Selection of territorial habitat in a declining population of Lapland Longspurs *Calcarius lapponicus*

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Abstract
The population of Lapland Longspur *Calcarius lapponicus* has declined drastically in the Scandinavian mountains over the last decades. One hypothesis is that the population decline has been caused by a change in vegetation composition, specifically an increase in lichen cover leading to a possible decrease in seed-producing plants. We tested the hypothesis by recording vegetation composition inside and outside Lapland Longspur territories in a 10 km² study area at Hardangervidda, southern Norway, where longspurs previously bred in high numbers. Vegetation composition was recorded by percentage coverage in 295 1 x 1 m quadrats laid out evenly over the study area and compared to a similar treatment of 85 points inside 17 territories of Lapland Longspurs. No difference in lichen coverage or coverage by seed-producing plants was found inside versus outside territories. Instead, Lapland Longspurs were found to establish their territories in the upper part of the study area, where the snow melts earlier. Also, the occupied territories had an orientation towards the sun (sector S–W). Precipitation has increased strongly in the western parts of the Scandinavian Peninsula in recent decades. Falling as snow in the mountains, the increased precipitation leads to delays in spring thaw which could reduce the availability of breeding habitat for Lapland Longspurs during territorial establishment. We suggest that changes in spring conditions could be responsible for the species' population decline in the western parts of the Scandinavian Peninsula.

INTRODUCTION

Alpine and tundra ecosystems are highly vulnerable to climate change (Gonzalez et al. 2010, Pepin et al. 2015), and climate warming is known to cause poleward and uphill range shifts in many species in such environments (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). Moreover, rising temperatures and increased nutrient availability can lead to increased cover of graminoids, while lichens and mosses are outcompeted (Cornelissen et al. 2001, Klanderud & Totland 2005, Jägerbrand et al. 2009). Nevertheless, ecological responses might vary according to local conditions (Gottfried et al. 2012) and between taxonomic groups (Chen et al. 2011). If species cannot adapt to the environmental changes, or shift their geographic range accordingly, they might face an increased risk of extinction (Sekercioglu et al. 2008). It is therefore worrying that many alpine and tundra species of birds are currently declining (Bech et al. 2013, Lehikoinen et al. 2014, Scridel et al. 2018, Lehikoinen et al. 2019).

The Lapland Longspur *Calcarius lapponicus* has a circumpolar distribution closely associated with the tundra biome (Cramp & Perrins 1994). Populations are increasing worldwide (BirdLife International 2022), but a mean annual population decline of 5% per year was reported from 2002–2012 throughout Fennoscandia (Lehikoinen et al. 2014), with declines of 7.9% per year in Norway in the period 2010–2019 (Stokke et al. 2021). Furthermore, at the Hardangervidda mountain plateau in southern Norway, at the south-western limit of the species' Eurasian distribution, Byrkjedal and Kålås (2012) reported an 85% decline in the breeding population between 1980 and 2010–2011. Hence, from previously being one of the most common breeding birds in this mountain region (Haftorn 1971, Breiehagen 1994), the species is now found much more sparsely (Heggøy et al. 2019, the authors pers. obs.). Lehikonen et al. (2014) evaluated recent population declines in Lapland Longspurs and other mountain

birds in Fennoscandia, and concluded that declines were principally linked to changes in the conditions on the breeding grounds rather than at wintering areas.

The vegetation at Hardangervidda is currently changing and most conspicuously so 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 in areas of Hardangervidda since the 1980's (Jordhøy & Strand 2009). The increases might be linked to a decline in the local reindeer population during the last few decades, which eases grazing pressure on lichens, especially during winter (Jordhøy & Strand 2009, Odland et al. 2014). Hardangervidda is also utilized by many farmers as a summer pasture for their livestock, especially domestic sheep (Rekdal et al. 2009). Moreover, in recent decades there has been a decline in the numbers of sheep utilizing Hardangervidda during the summer (Austrheim et al. 2008). Lower densities of sheep lead to less trampling, which could be beneficial for lichen growth.

