4 iterations.

	DCA1	DCA2	DCA3	DCA4
Eigenvalues	*0.6755*	*0.4637*	*0.3894*	*0.4031*
Decorana values	*0.7303*	*0.4211*	*0.3419*	*0.1907*
Axis lengths	*4.6711*	*3.6177*	*3.7757*	*3.4366*

ANOVA of the ordisurf-function

Family: binomial

Link function: logit

Formula:

y ~ s(x1, x2, k = 10, bs = "tp", fx = FALSE)

Approximate significance of smooth terms:

edf Ref.df Chi.sq p-value

s(x1,x2) 8.318 9.000 195.1 <2e-16

Outputs from model selection in R:

Table D. The AIC values for the different variables tested against the model consisting only of the intercept of presence of territories in the GLM-model.

Variable	Type of variable	AIC value (first order/second order)
Lichens	Percent cover	407.7/406.5
Bryophytes	Percent cover	407.9/408.8
Salix sp	Percent cover + presence/absence	403.4/405 + 404.8
Carex bigelowii	Percent cover + presence/absence	406.3/407.8 + 407
Eriophorum sp.	Percent cover	407.5/406.8
Empetrum nigrum	Percent cover	406.7/407.9
Betula nana	Percent cover + presence/absence	407.6/407.2 + 407.3
Salix herbacea	Percent cover	407.2/408.9
Nardus stricta	Percent cover	407.9/407.4
Forbs	Percent cover	405.5/407.4
Grasses	Percent cover	407.9/405
Luzula sp.	Presence/absence	406.3
Carex bigelowii + Luzula sp.	Presence/absence	408
Salix sp. + *Betula nana*	Percent cover + presence/absence	408/408+404.8
Altitude	---	386.4/370.6

Analysis of Deviance Table

Model 1: Territorie_10 ~ +1

Model 2: Territorie_10 ~ poly(Moh., 2)

 Resid. Df Resid. Dev Df Deviance Pr(>Chi)

1   379   403.96

Table E. The AIC-values for the different variables tested against the model consisting of the second-order polynomial regression of altitude against the presence of territories in the GLM-model.

Variable	Type of variable	AIC value (first order/second order)
Lichens	Percent cover	368.9/370.1
Bryophytes	Percent cover	372.5/373.9
Salix sp	Percent cover + presence/absence	364.3/366.2 + 365.4
Carex bigelowii	Percent cover + presence/absence	367.4/369.2 + 372.4
Eriophorum sp.	Percent cover	371.9/372.1
Empetrum nigrum	Percent cover	372/373.8
Betula nana	Percent cover + presence/absence	370.4/369.6 + 365.7
Salix herbacea	Percent cover	372.4/373.3
Nardus stricta	Percent cover	372.6/369
Forbs	Percent cover	369.8/371.8
Grasses	Percent cover	370.5/372.3
Luzula sp.	Presence/absence	370.1
Carex bigelowii + Luzula sp.	Presence/absence	371.9
Salix sp. + *Betula nana*	Percent cover + presence/absence	367.8/362.9 + 357.2

Analysis of Deviance Table

Model 1: Territorie_10 ~ poly(saldvergPA, 1)

Model 2: Territorie_10 ~ poly(Moh., 2)

* Resid. Df Resid. Dev Df Deviance Pr(>Chi)*

1   378   400.77

2   377   364.59 1   36.179 1.8e-09 ***

Table F. The AIC-values for the different variables tested against the model consisting of the second order polynomial regression of altitude and the presence/absence of *Salix* sp. and/or *Betula nana* against the presence of territories

Variable	Type of variable	AIC value (first order/second order)
Lichens	Percent cover	355.9/357.5
Bryophytes	Percent cover	359/360.2
Salix sp	Percent cover	356.6/358.5
Carex bigelowii	Percent cover + presence/absence	357/358.9 + 358.6
Eriophorum sp.	Percent cover	359.2/360
Empetrum nigrum	Percent cover	357.7/359.6
Betula nana	Percent cover	358.5/360.4
Salix herbacea	Percent cover	359.2/360.7
Nardus stricta	Percent cover	358.7/355.4
Forbs	Percent cover	355.9/357.2
Grasses	Percent cover	358.4/357.7
Luzula sp.	Presence/absence	356.8
Carex bigelowii + Luzula sp.	Presence/absence	359

Analysis of Deviance Table

Model 1: Territorie_10 ~ poly(Moh., 2) + poly(saldvergPA, 1)

Model 2: Territorie_10 ~ poly(Moh., 2) + poly(saldvergPA, 1) + poly(Nardus,

  2)

 Resid. Df Resid. Dev Df Deviance Pr(>Chi)

1   376   349.23

2   374   343.35 2   5.8766 0.05296 .

---

*Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

Need to test for interactions between the second order polynomial regression of altitude and the presence/absence of *Salix* sp. and/or *Betula nana*:

Analysis of Deviance Table

Model: binomial, link: logit

Response: Territorie_10

Terms added sequentially (first to last)

Df Deviance Resid. Df Resid. Dev Pr(>Chi)

	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)
NULL			379	403.96	
poly(Moh., 2)	2	39.369	377	364.59	2.825e-09
poly(saldvergPA, 1)	1	15.366	376	349.23	8.858e-05
poly(Moh., 2):poly(saldvergPA, 1)	2	0.078	374	349.15	0.9619

NULL

poly(Moh., 2)   ***

poly(saldvergPA, 1)   ***

poly(Moh., 2):poly(saldvergPA, 1)

---

*Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

T-test between altitude and presence/absence of *Salix* sp. and/or *Betula nana*

 Welch Two Sample t-test

data: Moh. by saldvergJN

t = 8.1738, df = 254.06, p-value = 1.424e-14

alternative hypothesis: true difference in means is not equal to 0

95 percent confidence interval:

 24.07616 39.36001

sample estimates:

mean in group N mean in group Y

    1225.133   1193.415