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of Life Sciences

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Faculty of Environmental Sciences and Natural Resource Management

# **Habitat Selection and Temporal Trends in Elevational Occurrence and Population Size of an Alpine Bird (*Eremophila alpestris*)**

Habitatvalg og tidseffekter på høydeforskyvninger og  
populasjonsstørrelsen hos fjellerke

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## Preface

This master thesis concludes five years of study within ecology and natural resource management at the Norwegian University of Life Sciences. During the MSc program in natural resource management, I selected this project because of my interest in population ecology and alpine regions. Through this project I have acquired valuable knowledge about the effects of changes in the mountain for alpine birds, and what problems may come for managers in the future.

I would like to thank my supervisor, Svein Dale, who contributed greatly to fieldwork, guided me through this project, provided great advice and was always present when I needed guidance. A special thanks also to Axel Brevig-Edfeldt for cooperation in field. I would also like to thank the County Governor of Trøndelag and Ola Bekkens fuglevernfond who financially supported this project. As well as the Norwegian Wild Reindeer Center at Hjerkin for accommodation in field, Roar Økseter at NMBU for GIS guidance and fellow students and family for discussions and feedback on the thesis.

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## Abstract

The global climate is changing, and this forces avifauna, vegetation, insects, and other animal species to shift their distribution towards higher elevation and latitude. These shifts can lead to population decreases and could be one of the causes of the observed declines in avifauna. The horned lark (*Eremophila alpestris*) is reportedly not in decline in Norway, but declines have been observed in some areas and neighbouring countries, and with limited data the population trend is uncertain. To assess the habitat preference and if there has been elevational shifts and changes in population size, 44 sites were surveyed in the region of Dovre in the breeding season (May-June). Further, citizen data from the Norwegian Biodiversity Information Centre were used to analyse elevational changes over time between 1971 and 2021 and population size between 2007 and 2021. In addition, two reports were used to compare the findings of this study to older surveys from the region. Habitat analyses showed that horned larks preferred nutrient-rich sites with moderate grazing, where a high density of sheep had negative effects. The elevational analyses showed that there has been an elevational shift of 2.17 m upwards per year since 1971 and 3.65 m/year since 2008 for southern Norway. Significant changes were also observed for a selection of surveyed study sites in Grimsdalen (1969 mean = 1337 m, 2022 mean = 1426 m) and in Einunndalen (1992 mean = 1337 m, 2022 mean = 1414 m). The population has been stable between 2007 and 2021, but with elevational shifts the available and preferred habitats will decrease over time. Managers should also note the importance of grazing and regulate this in the mountains to keep open grasslands in alpine regions. Climate change and associated changes in alpine habitats is likely to change the population trend of the horned lark and should be monitored for potential population decreases.



## Sammendrag

Klimaet er i endring og dette fører til at fugl og andre artsgrupper endrer utbredelse mot polene og forflytter seg høyere i terrenget. Disse endringene fører til nedgang i habitat og er antatt å være en av grunnene til de globale nedgangene i fuglepopulasjoner. Bestanden av fjellerke er ukjent, og det har både blitt rapportert nedgang og oppgang i Norge. For å innhente mer kunnskap om, og avdekke habitatpreferanser, samt mulige endring i foretrukket høyde og populasjonstrenden hos fjellerke, ble 44 områder taksert på Dovrefjell i hekkeperioden for fjellerke i 2022 (mai-juni). Videre ble også data fra Artsobservasjoner.no og tidligere rapporter brukt for å lage tidsserier for høyde mellom 1971–2021 og bestand mellom 2007–2021. Habitatanalysen som ble utført viste at fjellerka foretrekker intermediære og kalkrike områder med moderat beiting. Det har vært en forskyvning i høyde for fjellerka med 2.17 m/år siden 1971 og 3.65 m/år siden 2008. Det ble i tillegg observert signifikante forskjeller mellom feltobservasjoner fra Grimsdalen (1969 gjennomsnitt = 1337 m, 2022 gj. snitt = 1426 m) og i Einunndalen (1992 gj. snitt = 1337 m, 2022 gj. snitt = 1414 m). Populasjonen av fjellerke på Dovrefjell har vært stabil siden 2007, men med endring i foretrukket høyde vil det gradvis bli mindre tilgjengelig habitat. Derfor er det viktig at forvaltningen regulerer beiting i høyfjellet og forhindrer både gjengroing og degradering av alpine gressheier. Videre er det vesentlig at bestanden av fjellerke blir overvåket for eventuelle nedganger som følge av endring i klima og menneskers bruk av fjellet.





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## Introduction

The global climate is changing, and this affects wildlife and flora all around the world (Parmesan & Yohe, 2003). Climate change has led to higher temperatures, which forces species to adapt by changing their distribution towards higher elevation and latitudes (Chen et al., 2011; Walther et al., 2002). Higher temperatures have also led to higher primary production or “greening” of alpine and arctic biomes (Myers-Smith et al., 2020; Rumpf et al., 2022), which can threaten the species that naturally occur in these areas (Post et al., 2009). The relative abundance of wildlife populations has decreased with 69% on average between 1970 and 2018 mainly because of the change in land use, however, if the global warming is not limited to 1.5°C, climate change can be the dominant cause for biodiversity loss (WWF, 2022).

In alpine regions, the rate of warming has been twice the global average (Brunetti et al., 2009). This can have severe effects for species living in their upper margins of latitude or elevational occurrence (Theurillat & Guisan, 2001), because they gradually will get less available habitat if they move up in elevation (Chamberlain et al., 2016a; Freeman et al., 2018). Studying elevational shifts is relevant because mountain regions often represent biodiversity hotspots and are vulnerable ecosystems. In mountain regions there has already been evidence for upward shifts in vegetational zones and changing plant communities (Pauli et al., 2012; Vitasse et al., 2021) as well as upslope shifts for mountain birds (Couet et al., 2022; Flousek et al., 2015; Freeman et al., 2018; Hallman et al., 2022; Liang et al., 2021; Neate-Clegg et al., 2021; Pernollet et al., 2015). This could lead to population declines and potentially extinction (Sekercioglu et al., 2008; Thomas et al., 2004). Climate change is therefore now considered one of the major threats for the abundance of mountain birds (Chamberlain et al., 2016b).

Avifauna is declining in both Europe (Inger et al., 2015) and North America (Rosenberg et al., 2019). Declines in mountain birds have been recorded (Lehikoinen et al., 2019), while most declines are observed for common species (Byrkjedal & Kålås, 2012; Lehikoinen et al., 2014), the specialists that only breed in mountain areas will face population declines (Scridel et al., 2018). These declines could be caused by elevational shifts and loss of habitat (Maggini et al., 2011; Pernollet et al., 2015; Popy et al., 2010), but not all studies show these trends

(Archaux, 2004). The declining populations could also be a consequence of altered grazing regimes (Laiolo et al., 2004), or the increasing disturbance from human activities (Chamberlain et al., 2016b). While many studies have looked at climate change as the main driver for changes in distribution, other drivers should not be overlooked, and it is important to incorporate habitat change as a main driver together with climate (Chamberlain et al., 2016a).

Changes in climate leads to treeline shifts (Harsch et al., 2009) and altered habitat for alpine birds (Ferrarini et al., 2017). The impacts on alpine birds from upward treeline shifts could be significant (Sekercioglu et al., 2008). Climate is an important driver of treeline shifts, but the elevating treeline could also be explained by increased land abandonment and changed agricultural practices (Laiolo et al., 2004). In Norway, the agricultural use of the mountains has strongly decreased since 1900 (Stensgaard, 2017). Land abandonment and decreasing agricultural use of mountain areas leads to less grazing and thereby more shrubs and trees instead of alpine grasslands. A study from the Italian alps showed that bird species that prefer open grasslands will have a decrease in distribution with an increase in shrubland and forest (Chamberlain et al., 2013). Altered habitats in higher elevation due to warmer climate and less agriculture in combination with less available area at higher elevations will lead to less available habitat for alpine birds (Byrkjedal & Kålås, 2012), and it is claimed that a lot of alpine habitats will disappear between 2041-2060 (de Gabriel Hernando et al., 2021).

Habitat suitability is mainly limited by climatic factors (de Gabriel Hernando et al., 2021), but the presence of a habitat is strongly affected by several drivers. Alpine habitats have an absence of shading objects like trees and shrubs, and therefore factors like solar radiation and wind exposure determined by the terrain, play a greater role in the species compositions. Southern and eastern slopes have higher species numbers, mainly because they have a longer solar exposure and because of the leeward position from the prevailing westerly winds (Winkler et al., 2016). In addition, the same study found that eastern slopes would be thermally more favourable for vegetation compared with western oriented slopes. But these effects are more even in boreal and arctic areas, due to the longer days at low sun angles in higher latitude towards the pole.

Environmental factors such as microclimate are important drivers for community composition in alpine meadows (Li et al., 2011), but the vegetation compositions are also reflected by the

local bedrock type and fine-scale heterogeneity (Batllori et al., 2009). In the European Alps, plant cover has increased on calcareous mountaintops the last fourteen years, while the richness has decreased, mainly due to competition (Nicklas et al., 2021). In the Dovre region in Norway the species richness increased between 2001 and 2008, and changes in species composition were observed on the lowest summits (Holten et al., 2009). Bedrock geochemistry can also determine plant productivity through nutrient availability (Hahm et al., 2014). Therefore, both slope aspect, changing microclimates and bedrock are important in determining possible habitats for alpine birds.

The horned lark (*Eremophila alpestris*) is the only lark species to have successfully colonized tundra and alpine habitats. The preferred habitat contains barren terrain with short vegetation like lichen, grass, or heather (Stueflotten, 1994). Therefore, it mainly breeds in arctic tundra, barren steppes, dry stony patches in lichen tundra, high mountain areas and arctic-alpine zones (Cramp, 1988). Because the horned lark occurs in areas with high elevation, topographic isolation could have fragmenting effects and determine territory occurrence. But also, human presence in form of recreational trails or expansions of cabin areas could fragment the habitats of horned lark and other alpine birds. Studies on forest birds in France have found effects on territory occurrence from human recreational disturbances, but these effects were minimal on ground breeding birds (Bötsch et al., 2017). A vulnerability matrix conducted on 180 bird species living in Subarctic and Arctic areas selected the horned lark as a species that may need extra conservation attention (Hof et al., 2017). According to the IUCN red list assessments, the biggest threat towards the horned lark globally is agriculture abandonment (BirdLife International, 2021a), while in Europe, livestock farming and ranching is the main threat (BirdLife International, 2021b). In the Norwegian and Swedish Red Lists, declining food abundance in the winter areas, as observed by Dierschke and Barlein (2002) is mentioned as the main threat, while climate, predation and toxins are mentioned as possible additions where research is scarce (Artdatabanken, 2020; Stokke et al., 2021a).