The Lapland Longspur prefers habitats with tussock tundra, usually with a sparse cover of shrubs like *Betula nana* and *Salix* spp. (Haftorn 1971, Seastedt & MacLean 1979, Cramp & Perrins 1994, Henry & Mico 2002, Boelman et al. 2015). During the pre-nesting period, males defend their territory with song, flight chases, and ground postures (Drury 1961, Bjørnsen 1988, Cramp & Perrins 1994), but tolerate visiting males which do not exhibit territorial behavior (Drury 1961). Studies in Alaska have shown that territories containing large proportions of mesic areas had better feeding resources and were smaller than territories with less favorable feeding habitats (Seastedt & MacLean 1979). As incubation progresses, territory borders disappear (Drury 1961, Seastedt & MacLean 1979, Gierow & Gierow 1991). Little information is available on the habitat characteristics of Lapland Longspurs breeding in Europe. Information on habitat requirements is vital for an understanding of basic breeding ecology in species, and thus for species conservation.

Recent changes in the habitat on the alpine breeding grounds are thought to be a likely factor behind population decline in Lapland Longspurs (Byrkjedal & Kålås 2012, Lehikoinen et al. 2014). An increase in lichen cover (Jordhøy & Strand 2009) may result in lower availability of seed-producing plants and thus limited food availability for breeding longspurs (Byrkjedal & Kålås 2012). Seeds form an important and substantial part of the species' diet in early spring (Byrkjedal et al. 2022), and reduced seed availability during this period might be especially critical. An increased lichen cover suppressing herb and forb diversity could perhaps also negatively affect availability of insects for the birds, as well as possible nest sites. From this combination of ecological changes, we would predict that Lapland Longspur territories would be located where the lichen cover is relatively low, and where meadows with grass and herbs are relatively common.

We studied habitat selection in a declining population of Lapland Longspurs breeding in an alpine area at Hardangervidda, southern Norway. By mapping territories of Lapland Longspurs, and by recording plant cover within and outside occupied territories, we looked for evidence of habitat preferences by the birds. If habitat availability limits the breeding population of Lapland Longspurs, we predicted that habitats found within territories should differ from habitats available in surrounding areas without territories. We tested the hypothesis that longspur territories are more likely to occur in areas rich in seed-producing plants, and with a relatively sparse lichen cover. Based on previous studies of this species, we also predicted that areas with shrubs should be over-represented in Lapland Longspur territories compared with the surrounding habitat.

METHODS

Study area
We studied Lapland Longspurs in a 10 km^2 area around Bjoreidalshøgda and on the northern slope of Stigstudalen on the western part of the Hardangervidda mountain plateau in southern Norway (Eidfjord municipality, ca. 1250 m a.s.l., 60°21´ N, 7°33´ E; Figure 1).

The study area was selected due to observations of Lapland Longspurs early in the field season in 2016, as well as observations in 2011 indicating a minimum of 25–30 males present in this area (IB and TL pers. obs.).

The Hardangervidda mountain plateau covers ca. 8000 km^2 (Thorsnæs 2014). The study area lies above the tree line in the low- to middle-alpine zone. Due to a thick layer of snow during winter, 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).

Territory mapping
We searched the study area for Lapland Longspur territories between 21 May and 23 June 2016. Locations where singing males were either seen or heard were plotted with a GPS unit and categorized as a potential territory. Plots were transferred from the GPS unit onto the map «N50-Hardangervidda» using MapSource (version 6.16.3, Garmin Ltd. 2010). Within each presumed territory, reference points such as rocks or tall shrubs of *Salix* spp. where longspurs were often seen, were recorded with the GPS unit and added to MapSource to make the map more detailed. For each location, territory mapping (Sutherland et al. 2004) was conducted with printed maps from MapSource with 200 m scales and always by the same observer (VBF). Within each presumable territory, males were followed by sight for 10 minutes from the spot where they first appeared. To have a better view of the territory and
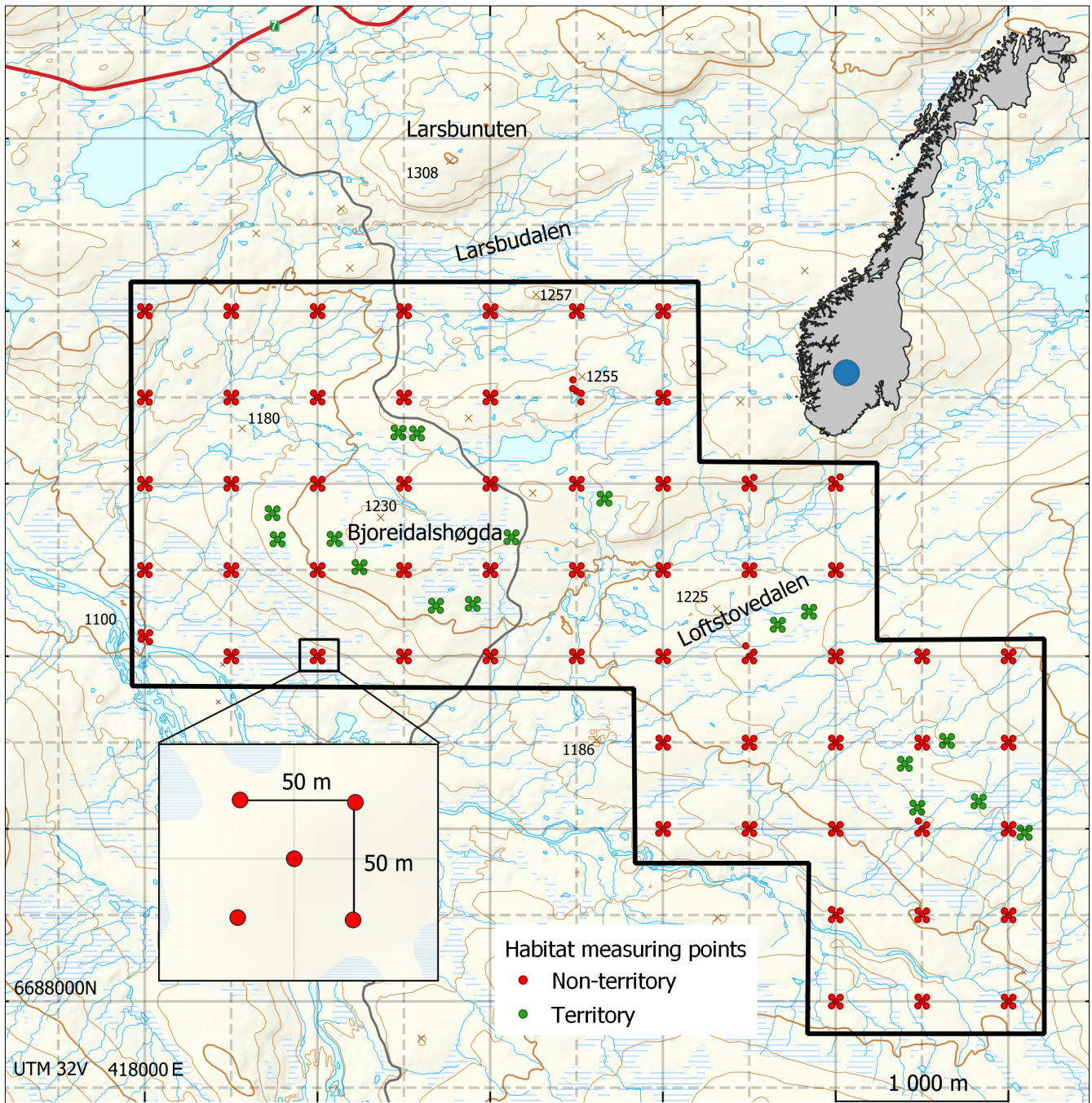
Figure 1. Study area with habitat measurement points. Green symbols represent territorial measurement points and red symbols show measurement points equally distributed over the study area as defined by the UTM grid system. Each habitat measurement point consisted of five 1 x 1 m squares for recording of plant species coverage as indicated in the inserted figure at lower left. Map data: Kartverket.

hence improve the quality of the territory mapping, VBF sometimes had to move to a better position after a bird was first spotted. Movements were always done as gently as possible not to affect the activity or behavior of the observed bird. The number of times the territories were mapped is given in Appendix 1. In addition to the position where the male first was spotted, its positions were marked on the printed map every minute, resulting in 11 records per territorial mapping sequence. Due to the size of the study area, territories could normally not be visited more than once per day. However, when they were, the area was left undisturbed for a minimum of one hour between mapping sequences to minimize the potential risk that the observer's presence affected the results. Position plots from the territory mapping were manually transferred into MapSource the same day as they were mapped, generating clusters of observations for each occupied territory.