Declines have been recorded for horned lark, but the global declines are not sufficiently rapid enough for the species to be categorized as threatened (BirdLife International, 2022), therefore it is categorized as least concern (LC) on the International Red List (BirdLife International, 2021a). According to the Norwegian Red List the horned lark is not in decline and has in contrary to many mountain birds shown a small increase the last years (Stokke et

al., 2021a). Recordings from Arctic breeding grounds in Norway has shown decreases in both Troms (Strann & Bakken, 2004) and Finnmark (Frantzen et al., 1991), while newer studies from Hardangervidda and Finnmark shows an increase in alpine populations of horned lark (Byrkjedal & Högstedt, 2022). The populations in alpine areas in Southern Norway have rarely shown noted declines, but according to Stueflotten (1994) there might have been some declines in the Dovre area. The population in Sweden has been stable the last years (Wirdheim & Green, 2022), after showing a massive decline for a longer period which resulted in the red list category vulnerable (VU) (Artdatabanken, 2020). Whilst the population in Finland is at a record low (Hyvärinen et al., 2019), after decades with rapid declines (Hildèn, 1987). The declines in Finland have been believed to be due to overgrazing of lichen by reindeer (*Rangifer tarandus*) (Donald & de Juana, 2014). The data for Norway is scarce, and a comprehensive study is needed to get a better image of the distribution and population trend of the horned lark. In addition, new knowledge on species distribution and abundance along altitudinal transects for mountain birds would be useful for managers to predict future endangered species, and how they might be affected by the changing climate (Chamberlain et al., 2012).

Here, line transects were conducted to assess horned lark distribution and abundance in the regions of Dovre, Oppdal and Folldal. The recordings are used to analyse habitat selection, based on the bedrock richness, grazing species and density, as well as geographical and field effort variables. To check for possible elevational shifts, which may be expected, the observed heights are compared to earlier observations for Grimsdalen in Spjøtvoll (1970) and Einunndalen from Svendsen (1997). In addition, citizen data from the Norwegian Biodiversity Information Centre (artsobservasjoner.no) will be used to analyse the elevational occurrence for all mountain areas in southern Norway from 1971 to 2021. Possible elevational shifts could also lead to decreases in abundance and therefore a decrease in abundance could be expected. The same database is used to analyse changes in population size for Dovre, as well as using the old recordings to check distribution across time in the different areas. Habitat analyses will be important to understand the possible future effects on the bird from a changing climate and human land use. Compared to findings from other areas an elevational shift could be expected for the horned lark and the data from our analyses will be important to determining if Norwegian birds are facing the same shifts as observed in Europe. Since the data on the population size is scarce, our findings should contribute towards a more accurate understanding of the size and trend for the population of horned lark in Norway.

## Materials and methods

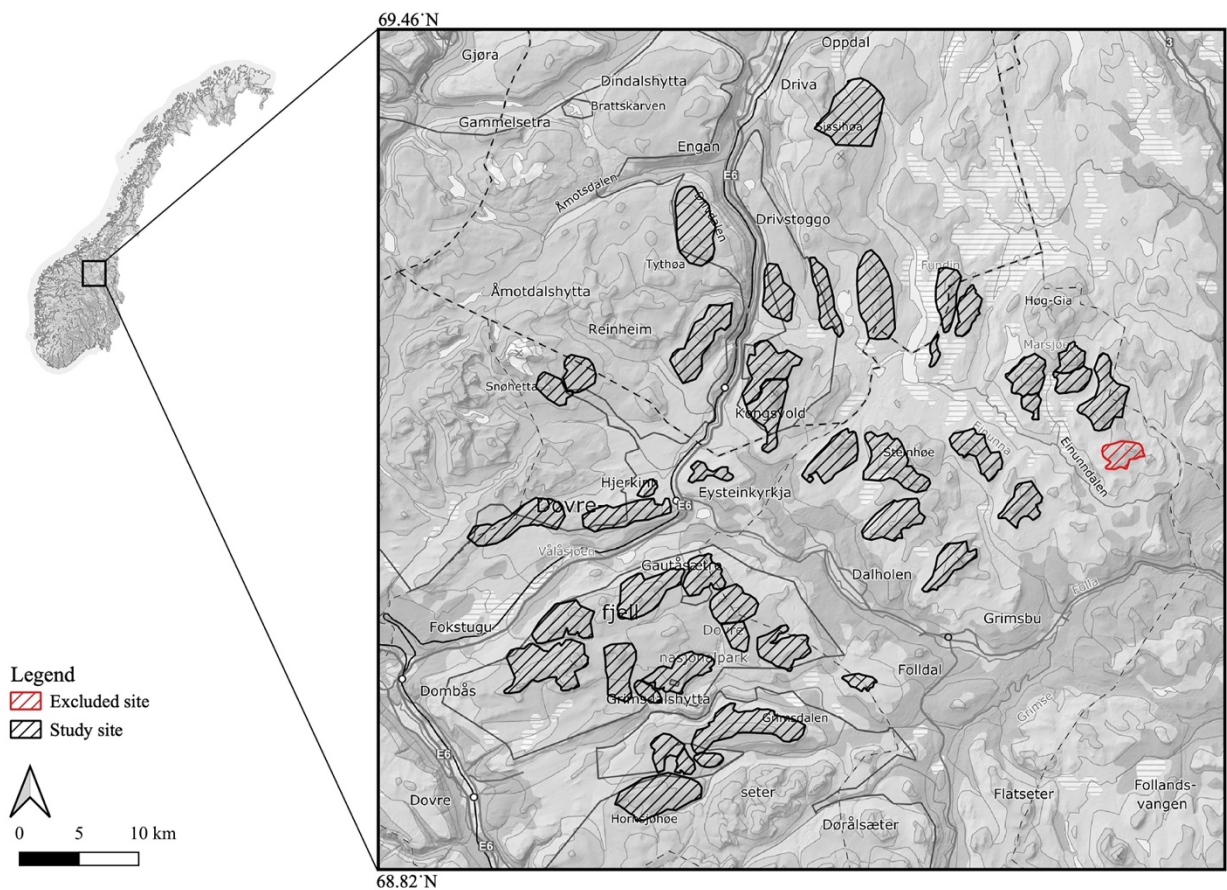
### Study area

The study was conducted in the north-eastern part of southern Norway. Specifically, the study area included the municipalities Dovre, Folldal and Oppdal in the counties of Innlandet and Trøndelag. In addition, two study sites were partly located in Tynset and Lesja municipalities (figure 1). The study area covered different mountains and alpine plateaus in the Dovrefjell-Rondane region. Some of the data collection took place in Rondane national park, Dovre national park and Dovrefjell- Sundalsfjella national park, preserved for their importance in protecting alpine flora and fauna in Norway (Norwegian Environmental Agency, 2023). Parts of the area were part of the biggest nature restoration project in Norway, and the region is especially important for the threatened populations of wild reindeer and arctic fox (*Vulpes lagopus*) (Hagen et al., 2022). The area is also important for alpine birds and with the large number of mountaintops and alpine plateaus we have selected this area because it is the preferred habitat for horned lark during their breeding season and there exists citizen and transect data from earlier years.

The climate in Dovre is strongly affected by the inland position of the region and is categorized as continental with little precipitation. Due to the elevation, the winters are cold, and summers mild. Dovre is exposed to heavy winds and the summer temperature therefore rarely exceeds 20°C with a mean temperature at Hjerkinn (1012 m a.s.l.) in June and July being 10°C in 2022 (Meteorologisk institutt, 2023). The bedrock in the Dovre area is separated into two; the western part with Precambrian gneisses and granites and the eastern part with Cambro-Silurian rocks (Thorsnæs & Askheim, 2021). The western part contains mostly of granite, gneiss, quartzite and sparagmite, and is characterized by high mountaintops (Thorsnæs & Askheim, 2021). The eastern part on the other hand has a flatter topography containing phyllite and tonalites (Thorsnæs & Askheim, 2021). The calcareous bedrock has led to the presence of threatened habitats, both strongly calcareous boreal heaths and calcareous peatlands has been mapped in the area (Norwegian Environmental Agency, 2022) and the area is therefore well known for being nutrition rich with numerous red-listed and endemic plants (Norwegian Environmental Agency, 2023).

We selected 45 study sites based on the existing citizen data for many of the sites and based

on height and placement of the mountain (figure 1). Ten of the study sites are selected because Spjøtvoll (1970) surveyed them in 1969 and four of them was again visited by Sonerud (1982) in the period 1977-1980. In addition, eight further sites had historical data from Svendsen (1997) in 1992 and were therefore included. All sites were defined from the 1200 m contour line and upwards and covers the whole mountaintop. For some sites there were access restrictions, or the lowest elevations overlapped and therefore some study sites started at a higher elevation up to 1460 m (a.s.l.). The sites varied in size from 1.33 km<sup>2</sup> to 21.69 km<sup>2</sup>. Several mountaintops have been divided into two sites because of their size, and then they have been separated along the watershed, or north-south. All sites were in areas where the occurrence of horned lark was regarded to be likely, but we have tried to cover different areas with diverse nutritional richness.



*Figure 1: Map over the sites for data collection marked in black, and the excluded site marked in red (see details in the paragraph Field surveys). The field work was conducted in the Dovrefjell region, located in inland Norway in the counties of Innlandet and Trøndelag. Map made in QGIS 3.8 with EU89 UTM33 as coordinate system.*



## Study species

The horned lark (formerly called shore lark) is an alpine bird with a global distribution covering all continents in the northern hemisphere (Beason, 2020). In Northern Europe it is a migratory bird and breeds in the mountains of Fennoscandia (Cramp, 1988). The horned lark is cryptically coloured with a yellow face and black band across its breast as seen in figure 2 (Haftorn, 1971), but gets its name from the small horns above the eyes found on male adults (Cramp, 1988). It usually arrives to the breeding areas during the end of April and egg laying can start as early as May but is usually during June. As one of very few alpine birds, the horned lark can have two broods a year and the generation length is three years (Cramp, 1988). The clutch size varies between one to eight eggs, but mostly they lay between two and five, and the clutch size can increase with latitude (Donald & de Juana, 2014). In September or October, it leaves the mountain areas and migrates south, some individuals can spend the winter in southern Norway, whilst most go further south around the North Sea, typically to the Wadden Sea (Dierschke, 2001; Svensson, 1997).



*Figure 2: Cryptically coloured horned larks (Eremophila alpestris) where one can see similar colours in the rock, grass, and lichen from the study site Finnshøa in Oppdal. Photo: Oscar Østvold*

The preferred habitat for horned lark in Norway is barren mountain plateaus in gradual inclinations preferably with little vegetation containing lichen, moss, or grass species (Haftorn, 1971). Typically, the horned lark is found between 1200-1400 meters above sea level (m a.s.l.), but it can range from 1000 m and upwards to the mountaintops, with the highest observation in this area being a sighting in 1946 on the Rondslottet mountaintop which is 2178 m (Spjøtvoll, 1970). Inclining mountain plateaus are thought to be preferred for nesting because they lose snow cover early (MacDonald et al., 2016). The nest is typically in open places like natural depressions on the ground in areas with low vegetation (Haftorn, 1971). Typically, the nest is made of woven plant material and feathers or other fine

materials, and is then surrounded by stones, bark, earth, animal dung and other materials (Donald & de Juana, 2014). The selected materials and position of the nest is to reduce the wind flow and in warmer regions to maximize shade (With & Webb, 1993). The preferred diet consists mostly of insects but can also be supplemented by seeds and moss spores (Byrkjedal et al., 2022), while they mostly eat seeds during winter (Dierschke, 2002).

Since the horned lark breeds scattered in alpine areas that often are difficult to access, the habitats are rarely visited. The horned lark is therefore often overlooked and underreported, which makes the population size uncertain. In the municipality of Oppdal the population has earlier been declared as vulnerable with approximately 50-100 breeding pairs (Opheim, 1998), while the population around Grimsdalen was estimated to be around 100 pairs (Sonerud, 1982). The Norwegian population has been estimated to be between 2000-3000 individuals (Shimmings & Øien, 2015). This is a reduction from earlier assumptions of up to 20 000 individuals (Stueflotten, 1994), which could be explained by unfavourable conditions in the overwintering areas in northern mainland Europe (Hildèn, 1987).

## Field surveys

The field surveys were conducted from 23 May – 29 June 2022, and the 45 sites were visited over a period of 27 days. In this period a total of 435.75 kilometres was covered in a total of 143 hours. The mean distance covered per site was 9.8 kilometres (2.2-18.3 km), while the mean time used was 192 minutes (33-360 min). In addition, a total of 17 876 elevational meters were covered inside the study sites. Further details on each site are reported in table A1. One of the sites (Snøfonnhøa, marked in red in figure 1) was excluded from the analyses because of non-optimal weather for observing birds and locate horned larks. Several other sites had bad weather as well (fog, snow or rain and wind), but here we managed to register all the other usual species for these areas and therefore these sites were included. This can potentially lead to some noise in the data but are not likely to affect the main findings of the research.

The master thesis is an observational field study where we conducted line transects in selected sites across the region. The transects were walked as a route in the site with the highest point being roughly in the middle of the route to avoid replicated observations (figure 3A). When we were more than one observer, we tried to cover wider areas as shown in figure 3B, to cover as much of the site as possible. All observations regardless of the distance from the observer were recorded. We started at 1200 m a.s.l. or higher, depending mainly on topography. In addition, we started to note observations of horned lark before we reached the 1200-meter line from 1000 m a.s.l., to detect any individuals below

the defined sites. All tracking data was recorded with a Garmin Instinct watch or the Strava application, and almost all the transect routes are available on Strava ([www.strava.com](http://www.strava.com)). The coordinates of observations were set using a GPS watch or with the application “Norgeskart friluftsliv” on our phones.

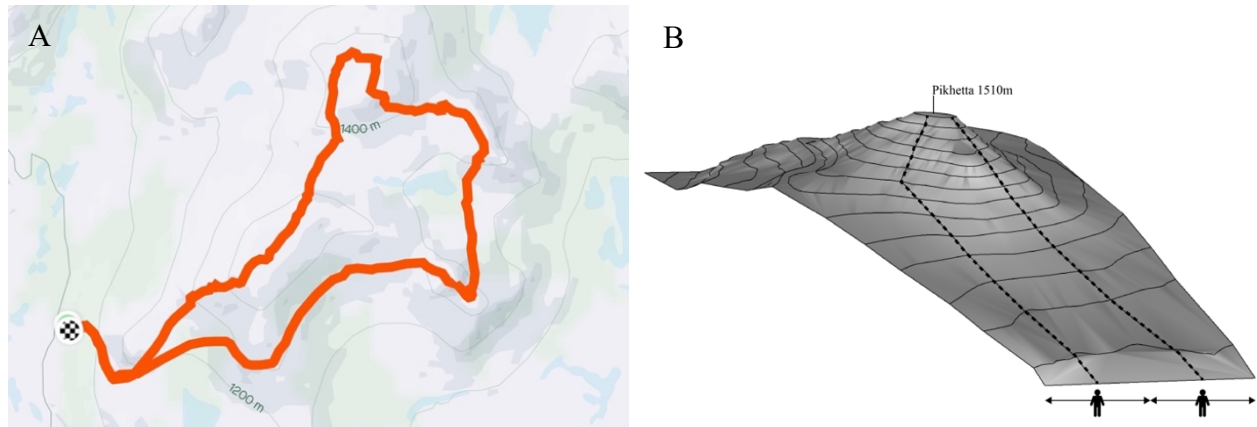


Figure 3: A: Map over one of the sites (Fatfjellet- Skardhøa) and how the transect ended up being, to cover all hillsides and as much area as possible without overlap. Figure is output from Strava. B: Illustration of how the recording of horned larks (*Eremophila alpestris*) could be conducted to cover more area of the hill. Made in Adobe Illustrator.

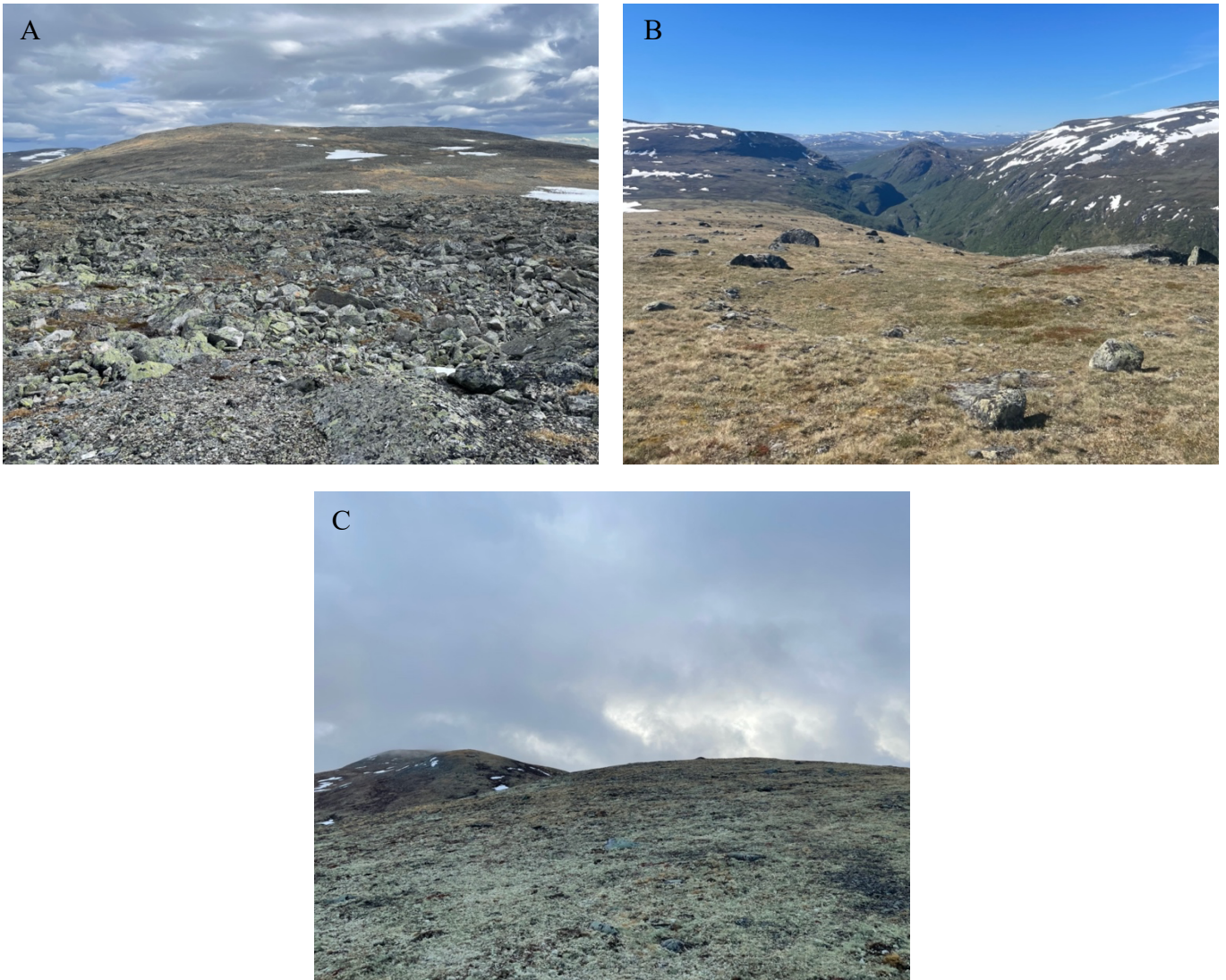
As well as the number of individuals, the behaviour (singing, calling, silent etc.), coordinates, meters above sea level, time of observation and date was noted for each observation. The start time was between 0430 h and 1223 h, with the mean start time being 0630 h. We detected birds both by song/call and by visual detection with binoculars or telescope, if several calls were heard simultaneously from different directions, these were thoroughly checked for the possibility of two territories but could often be one pair. If several songs were heard simultaneously, they were classified as different territories. All observations of horned lark, including other interesting species were uploaded in the citizen data database “Artsobservasjoner.no” to make it accessible for later studies. In addition, plant species characterized for calcareous bedrock, vegetation cover, the weather, and observations of grazing species (based on sightings and excrements) were recorded for each site. As grazing species ordinary livestock like domestic sheep (*Ovis aries*), cow (*Bos taurus*) and goat (*Capra aegagrus hircus*) were recorded, in addition, reindeer and muskox (*Ovibos moschatus*) were included as grazing species because they are abundant in at least parts of the area. The free and open-source geographical information system QGIS 3.8 was used to plot coordinates and to find the radial aspect of all observations.

## Habitat variables

To extract geographic data from the study sites for analyses the program QGIS 3.8 was used. I calculated the isolation of each habitat by measuring the distance in kilometres between the highest point of the studied site to the mountaintop (highest point) of the nearest possible habitat, in many cases these were also study sites. The area of the study sites in square kilometres and highest point of the study site was also extracted.

Data over the bedrock and nutritional richness in the sites for analyses were found using the Norwegian map service “Økologiske grunnkart” by the Norwegian Biodiversity Information Centre (*Økologiske grunnkart*, 2017). The layer is called “Kalkinnhold berggrunn” and is under the Norwegian Licence for Open Government Data (NLOD) made available by Geological Survey of Norway (NGU). The data was used to create the factorised variable ‘bedrock richness’ with the groups: “poor”, “intermediate” and “rich”, based on the labels from the layer. As seen in figure 4 the vegetation cover and species composition vary between the groups.

Data over grazing species was collected by sightings as mentioned earlier and cross checked with the species information in the layer “Beitelagskart” in the map service “Kilden” (*Beitelagskart*, 2021). The same map service was also used to extract density data for sheep called sheep per km<sup>2</sup>, which describes the density of grazing in each site (*Beitelagskart*, 2021). Here the density of sheep is recorded inside selected “sheep areas”, which is the area that one farmer or collective uses for grazing. In our study area there were 16 different sheep areas, which means that some study sites will have the same density value. On average one “sheep area” covers 2.6 study sites. Three study sites were not covered by a sheep area, which indicates that there is not grazing by ordinary livestock there, although this could not be confirmed, and they are therefore included in analyses without a value as NA.



*Figure 4: Habitats of the horned lark (*Eremophila alpestris*), represented by the nutrient poor site Nystugguhøa, Oppdal (A), intermediate site Finnshøa, Oppdal (B), and calcareous rich site Sletthøe, Folldal (C). Photo: Oscar Østvold*

## Historical data

To assess changes in elevational occurrence and population size, historical records from the Norwegian Biodiversity Information Centre ([artsobservasjoner.no](http://artsobservasjoner.no)) were collected. This website contains sightings of species made by private persons and professional ornithologists. Most of the bird registrations are made by members of Birdlife and can be trusted as valid registrations. For the elevational analyses all sightings between May and July in Southern Norway (counties of Agder, Vestfold and Telemark, Viken, Innlandet, Rogaland, Vestlandet, Møre and Romsdal, and Trøndelag) were included. To extract height data of historical observations a Digital Elevation Model (DEM) was used in QGIS. The coordinates of the observations were placed in a DEM to find the elevational

position in meters. All sightings below 900 m a.s.l. were excluded to avoid potential non-breeding observations. This resulted in 1632 observations between 1971 and 2021. Data from 2022 were not included to avoid our own observations which may potentially be biased towards higher elevations, due to our systematic surveys. In addition, our own field data was compared to the older recordings from two valleys with ten sites in Grimsdalen from 1969 (Spjøtvoll, 1970) and eight sites in Einunndalen from 1992 (Svendsen, 1997) to see if the trend from Southern Norway also occurred within our study area.