Vegetation sampling
From the clusters of observations that helped define the territories in MapSource, we calculated the center
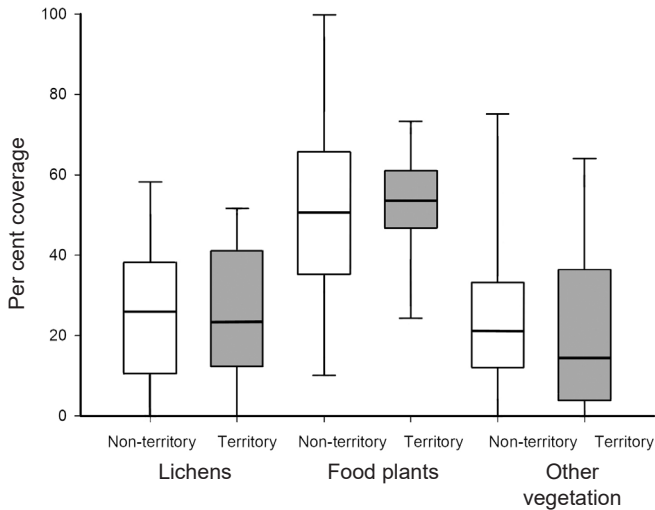
Figure 2. Per cent coverage inside territories (grey bars) compared to UTM-based points (open bars) across the study area, based on average values in five-point units (cf. Figure 1). Medians shown by horizontal bars, upper and lower quartiles by boxes, and maximum and minimum values by whiskers.
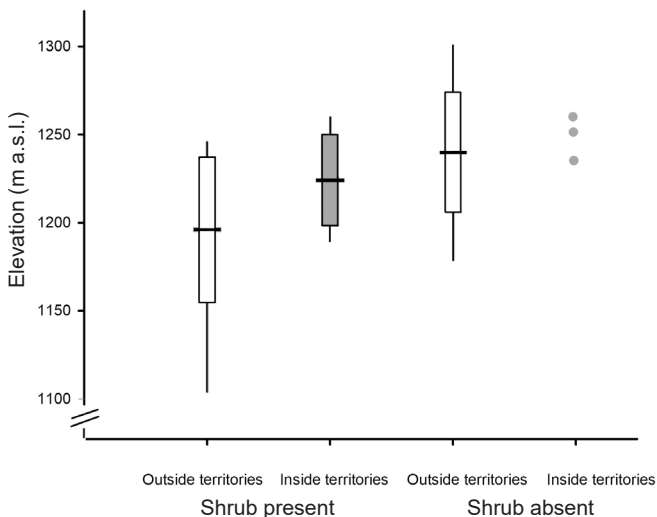

Figure 3. Elevation of territories with shrubs present and absent compared to sample points distributed over the study area. Presence and absence of shrubs was scored for the pooled five vegetation analysis points within each territory (n = 17 territories; grey bars) as well as for each of the five-point groups outside the territories (n = 59 five-point groups; open bars). Averages (horizontal bars), +/-SD (boxes), and maximum and minimum (whiskers) are shown. Single values for the three territories without shrub are shown as dots.

of each territory by arranging the observation points along latitudinal and longitudinal axes and calculating the median position. The center of each territory was chosen as a point for recording vegetation by using a 1 x 1 m quadrat frame to estimate the percentage cover of different plant species present at the ground layer (Bullock 1997). To better account for the variation of vegetation within each territory, the quadrat frame was

also used at four additional sample points arranged in a square around the center of the territory. We arranged the four points parallel to the north-south and east-west directions and with a standardized distance to the center of the territory, with sides of the square measuring 50 m each (Figure 1). Although the distance of 50 m was arbitrary, we assumed from the clusters of territorial observations that all sample points were within the focal territories.

To estimate the available vegetation in the whole study area, examination points were systematically selected from the UTM grid system where the grid lines of 1x1 km crossed each other (Figure 1), and additionally at 500 x 500 m grid squares between the main UTM lines. Line-crossings at each 500 and 1000 m intersection were treated as a vegetation examination point with 1 m² and surrounded by four additional sample points, in the same sampling protocol as for the territories. Our procedure resulted in a total of 295 points examined by vegetation frame.

Altitude and slope direction were recorded for each frame examination points, both at territorial and non-territorial sites.

Vegetation sampling was conducted after the territorial mapping was completed. If some of the examination frame points occurred on streams, small ponds, or snow, the location was classified as an unsuitable surface and the frames were moved directly northwards until the first possible examination surface.

Dwarf Willow *Salix herbacea* was recorded at a species level, whereas other *Salix* species, which were mostly taller than 20 cm, were marked as *Salix* sp. Lichens, bryophytes, forbs, and grasses were only treated as vegetation groups and not identified to species. To ease the estimation of plant cover, the 1 x 1 m frame was subdivided into 100 equal-sized squares by thin metal strings. In areas with *Salix* sp., the shrub sometimes had to be pushed aside to fit the frame for measuring the plant cover at the ground level. However, the area covered by the lower part of the trunks (which could cover a considerable proportion of the ground layer) was estimated and included.