To see if there has been changes in population size within our study sites, both historical survey data and citizen data were analyzed. Spjøtvoll (1970) has data for the period 1968-1970, but only data from the year 1969 was used because this is the only year when a thorough survey was conducted. The ten sites from Spjøtvoll (1970) in Grimsdalen were compared to our own field data, in addition to the eight sites from Svendsen (1997) in Einunndalen from 1989-1992. Citizen data from [artsobservasjoner.no](http://artsobservasjoner.no) in the periods 2000-2021 (n= 231) and 2007-2021 (n= 189) were used to analyze the population trend for all 45 sites. Negative reports for the analyses were included and selected based on reports that included at least two other alpine bird species that live in the same elevational area. Reports that only included raptors or rare species were considered likely to have omitted sightings of other birds such as the horned lark, and therefore not included as negative observations.

## Statistical analysis

The observed heights of horned lark territories were plotted as a histogram to see the elevational range. To check if any observations were beneath the study sites and how many territories there were per km, the observed heights were then separated into the elevational ranges from the field survey and territory per km was calculated. The differentiation between the observed heights and the height of the highest point in the site was calculated to check how far from the elevational limit the horned lark occurs. Further, the aspect of each observation was plotted as a radial plot with the cardinal directions as x-axis, and the number of occurrences as y-axis. The significance of the aspect-variable was found with a chi-squared test.

For the habitat selection analyses, several variables have been recorded and used in different stages of analyses. The response variable for occurrence and habitat selection analyses was the number of territories recorded per site during surveys in 2022. The predictor variables were as listed in table A2: max height, time used, distance, area, isolation, sheep per km<sup>2</sup>, livestock, bedrock richness, observers, and mean height. Maximum height is the elevation (m a.s.l.) of the highest point in the study site.

Time used is the time spent in each study site above the 1200 m contour line and is recorded in minutes, this means that the time spent up to 1200 m was not included in this variable. Distance is the distance covered by foot in each site and recorded in km. The variables area and isolation are recorded in QGIS as described in 'Data collection and historical data'. The isolation variable was log transformed to deal with a skewed distribution. Sheep per km<sup>2</sup> was extracted as described earlier and log transformed because the distribution was skewed. Livestock is the number of different grazing species in each site, sorted into two groups of "2 species" and "3 species" (few sites had more than three species present, and these were included in the group "3", all sites had at least two species). The variable 'bedrock richness' is divided into three groups based on the levels of calcareousness "poor", "intermediate", and "rich". The variable 'observers' is included instead of date because there were different efforts for each date and in each site, therefore the sites have been divided into three groups ('1', '2', '3') based on how many observers there were in each site. In addition, a variable called mean height was included to analyse relations between our observational heights of horned lark and grazing density and if this varied in height, here the average height of territories was calculated for each study site and the sites without observations of horned lark were excluded.

Predictor variables were checked for collinearity. For the variables "time used" and "distance covered" the correlation value was 0.91 and therefore the variable "distance" was excluded from the analyses because "time used" has significant effects and was concluded to be a more correct measurement of effort. The variables "height of mountaintop" and "area" correlated with a value of 0.66, this is not too high to exclude one, but should be kept in mind when analysing the data. The numerical variables are analysed towards the number of territories with a linear regression to see the relationship before finding the best model for habitat selection. For the categorical variables "Bedrock richness", "Livestock" and "Number of observers", ANOVA analyses were used. Since the ANOVA gave significant results, a Tukey post hoc test was conducted to see the significance and differences between the different groups. To assess which variables describe the habitat preferences a general linear model (GLM) with a Poisson distribution was conducted, with all variables included in the model. StepAIC from the R package 'MASS' (Venables & Ripley, 2002) was used to find the best fitting model according to significant effects on the number of territories and lowest AIC, see table A4 for all the AIC values. The number of territories were used as response and the best fitting model is presented with predictions based on our data.

To see if there has been an elevational shift for the distribution of horned lark, a Welch Two Sample t-test between the two time periods on the observed height variable for Grimsdalen and Einunndalen was conducted. A linear regression based on citizen data in the period 1970-2021 was also conducted

to assess the rate of change for Southern Norway with region as a random factor (same regions as in figure A4). Since the citizen data website was launched in 2008, there is much more data from that year and onwards compared to before 2008. Therefore, the same linear regression was conducted for the period 2008-2021 as well. Data from 2022 were not included to avoid potential noise by our own observations uploaded to the database. Additional analyses were made to strengthen the results of a possible elevation shift. Data for horned lark was compared to data for the species snow bunting (*Plectrophenax nivalis*) and rock ptarmigan (*Lagopus muta*) (figure A2), this to further investigate if the lack of higher observations of the horned lark was due to the observer's lacking presence in high elevation or is representative data. The elevational shift was also checked for regional variances between the counties (figure A3) and the regions have been checked for any possible trend shifts in where birders have made observations (figure A4).

To analyse the population changes I used the package 'rtrim' (Bogaart et al., 2018) which is a package that is specialized on time series of population counts. Here a Poisson regression is used to make linear models for time series with missing observations for some years. The model 2 was chosen because it generates indexes per year and assumes that it is the same growth rate for each site regardless of varying populations across sites. The only demands are that each site needs to have observations for minimum two years. In this way the populations can vary between sites, but it will still generate a growth rate for every area regardless of missing counts for some sites for some years. Data from 2007 to 2021 for our study sites in Dovre was used in the trim because that is the period with most citizen data, but a trim was also conducted for the period 2000 to 2021, to check for a longer period (figure A5). In addition to the trim, a two-sample t-test was conducted for both Grimsdalen (1969 vs. 2022) and Einunndalen (1992 vs. 2022) to check for the same population trends based on field surveys instead of citizen data. The statistical analyses in this thesis were conducted using R Statistical Software version "R.3.6.1 GUI 1.70 El Capitan build" or newer (R Core Team, 2021).





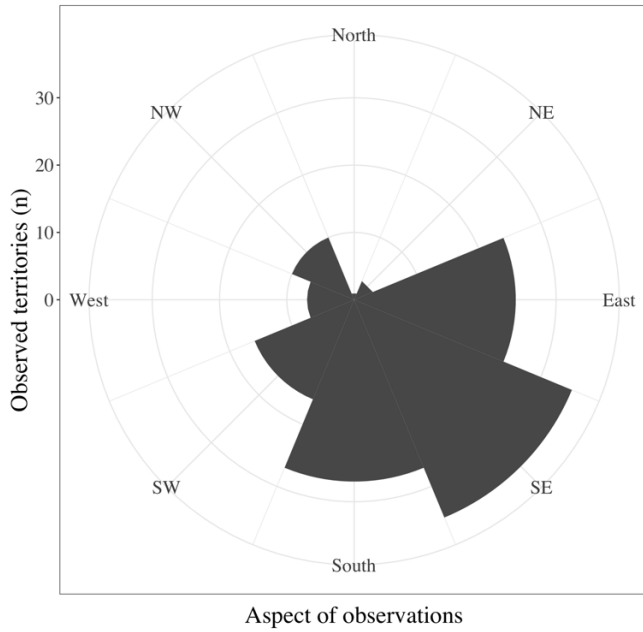


Figure 4: Density of observed horned lark (*Eremophila alpestris*) in the representative slope aspects in the Dovre region, y-axis is the number of observed territories.

The mean observational height was 1430 m a.s.l. (figure 7A) (table A3; SD = 87.22, SE = 7.42) with only one observation being below 1200 m a.s.l. (figure 7B). The density of territories inside the survey interval (1200-1700) was 0.28 per kilometre (figure 7B), and the median difference between the maximum height of the peak and elevation of each territory was 90 meters (figure 8).

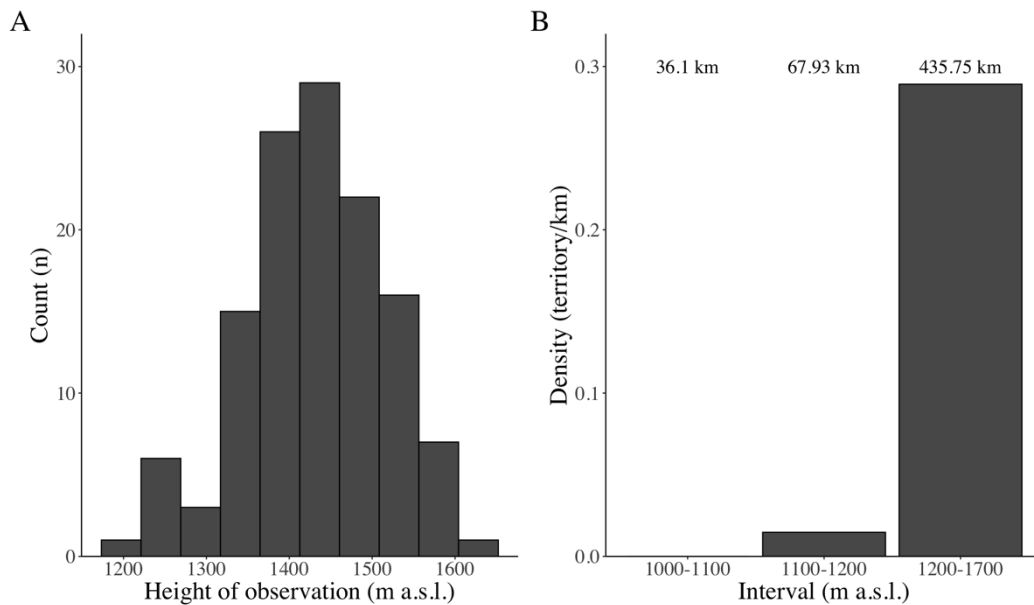


Figure 5: A. Histogram over the distribution of observed heights of horned lark (*Eremophila alpestris*) during field surveys in the region of Dovre in 2022. B. The density of territories of horned lark (*Eremophila alpestris*) per kilometres covered inside the three elevational intervals shown as a bar chart. Annotation is the total distance covered inside the intervals.

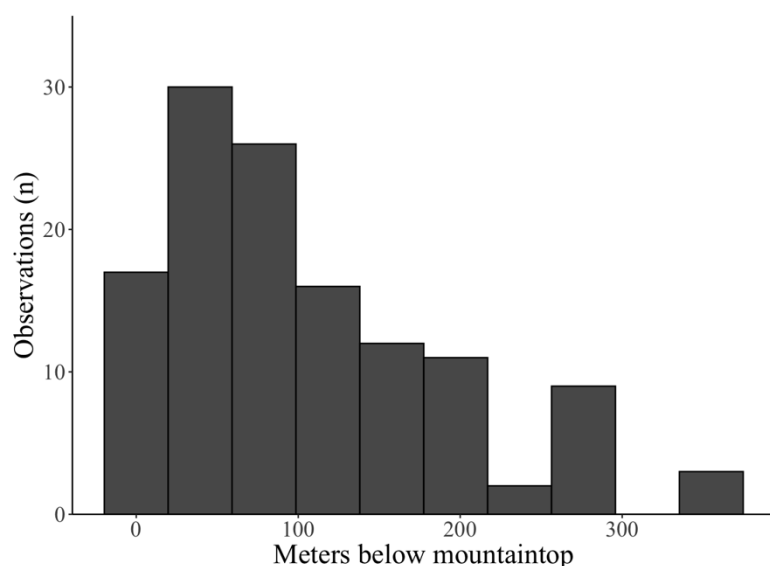


Figure 6: Histogram over the difference between the maximum height of mountaintop and observation of horned lark (*Eremophila alpestris*) on the same mountain during field surveys in Dovre, Norway.

## Habitat selection

The time used in a site was significantly correlated with the number of territories registered in each site (table 1, figure 9A). The other variables were not significant in the single-factor analyses (table 1, figure 9), although max height could show a positive trend with increasing heights (table 1, figure 9B) and isolation has a non-significant possible negative trend with increasing distances (table 1, figure 9D).

Table 1: Pearson correlation between the number of territories of horned lark (*Eremophila alpestris*) and the recorded variables.

Variable	N	R-value	P-value
Time used	44	0.47	<b>0.001</b>
Max height	44	0.25	0.09
Isolation	44	-0.25	0.09
Sheep per km <sup>2</sup>	44	0.16	0.30
Area	44	0.20	0.18

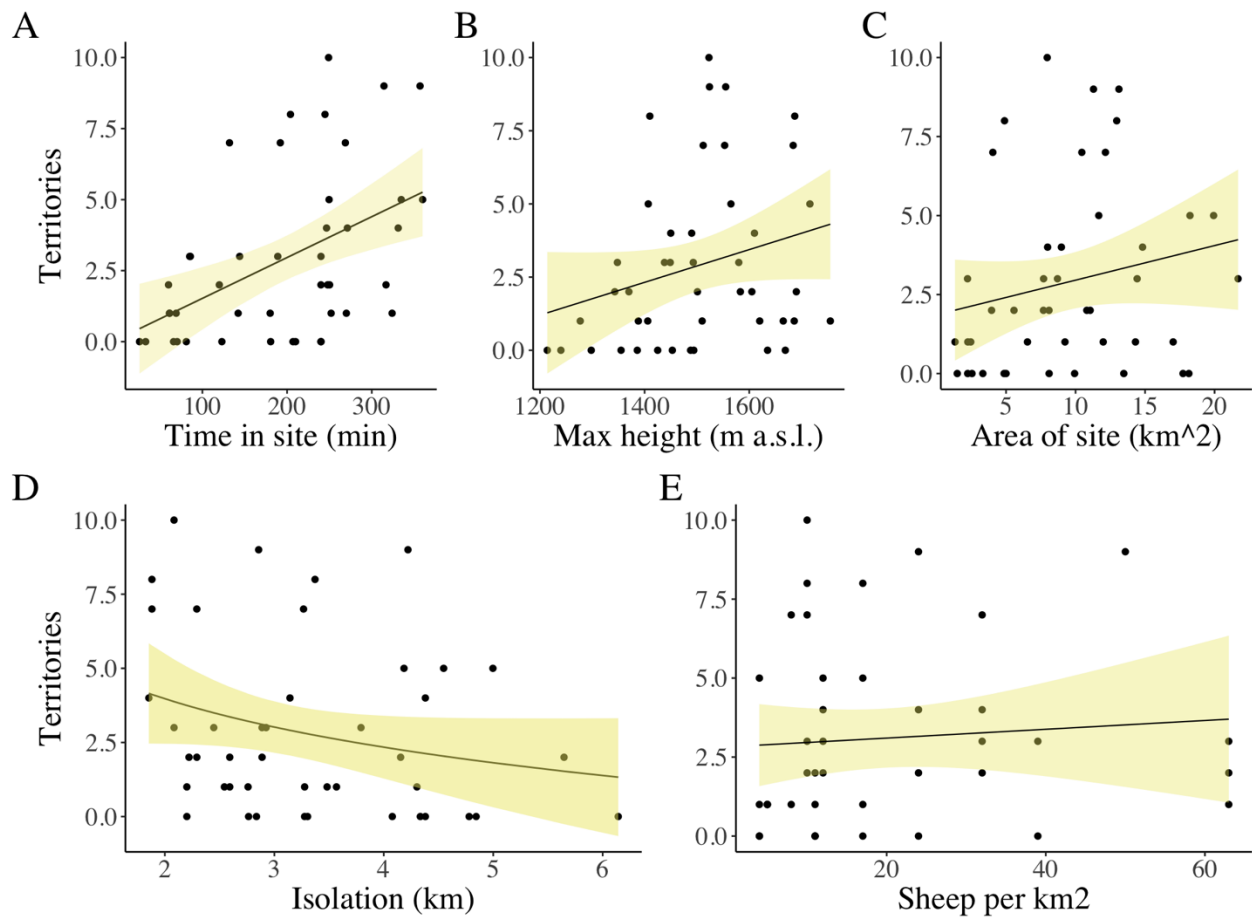


Figure 7: The recorded numeric variables from field surveys in the Dovre region on the x-axis and the relationship towards the number of observed horned lark (*Eremophila alpestris*) territories (y-axis), with additional linear regression lines.

For habitat selection it seems that horned larks preferred areas with fewer grazing species (figure 10A) although this does not necessarily mean less grazing. On average, sites with two grazing species will have 2.18 more territories than sites with three species ( $F = 4.63$ ,  $df = 1,42$ ,  $P = 0.03$ ). The bedrock richness (figure 10B) showed that horned lark had a high preference for intermediate ( $n = 19$ ) and rich ( $n = 17$ ) sites instead of poor ( $n = 8$ ) ( $F = 6.78$ ,  $df = 2,41$ ,  $P = 0.002$ ) with significant comparison between the groups (P-I:  $diff = -3.86$ ,  $P = 0.002$ , R-I:  $diff = -2.01$ ,  $P = 0.06$ , R-P:  $diff = 1.85$ ,  $P = 0.23$ ). The number of observers ( $F = 3.07$ ,  $df = 2,41$ ,  $P = 0.05$ ) showed a significant difference between the groups one and two ( $P = 0.05$ ) as seen in figure 10C.

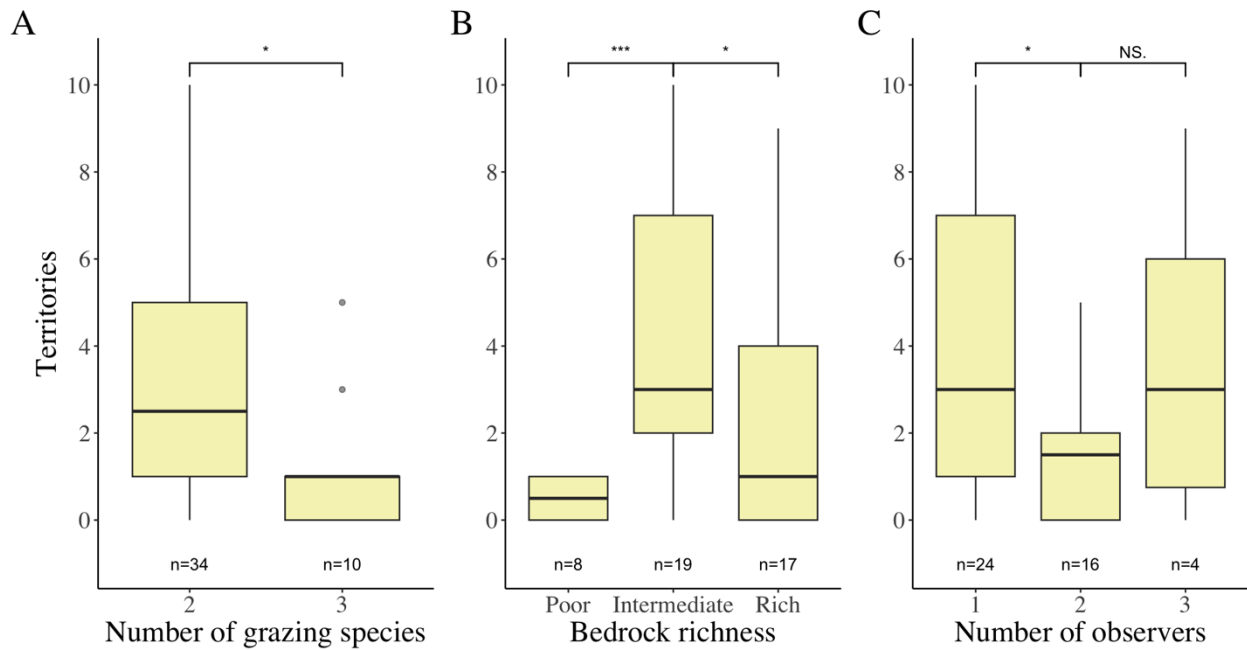


Figure 8: Boxplot over the three categorical variables used in habitat analyses for the horned lark (*Eremophila alpestris*), points represent outliers, stars represent the significant differences between the groups and “n” is the number of sites within the group. A. The number of occurring livestock species (2: sheep and reindeer, 3: cow or muskox in addition) in each site and how this affects the number of territories. B. The collected data on bedrock richness in a factorized scale from poor to rich. C. The number of observers in each site and the accompanied observed territories.

According to the StepAIC conducted to find the best fitting model, the field effort variables time used and number of observers, and biological variables bedrock richness and density of sheep predict the preferred habitat best (table 2). The number of territories declined with increasing density of grazing sheep per square kilometre (figure 11), while the intermediate and richer bedrock had higher numbers of territories, compared to the poor sites (table 2). The relationship between sheep density and the average elevational occurrence of horned lark for each of the study sites with recorded territories was analysed. Here, no significant relationship was found, which indicates that grazing is not height dependent (table A5).

Table 2: Output from the best fitted general linear model (GLM) for the horned lark's (*Eremophila alpestris*) habitat selection, the group "1 observer" and "poor" are reference groups in the analyses. AIC: 157.39.

Predictors	Estimate	SE	Z-value	P-value
Intercept	-0.8	0.56	-1.41	0.15
Time used	0.005	0.001	4.68	<0.001
2 Observers	-1.13	0.23	-4.8	<0.001
3 Observers	-0.34	0.35	-0.99	0.32
Bedrock richness: Intermediate	2.07	0.53	3.86	<0.001
Bedrock richness: Rich	1.54	0.56	2.73	0.006
Sheep/ km2	-0.23	0.12	-1.93	0.05