Numerical analysis

For comparison of plant coverage and presence/absence of shrubs (*Salix* spp. and/or *Betula nana*) inside the territories with examination points outside the territories, we pooled the results for the frames belonging to the same five-frame group. Elevation was averaged for the five points belonging to the same five-frame group. When analyzing the distribution of slope orientation, we used the recorded orientation of the central frame of each five-point unit. The five-point units are hereafter referred to as «habitat measurement points».

Plants used as food resources were identified from seeds found in the stomachs of Lapland Longspur (Byrkjedal et al. 2022, Appendix 2). For the comparison of seed plants the coverage of each such plant taxon was

summed for each habitat measurement point (coverage of the taxa, see Appendix 2).

Statistical analyses were performed in SPSS Statistics Version 25. The distributions of plant coverage expressed by percentages deviated from normality, and we used non-parametric statistics for analyses of these variables. Elevation of plots within and outside territories were normally distributed, hence we used a t-test to compare the groups.

RESULTS

The percent coverage of lichens in habitat measurement points within the 17 territories (23.4%) did not differ from the 59 points that were evenly distributed over the study area (26%; Mann-Whitney U = 470.0, p = 0.7, Figure 2). Moreover, the coverage of seed producing plants potentially relevant as food for Lapland Longspurs did not differ between territories (53.6%) and other parts of the study area (50.6%; Mann-Whitney U = 436.0, p = 0.4, Figure 2). Shrubs were found in 14 of 17 occupied territories (82.4%), which also did not differ from the frequency found in the 59 habitat measuring points outside of the territories (71.2%; Fisher's Exact Test, p = 0.53)

Territories were on average situated at higher sites in the study area compared to habitat measuring points distributed outside territories, even though shrubs were distributed well below the elevation zone where territories were found (Figure 3). The average elevation of territories with shrubs was significantly higher than non-territory points with shrubs (t = 2.74; df = 54; p = 0.008). Longspur territories were found as high up as the shrubs were found, with three territories located even above the shrub zone.

The habitat measuring points within territories were all found on mountain slopes with an orientation facing south, southwest, or west (Figure 4). A large proportion of the measuring points outside the territories had similar orientation, but the territories showed a significantly stronger connection to S, SW and W slope directions than the measuring points located outside of the territories (Likelihood ratio test of distributions in the nine directional sectors including the category «flat ground»; G = 54.39; df = 8; p < 0.001).

DISCUSSION

To our knowledge, the current study of breeding habitat characteristics in Lapland Longspurs is the first detailed investigation of its kind from the Western Palearctic. In addition to improving our understanding of the breeding ecology in focal species, such baseline information about breeding habitat use is important also for species management and conservation of birds (Petit 2000). Hence, our studies shed light on the drivers of recent severe population decline in
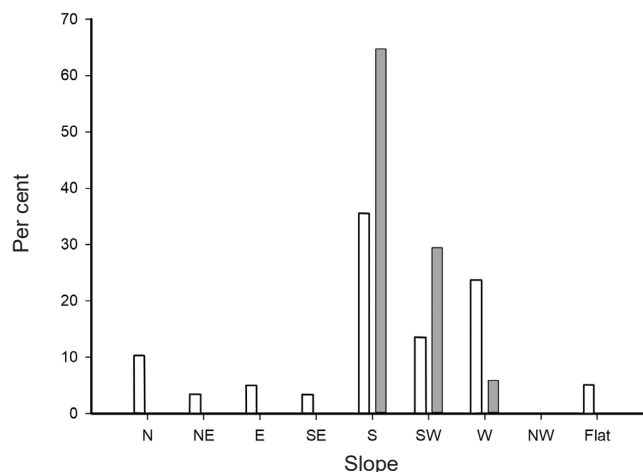

Figure 4. Aspect of ground slope at measuring points inside territories (grey bars) and distributed over the study area (open bars), recorded at the central point of each five-point unit (given as per cent).

Lapland Longspurs recorded throughout large parts of Fennoscandia. While our data are useful for testing existing hypotheses of the population decline, they also raise some important new questions about ecological change in mountain areas.