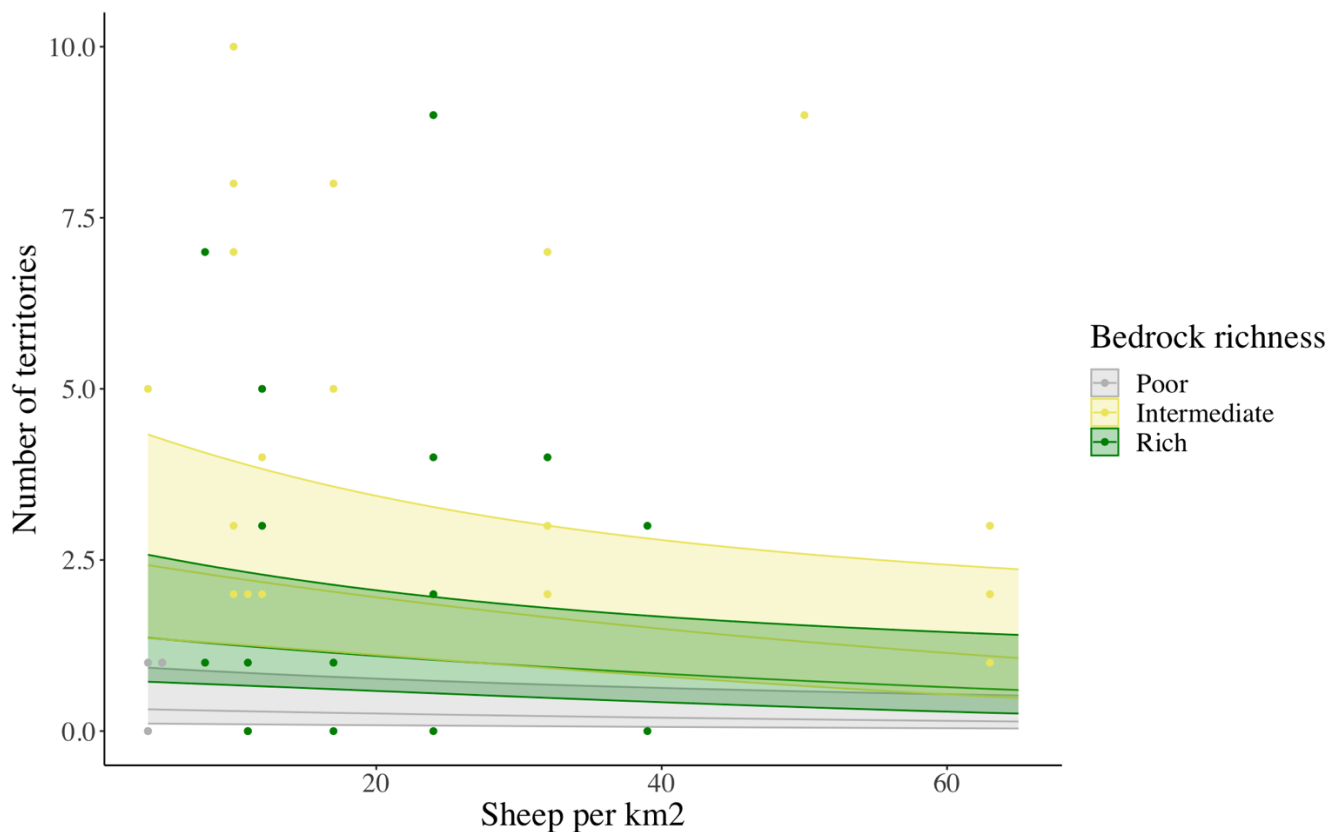


Figure 9: A prediction of preferred habitat for the horned lark (*Eremophila alpestris*) from the best fitting model (GLM) plotted without the variables "time used" and "observers" because they are not biological variables, but describers of effort. The points are the observed data from 2022, while the regression lines are predictions based on the model. The x-axis is showing the actual density of sheep (in km<sup>2</sup>) instead of the logarithmic values.

## Elevational occurrence

In a Welch Two Sample t-test there was a significant difference ( $T = -3.92$ ,  $df = 37$ ,  $P = <0.001$ ) between the mean height occurrence for Grimsdalen between the years 1969 (1337 m a.s.l.) and 2022 (1426 m a.s.l.) (figure 12A). With the same test conducted for Einunndalen there was also a shift of elevational occurrence with the mean for 1992 being 1337 m a.s.l. and 2022 being 1414 m a.s.l. ( $T = -4.14$ ,  $df = 32$ ,  $P = <0.001$ ) (figure 12B).

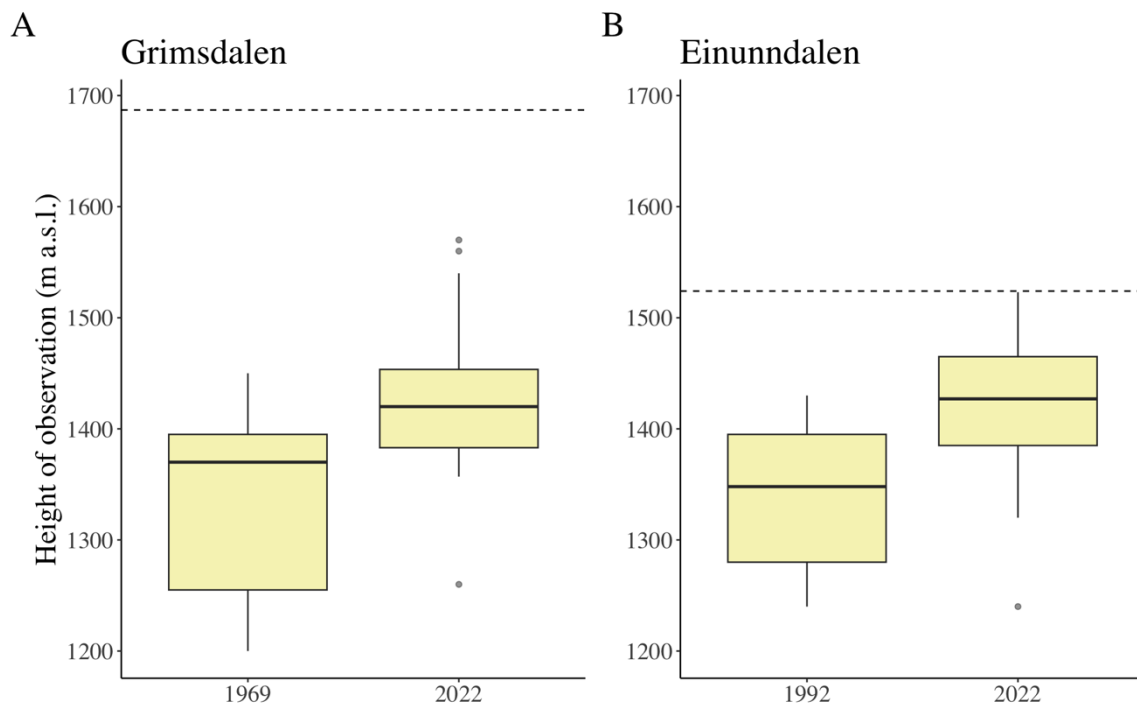


Figure 10: Historical elevational observations of horned lark (*Eremophila alpestris*) made by Spjøtvoll in 1969, compared to field data from 2022 in the region of Grimsdalen (A), and the region of Einunndalen in 1992 compared to field data from 2022 (B). The dashed line represents the maximum height of the highest sampled mountain in each region, and points represent outlier data.

The linear regression of historical citizen data for the period between 2008 and 2021 showed a height increase of 3.65 meters per year ( $df = 1222$ ,  $SE = 0.77$ ,  $P = <0.001$ ). While the same analysis for the whole period (1971-2021) with available data (figure 13) shows an elevational increase of 2.17 meters per year ( $df = 1630$ ,  $SE = 0.26$ ,  $P = <0.001$ ). In both regressions the variable region was used as a random factor to control for temporal changes in height variances between the regions.

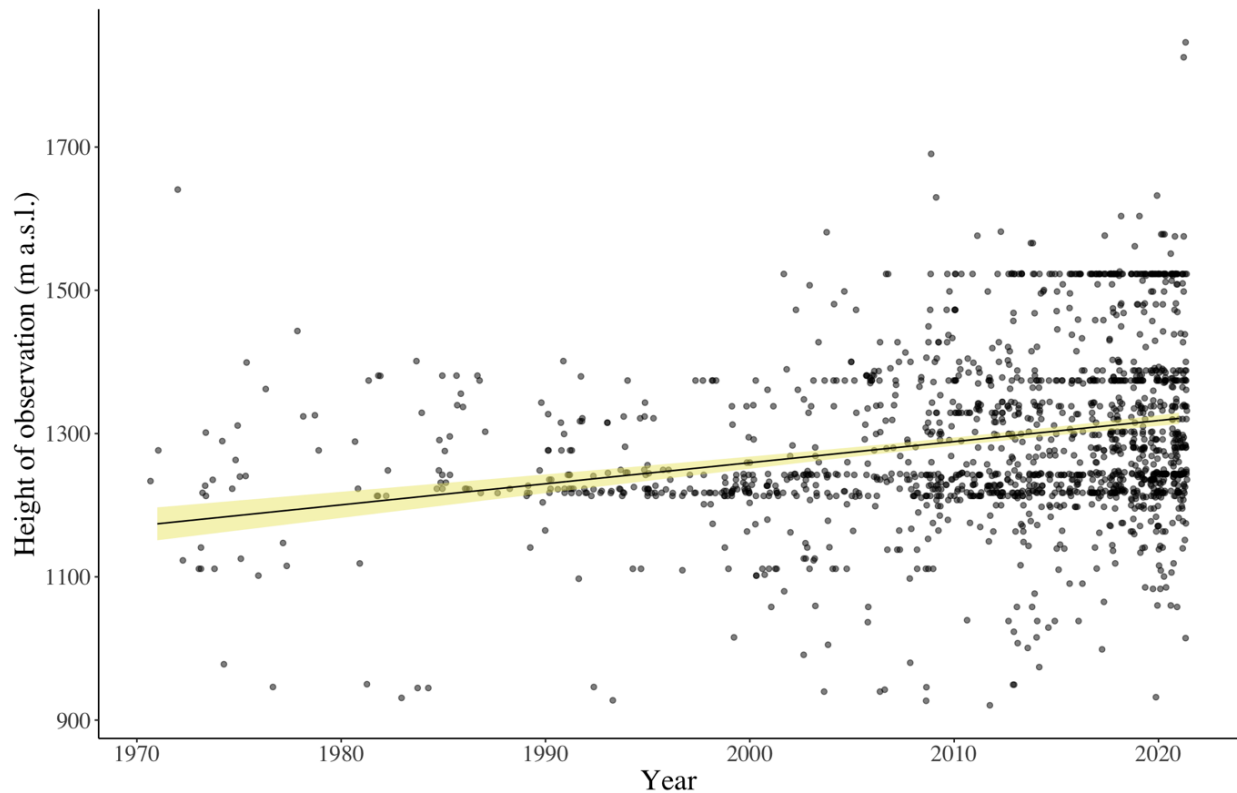


Figure 11: Historical elevation data of horned lark (*Eremophila alpestris*) from Southern Norway ranging from 1971 to 2021 with a regression line. The number of observations per year increases exponentially after 2008.

### Population trend

A paired sample t-test between the transect conducted in 1969 (mean = 1.9) and 2022 (mean = 2.3) showed a 0.4 population increase per site in Grimsdalen, although the results were not significant ( $T = -0.41$ ,  $df = 9$ ,  $P = 0.68$ ) (figure 14A). The same test conducted for Einunndalen as seen in figure 14B gives a mean of 1.25 territories per site in 1992 and 5.25 in 2022 ( $T = -2.58$ ,  $df = 7$ ,  $P = 0.03$ ).



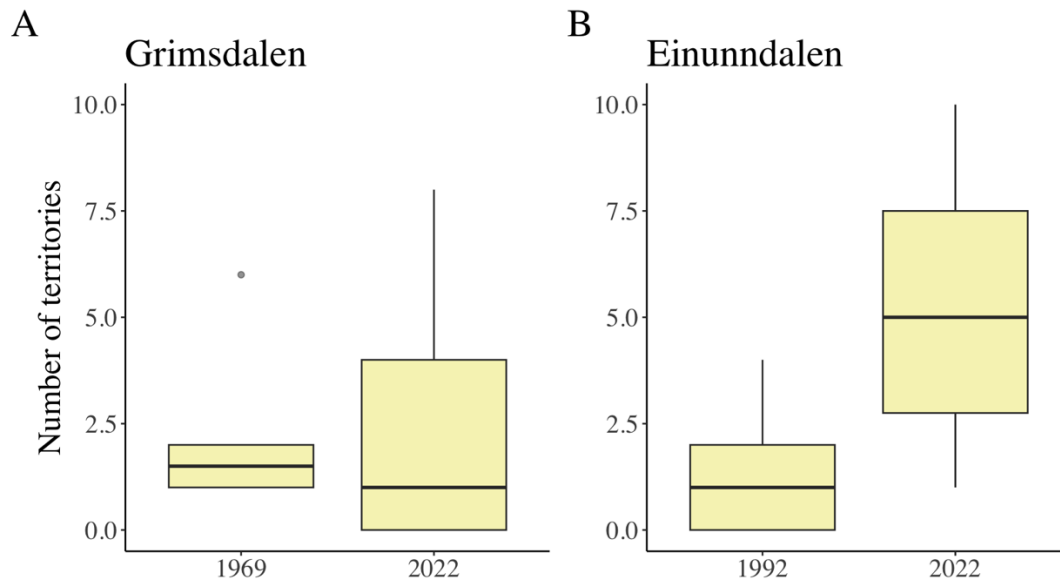


Figure 12: Boxplot of the number of surveyed horned lark (*Eremophila alpestris*) territories in Grimsdalen (A) and Einunndalen (B) from historical surveys and field work in 2022, where the x-axis represents year. Note that the bold lines are median and not the mean value as is given in the text, the point is an outlier value.

The population trend across all sites (including zero-observations) showed a stable population size over time (figure 15) with a non-significant additive growth rate of  $-0.003$  ( $SE = 0.01$ ,  $P = 0.86$ ; Wald test for significance of slope parameter:  $Wald = 0.02$ ,  $df = 1$ ,  $P = 0.88$ ). The same trend is seen for the period 2000-2021 (figure A5).

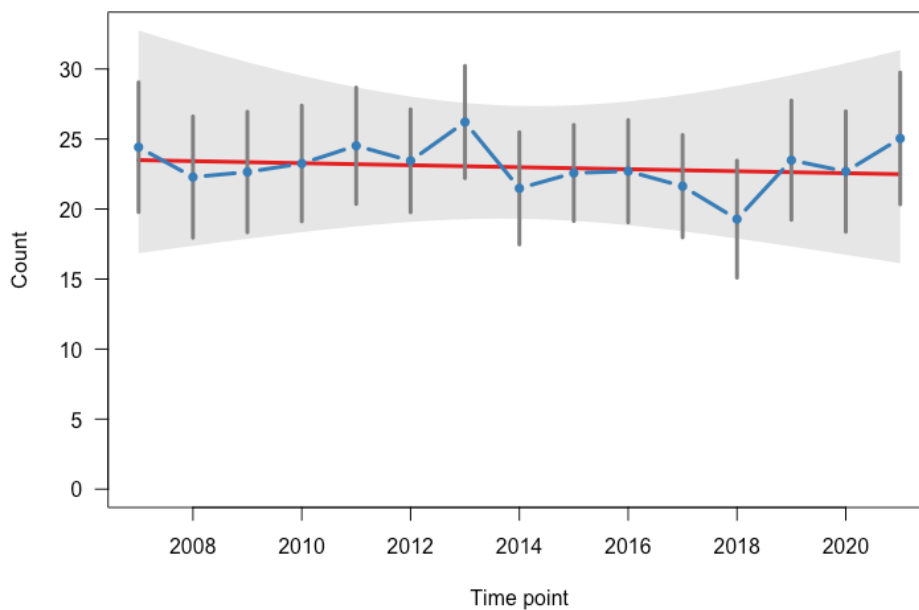


Figure 13: Number of territories and overall population slope with 95% CI for the horned lark (*Eremophila alpestris*) between 2007 - 2021 in our study sites in the Dovre region with recorded zero-observations.

## Discussion

### Habitat preferences

Field surveys recorded a high number of territories compared to other older surveys, which could be a result of the different changing variables further discussed in this thesis. The elevational occurrence was normally distributed around 1430 m which is higher than the formerly believed range of the horned lark in Norway. Just as our study hypothesized the number of territories was minimal under the 1200 m line with only one observation just below at 1196 m a.s.l. at the site of Steinhøe in Einunndalen. One interesting result is that most of our observed territories occur between the mountaintop and 100 m below, which indicates that many of the territories already are located at the upper limit of their possible occurrence. As hypothesized the horned lark preferred southern facing slopes with a high density also on the east slope. This could confirm the findings by Winkler et al. (2016) that showed that east and southern slopes in the alps were warmer and therefore was preferred by alpine plant species and therefore also by alpine birds. In addition, there was a close to significant negative relationship between isolation and the numbers of territories, which indicates that the horned lark settles on peaks that are close to other peaks with existing territories. This could be because young birds are familiar with the location of their parent's territories and settle in near sites. The variable maximum height was also close to significant with a positive relationship, which indicates that the higher the mountain, the higher the number of territories in the site. This could be because there is more available area on higher mountains that can facilitate for more territories, or because there is some sort of elevational shift where the horned lark selects the sites where they can move up in elevation.

Interestingly, there was a significant larger number of territories in study sites where only sheep or reindeer occurred as grazers, while the study sites with more species like cow and muskox had almost no observed territories. This can indicate that heavy grazing is not preferred by the horned lark and could have effects on habitat availability in the future, or it could be simply because cows graze in lower elevation and rarely overlapped with our study sites. Compared to this, when combined with other variables in the habitat model, horned lark territories correlated with lower density of sheep grazing. This is similar to the findings of Evans et al. (2006) where lower grazing promotes higher abundance of birds, but some grazing seems to be better than no grazing. In contrast, Loe et al. (2007) found a small positive effect of grazing on alpine bird species in lower alpine zones, and Laiolo et al. (2004) found a clear negative effect on alpine birds with less grazing and pasture abandonment. These different findings could indicate that the effect of grazing changes between the different alpine zones.

But as Knopf (1994) describes, we can rarely point out one single factor as the cause, and that the relative effect of grazing is poorly understood.

The effect of grazing on the vegetation is better understood and studies from Norwegian mountain habitats showed small positive effects at low grazing levels and small negative effects at higher grazing levels (Evju et al., 2011). Higher density of grazing can lead to less vegetation, but also higher plant species richness, and while lower abundance and diversity of beetles has been observed in grazed habitats, it is not thought that grazing will lead to less food for insectivorous birds (Myserud & Austrheim, 2005). Vandenberghe et al. (2009) mentions that reduced food accessibility seems to be an effect of grazing and could be more important than reduced food abundance, which fits with the suggestion by Loe et al. (2007). This paper showed that grazing can lead to increased catchability of insect prey but does not lead to decreased insect abundance. These findings could be stronger for lower alpine zones with shrubs and not be valid for higher alpine zones with grass and lichens, where the insects could be more accessible regardless of grazing. The true rate of grazing in each site is unknown and even with a high density of sheep, it is possible that little grazing occurred inside our study sites. We did not find any relationship between the density of sheep and elevational occurrence of horned lark, which rules out the hypothesis that heavy grazing forces the birds higher in elevation, or that sheep generally graze in the lower alpine zones. This should be further studied to give managers information of the true occurrence and density of grazing and how it might affect alpine bird species.

Horned larks had a clear preference for calcareous sites with most territories being in intermediate or rich sites, with very few observed in poor sites. These clear significant differences had some overlap in the habitat model, but we can conclude that poor alpine habitats will have few to no territories of the horned lark. The data behind the variable for bedrock richness is accurate, but only describes the bedrock and not the other factors that would determine the habitat richness. Therefore, some sites may be categorized as intermediate in our study, but can be perceived as rich in field, or the other way around. We decided to use the data as it is instead of affecting it by our own perceptions from field, but this means that we lack good variables that describe the actual quality of habitat with vegetational and nutritional values. This could be the reason why the hypothesis is not fully met, with the rich sites varying a lot in preferability.

The best fitting model for habitat selection included the variables observers and time used, which can give an input on the effect of area because area and time used correlates with a value of 0.65 ( $P = <0.001$ ) in a Pearson correlation test. The model also included the biological variables bedrock

richness and density of sheep grazing. When combining these two variables we see that the lower density of grazing combined with intermediate bedrock gives the most preferred habitat for the horned lark. While there is some overlap between the different scales of bedrock richness, the overall slopes gradually decline with increased density of sheep grazing in both intermediate and rich sites. This indicates that grazing alters the preferability of the habitat, and with only the nutrient poor sites reaching levels of zero territories, we can say that poor sites with heavy grazing is the least favourable for the horned lark. With grazing having a negative effect this is a possible limiting factor, in addition, it seems that the vegetation richness is important in determining possible habitats. Therefore, these factors need to be combined when selecting possible hotspots for horned lark and where potential management activities should be prioritized.

## Elevational shift

In both Grimsdalen and Einunndalen the median elevational occurrence has had a significant shift since the previous field surveys. In Einunndalen the occurrence is already nearing the elevational limit in the surveyed sites and in Grimsdalen we see a clear shrinking of the preferred height interval. This shows clear signals of an elevation shift in the area and supports the hypothesis of an elevation shift happening for the horned lark in southern Norway. As Chamberlain et al. (2016a) notes, the impact of climate change and elevational shifts will be most severe in areas where there are limited possibilities to move up in elevation.

The linear regression conducted on height data for the whole region of southern Norway including Trøndelag shows a significant positive slope which can be concluded as evidence for an existing elevation shift. Between 1971 and 2021 the horned lark has on average occurred 2.17 m higher in elevation each year, while for the shorter period between 2008 and 2021 the shift is 3.65 m per year. This is similar to the findings of Pernollet et al. (2015), who found a yearly shift for the rock ptarmigan between 1.5–9.4 m/year varying between different regions of the alps. This also supports the findings of several other studies from the alps and other mountain areas in the world which show elevational shifts happening for different alpine birds (Bani et al., 2019; Maggini et al., 2011; Neate-Clegg et al., 2021; Popy et al., 2010; Scridel et al., 2018; Sekercioglu et al., 2008). Couet et al. (2022) found a mean elevational shift of 0.9 m per year for birds in the Scandinavian mountains, and although the horned lark was not included in this study, they found a greater effect on short-lived birds than on long-lived birds. In the tropical Andes of Peru elevational shifts have been observed and it is expected to lead to extinctions of high-elevational species (Freeman et al., 2018). This study concluded that climate change would affect tropical species more than those living in temperate areas,

which matches the findings of Pernollet et al. (2015) who found greater effects of climate change in the southern alps in contrast to the northern parts of the alps. Some studies have pointed to other factors rather than just temperature changes as drivers for elevational changes. Hallman et al. (2022) found that the elevational preference was habitat dependent, and that species with smaller mass, brain size and hand-wing index in addition to migratory behaviour had greater upslope shifts. This matches the traits of the horned lark and could describe the elevational shifts discovered in our study.

Based on our findings we can conclude that there is an elevational shift occurring for the horned lark in southern Norway, which is an important finding that could also be applied to other alpine bird species. Although when we compared the horned lark with two other species in Norway, conducted for methodological reasons, the short-term analysis only showed a shift for the horned lark. The long-term analysis also showed an elevational shift for the snow bunting in addition to the horned lark, while the rock ptarmigan had a stable trend for the whole period (figure A2). Although this is a preliminary analysis, the findings could indicate that changes in temperature impact species different based on their life strategies and traits. Here further studies on elevational occurrence for alpine birds should be prioritized in the future to assess possible drivers for population decreases.