Interestingly, we found no support for the hypothesis proposed by Byrkjedal and Kålås (2012), that increases in lichen cover have had a negative effect on the territorial establishment of Lapland Longspurs. The recent years' increase in lichen cover on Hardangervidda might have less impact on the abundance of plants producing seeds fed on by Lapland Longspurs, particularly at an early phase of territorial establishment (Salomonsen 1950; Custer & Pitelka 1978; Byrkjedal et al. 2022). Actually, grounds with high coverage of seed producing plants were not found to be especially selected for as a territorial habitat component. The coverage of such plants was generally high with ≥ 50% coverage, which might be adequate for the birds to feed comfortably on early in the season. Lapland Longspurs often feed a distance away from their breeding territories (Drury 1961, Tryon & MacLean 1980, the authors pers. obs.) and thus may not be entirely dependent on the food inside their territories. Moreover, Lapland Longspurs rapidly increase the inclusion of invertebrates (Arthropoda) in their diet as the season progresses and thus shift their diet away from plant seeds (Haftorn 1971; Custer & Pitelka 1977, 1978).

A most striking result of this study was that the territories of Lapland Longspurs were situated at higher elevations in the study area. Instead of an even distribution over the study area, the territories were found along the highest part of the shrub zone, where the zone merges into the shrub-free and bare heath vegetation. The pattern might seem like a surprising result, as also the lower part of the study area earlier held breeding Lapland Longspurs in good numbers (the authors pers. obs.) and still had shrubs that might

Figure 5. Snow cover seen from the study area on the dates of 31 May, 4 June, 15 June, and 22 June 2016. Photos: Vegard Bang Fjeldheim.

seem appropriate for the species.

Increasing precipitation over the last decades due to climate change (Hanssen-Bauer et al. 2009) has caused an increase in snow depth in the mountains of western part of the Scandinavian Peninsula, leading to an increasingly later spring thaw (Dyrrdal et al. 2013). The lower parts of the study area are more sheltered than the upper parts which gradually merge into the exposed and windswept ridges. Variation in topography might lead to increased snow accumulation in the more sheltered hillsides and depressions of the study area, especially where shrubs are present. On the other hand, exposed, windswept ridges accumulate little snow during the winter, resulting in an earlier spring thaw where food plants as well as dry nesting ground appear earlier than in lower areas. The later thaw in the sheltered areas can result in snow covering the ground several weeks longer, and wetness as well as ice can remain longer in the ground. For the Lapland Longspur, persistent snow can lead to decreased area availability because snow cover in suitable habitats melts too late to allow a successful breeding attempt, and the only available breeding grounds are found close to the wind-swept upper parts. The longspurs' preference for south-facing slope directions facing the mid-day and afternoon sun supports the idea that early thaw is an important factor in the longspurs' territorial establishment. Sun-facing

orientation of Lapland Longspur nests has also been found elsewhere (Hussell and Montgomerie 2002, Boal & Andersen 2005). We suggest that the increased snow depth and increasingly later thaw over the last decades might, at least partly, explain the population decline of the species at Hardangervidda and other mountain regions of western Scandinavia (Lehikoinen et al. 2014; Stokke et al. 2021). Delayed breeding due to late thaw has been shown to have a negative effect on the clutch size of Lapland Longspurs in Greenland (Fox et al. 1987).

Two previous studies clearly demonstrate that the Lapland Longspur was a much more common bird species close to our study area than today. First, in the summer of 1978, censuses of breeding pairs of birds were conducted in a 4.4 km² area with its closest border about 500 m from our present study area, extending westwards on the same slope (Innes 1980). The area had an SSW aspect, an altitudinal range from 1075 to 1255 m a.s.l., and a habitat similar to that of our present study area. Shrubs were distributed over most of the plot but diminishing toward the higher areas of the study area. In this area, a total of 56.5 territories of Lapland Longspur were mapped, with a majority found in the willow shrub in the downhill part of the area, below the 1120 m elevation and well below the elevations at which the species nested in our study

area. Second, Bjørnsen (1988) studied the breeding behaviour of Lapland Longspurs in a lower part of the same area in 1986 and 1987 (50 ha plot 1080-1100 m a.s.l.) and found that the birds arrived during the first 10 days of May and laid eggs in the period 2–12 June. The species is nowadays virtually absent from both of these study plots, which retain substantial snow cover throughout most of June (the authors pers. obs.). A view of our study area and surroundings photographed from the same point 31 May, 4 June, 15 June, and 22 June 2016 gives an impression of the snow conditions at the time of Lapland Longspur establishment and nesting (Figure 5).

The increased snow cover in sheltered shrub-grown areas could have a negative effect also on other montane birds utilizing such habitat for breeding. Lehikoinen et al. (2014) reported declines among several species in the Scandinavian mountains, and the declines were most pronounced in the western parts of the mountains, which include the areas with increasing snow cover (Hanssen-Bauer et al. 2009, Dyrrdal et al. 2013). At Hardangervidda, declines of other common species, in particular Meadow Pipit *Anthus pratensis* and Northern Wheatear *Oenanthe oenanthe*, have also been recorded (Byrkjedal & Kålås 2012) but with a far less dramatic declines than the Lapland Longspur. Although sharing breeding habitat with the longspurs, the other species occur over a wider range of habitats (Lien et al. 1974, Østbye et al. 2002) and are thus presumably less affected than the longspurs by delayed snow cover. If an increased snow cover caused a decline in the Lapland Longspur population at Hardangervidda, we would expect the species to have decreased less in any mountain areas with stable or decreasing snow cover. However, this prediction remains to be tested. Since the species has declined throughout Norway in recent years (Stokke et al. 2021) it is possible that more than one factor has negatively affected the species.

While climate change predictions usually point at a gradually earlier uphill and poleward phenology, with a corresponding shift in flora and fauna (Cornelissen et al. 2001, Klanderud & Totland 2005, Hickling et al. 2006, Lenoir et al. 2008, Jägerbrand et al. 2009, Chen et al. 2011, Myers-Smith et al. 2011, Pauli et al. 2012, Tingley et al. 2012), the Scandinavian mountains, in particular the western parts, face an environmental change opposite to those predictions, involving increased snow cover and a delayed spring phenology over substantial areas. Changes in the environmental conditions could clearly have effects on alpine plants as well as animals, and the biological effect of increasing snow depth and accompanying phenological shifts in the mountains would be worth further study.

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Appendix 1. The different territories of Lapland Longspurs, the date of first territorial plotting sequence and the number of times mapping was conducted on each territory in the study area. The codes for territories are those used during the field work.

Territory number	Date of first territorial plotting	Total of mapping attempts
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 2. Median percent coverage of plant taxa for units of five 1 x 1 m quadrats in territories (n = 85 quadrats at 17 territories) and in UTM-defined squares distributed over the study area (n = 295 quadrats at 59 units). Plant taxa marked with an asterisk (*) include plants where seeds were found in stomach samples of Lapland Longspur from the same general area (Byrkjedal et al. 2022).

Taxon	Territory (T) Non-territory (N)	Median	Upper quartile	Lower quartile	Range
Lichens	N	26.0	34.9	10.6	0–58
	T	23.4	38.2	13	0–51.6
Bryophyta	N	5	12.3	0	0–46.6
	T	6	10	2	0–36
Huperzia apressa	N	0	0	0	0–0.4
	T	0	0	0	0
Diphasiastrum alpinum	N	0	0	0	0–0.4
	T	0	0	0	0
*Salix reticulata**	N	0	0	0	0–3
	T	0	0	0	0
Salix herbacea	N	0	0	0	0–52
	T	0	0	0	0–13
Salix excl.*herbacea* & *reticulata**	N	0	1.1	0	0–9
	T	0	2.4	0	0–18
*Betula nana**	N	4.8	18.2	0	0–71
	T	3	22	0	0–35
Vaccinium myrtillus	N	0	0	0	0–10
	T	0	0	0	0
*Empetrum nigrum**	N	14.2	22.6	7.2	0–48.2
	T	16.6	28.4	10.2	0–49.8
*Herbs**	N	1.8	8.8	0	0–30.4
	T	6.2	15.2	0	0–31.6
*Juncus trifidus**	N	0	0	0	0–5.6
	T	0	0	0	0
Trichophorum caespitosum	N	0	0	0	0–8
	T	0	0	0	0
Eriophorum spp.*	N	0	4.6	0	0–57.2
	T	0.4	7	0	0–22
Carex spp.*	N	4.8	9.1	1.5	0–27.2
	T	3	5.6	1	0.4–16.8
*Graminaeae**	N	0	5.5	0	0–34.2
	T	0	6.2	0	0–17.6
Nardus stricta	N	9.4	20.9	1.4	0–48.2
	T	6	23.8	1.6	0–50