The elevational shift will lead to a decrease in habitat as described for northern Europe (Virkkala et al., 2008). For the rock ptarmigan in the Italian Alps, it is projected with a climate warming prospective that the habitat decrease will be 28 % towards 2038 and that the decrease will accelerate in the years after (Ferrarini et al., 2017). Our data shows that there can be a drastic decrease in available habitat for our study sites with the ongoing elevational shift, with the available habitat over the 1200 m line being 392.88 km<sup>2</sup> (table A6). The lower 10% quantile of the observed horned lark heights in 2022 is at 1320 m a.s.l., and the upper 90% quantile is at 1540 m a.s.l., which gives an available habitat of 240 km<sup>2</sup> for the preferred elevational occurrence in 2022. Considering the elevational growth rate from 1971 to 2021 (2.17 m/year), the available habitat in our study area will be approximately 169 km<sup>2</sup> in 20 years, 127 km<sup>2</sup> in 50 years and 31 km<sup>2</sup> in 100 years. With the growth rate found between 2008 and 2021 (3.65 m/year) the available habitat will be 117 km<sup>2</sup> in 20 years, 56.8 km<sup>2</sup> in 50 years and 3 km<sup>2</sup> in 100 years. These comparisons indicate a possible regional extinction of the horned lark in this century for our surveyed sites. With 90% of the elevational occurrence in 100 years being between 1685 m and 1905 m a.s.l. (based on the most rapid rate of increase) the horned lark can still occur in southern Norway. Although, it can only occur in small numbers and depending on an elevational shift also occurring for the vegetation and preferred habitat. These calculations are similar to the findings of Elsen and Tingley (2015) where they analysed mountain areas and suggest that species living in the middle and upper zones of the mountain may

encounter decreases in available area, whereas foothill and lower-alpine species will get habitat increases. The same effects seem unlikely in Norway although it could occur for mountain species depending on forest. With increasing annual temperatures, the elevational growth rate can increase over time which could lead to an even quicker reduction in available habitat.

Peringer et al. (2022) have simulated the vegetational shift in summer pastures in the Alps which indicates that the vegetational zones, and especially alpine and boreal heaths, will not necessarily follow the shift of the climatic zones. This could also be the case in Norway where the bedrock and soil establishment in higher elevation is not necessarily suitable for plant growth with harsh weather. A study from Dovre found a decrease in lichen richness and an increase in bryophyte richness on mountaintops between 2001–2015, as well as a progressive increase in dwarf-shrub abundance at the expense of lichens (Vanneste et al., 2017). These changes could be a result of changing temperatures but could also be a result of a decrease in grazing. With an expected tree line shift (Harsch et al., 2009), the combined result could be that the elevational range of alpine grasslands stands still and that the total area decreases with the lower vegetation zones shifting upslope. Therefore, an elevational shift of the horned lark could lead to further population decreases with decreasing available habitat and if the habitat and food source does not follow the upslope shift as well.

The preferred diet of the horned lark is insects and seeds (Haftorn, 1971), and studies predict elevational shifts also for insects (Shah et al., 2020). This means that the food source will likely move upslope together with the horned lark. However, observations have shown that insects might move faster in elevation than the vegetation (Kerner et al., 2023). With the horned lark moving upslope the elevational occurrence could overlap more with other alpine species such as snow bunting and potentially lapland longspur (*Calcarius lapponicus*). This however relies on elevational shifts also occurring for the lapland longspur, and if all reach the upper limit of elevation in the area. Then it could lead to interspecific food competition between the three species. Byrkjedal et al. (2022) found that the three bird species have diet overlap on the Hardangervidda where they have a more natural habitat overlap and that over half of the dry mass diet consists of seeds for the three species. Lapland longspur and the horned lark had both high percentages of insects in their diet and therefore a huge overlap of diet, while the snow bunting only had 17 % insect in the dry gut mass. The lapland longspur is in decline in Norway (Byrkjedal & Kålås, 2012; Stokke et al., 2021b), and during field work we did only observe few individuals in Folldal (Dale et al., 2022). In addition, lapland longspur generally occurs lower in elevation than the horned lark, and a potential competition between these two species is unlikely in the region. The snow bunting on the other hand was in abundance on most mountaintops in the region, and therefore overlapped with the horned lark where it occurred near the

peak. An interspecific food competition is therefore possible, especially with the horned lark moving upslope. In Subarctic and Arctic zones, the horned lark has showed an advantage in breeding success over the snow bunting with warmer temperatures (Ryzhanovsky, 2015), and thus it seems like the horned lark could have advantages with increasing temperatures. If the competition will lead to harsher conditions for the horned lark is unknown and should be further studied. However, Byrkjedal et al. (2022) suggest that the horned lark has had population increases in contrast to declines observed for the snow bunting and lapland longspur in areas where they overlap.

## Population trend

Flousek et al. (2015) predicts that high elevational bird species will have serious population decreases because of warmer climates and elevational shifts. Our short-term analyses from 2007-2021 showed a stable population trend which can indicate that the elevational shift has not reached a critical elevation in Dovre. The population in Dovre was thought to be in decline during the 60s and 70s (Stueflotten, 1994), because of disturbances in their overwintering areas. These declines were not reported for any other place in Norway, and Svensson (1997) concluded that observed declines in Lapland could not be caused by effects in the winter areas because the population in southern Norway who uses the same wintering areas was stable. Dierschke (2001) confirmed that horned lark from both southern Norway and Lapland has their wintering areas in the North Sea, preferably in the low salt marshes of the Wadden Sea. For granivorous passerines it is suspected that the amount of winter food is a key factor that regulates population size (Dunning & Brown, 1982). After huge floodings in 1963, Germany and the Netherlands decided to embank huge areas as well as intensify grazing (Kramer, 1991), which resulted in a 60% loss of salt marshes (Stock, 1993) and the main winter food source for the horned lark (Dierschke, 2002). Since the Wadden Sea became a National Park, the population of horned lark has increased during winter (Dierschke & Barlein, 2002) and a recent study from Norway showed a mean territory increase of 177% per study site on the Hardangervidda since 1985 (Byrkjedal & Högstedt, 2022). Though the general conception for alpine birds in Europe and Fennoscandia seems to be ongoing and future declines with significant 10% population decreases for mountain specialists (Lehikoinen et al., 2019), it seems that the disturbances that has been during winter is eliminated and that further disturbances to population size would appear at breeding sites.

Changing trends in weather conditions seems to favor generalists over specialist bird species in alpine habitats (de Gabriel Hernando et al., 2022). A study from Canada on a horned lark community with similar life strategies to the community in Europe, showed a clear negative effect on reproduction from later clutch initiation as a result of longer snow cover or harsher climate during spring (de Zwaan

et al., 2022). Climate change is supposed to lead to more precipitation and heavier snow coverage in alpine areas, which could lead to delayed clutch initiation, as suggested for the lapland longspur (Fjeldheim et al., 2023). This again could lead to reproduction failures and potential population decreases. In addition, climate change will most likely also lead to warmer summer temperatures, which can make chick survival easier, because the horned lark chicks are good at handling periods with both higher and lower temperatures than normal. It gets more critical for chick survival if there are heavy multi-days storms (which is predicted to occur more often), since the horned lark chicks does not cope well with sudden extreme changes (de Zwaan et al., 2020). Changing climates and changes in local weather should not be underestimated as a potential critical factor on the population of horned lark. However, as an alpine bird who already lives on the edge it should be capable of adaptation (Maggini et al., 2011), and we might also underestimate the capabilities of handling changes in weather, as observed on the Tibetan Plateau where breeding strategy was adjusted according to temporal changes in food availability and nest predation (Du et al., 2014), although the ongoing elevational shift as a possible adaptation to changing climates will affect the horned lark.

Changing climates leads to increased primary productivity and a greening of arctic tundra and boreal alpine areas (Myers-Smith et al., 2020). Ims et al. (2019) found that nest predation increased with primary productivity as an independent relation of simultaneous effects on vegetation cover around the nest. In addition, the predation risk steeply increased with elevation, implying that species in high elevation in boreal and arctic alpine ecotones are particularly vulnerable. In contrast, McKinnon et al. (2010) found lower predation risk for migratory birds that migrate into high latitudes like the tundra in arctic Norway. This could favor the population of horned lark living in Troms and Finnmark who lives on arctic tundra instead of alpine mountain ranges. Although the predation risk can increase, the total effect on population size of nest predation for the horned lark is not well known, but as for other species, nest predation could lead to lower population sizes (Bowler et al., 2020). The knowledge of breeding success and possible effects of predation for the horned lark in Norway and Europe is scarce and should be further studied to assess the impact of changing weather.

According to Chamberlain et al. (2016b) the biggest threats towards alpine birds are land abandonment and climate change. This is confirmed by our findings together with other studies where we see a clear elevational shift, likely driven by climate change. In addition, to impacts on open alpine grasslands from a shift towards grazing species that could have a greater impact on the vegetation. Changes in how humans use the mountain can also affect alpine birds and the horned lark negatively. Caprio et al. (2011) investigated if the extended ski-piste constructions in the alps impacted the alpine grassland bird communities, the findings indicate that grass covered ski hills are generally perceived



as alpine habitats, whereas heavier degradation of the mountain with roads and dirt tracks will lead to decreases in bird occurrences. This is important to note for Norwegian mountains where ski areas are abundant, and it is important to implement grassland restoration when constructing new ski tracks or resorts, although ski areas generally cover little of the preferred areas by the horned lark. Other human impacts in the mountains like wind power and cabin establishments are poorly studied on the effects on alpine birds. As for now wind power does not occur in mountains in southern Norway, although they do occur in the areas where horned lark breeds in Finnmark. For cabins and human recreation, these are rarely built in high alpine zones where the horned lark occurs, but if it were built in these areas it would contribute to a decrease in available habitat. The negative effect of trails and recreational traffic has been studied in the Alps, and no negative effect on breeding were found for ground nesting species such as the horned lark (Bötsch et al., 2017). This would also apply for the Norwegian mountains where people generally uses the established trails, and the disturbance outside these is limited, although Vallino et al. (2019) has found negative effects on foraging in an Alpine bird caused by human recreational disturbances. In Norway, the preferred season for hiking is mostly after breeding is finished and the possible disturbances is therefore not likely to have severe effects. In conclusion, the most plausible threats to the population of horned lark must be changing habitats by climate, land use, and the ensuing temporal changes in elevational occurrence.

## Management

Dawson et al. (2011) states that it is important to have a science integrated management when tackling climate change effects on species. To achieve this, it is important with species specific management and to monitor populations. Further, managers should prepare contingency plans so that conservation actions can be started when it is needed. Intensive intervention matters could be necessary if the status of the species gets severe. Possible methods would then be restoration of alpine habitats and removal of predators or drastic measures like assisted breeding and reintroduction. Hof et al. (2017) stresses the importance of looking beyond climate change when conservation is the aim, because the main threat is decreasing breeding ranges.

Our findings from the habitat model implicates that grazing should be managed. As seen in our results (figure 11) heavy grazing has a negative impact on the number of horned lark territories. To limit grazing, the density of grazers should be decreased by having less grazers in the mountain, especially in areas with high quality habitats for the horned lark. The results from livestock analyses show that sites with sheep and reindeer had more territories, therefore, species like cow or muskox which could have negative grazing effects, should be excluded from alpine habitats to reduce negative grazing that

can degrade the quality. This could raise a dilemma for Dovrefjell- Sundalsfjella National Park, where the muskox is important for attracting tourists. Although it has been discussed to remove the species from the alpine ecosystem (Gregersen & Noreng Trøen, 2023). In addition, the number of sheep in each site should be limited for the same reason since it is the abundant grazer in the area. Grazing by wild species such as reindeer could be discussed, and the real impact on lichen and grass species is unknown, although Donald and de Juana (2014) suggested that reindeer could be the cause of population declines in Finland, but for now it is unlikely that reindeers limit the number of horned larks in each site.

In Norway, national action plans are used for defining management actions for threatened habitats and species. One alpine bird species that has such a plan in Norway is the lesser white-fronted goose (*Anser erythropus*) which is critically endangered (Stokke et al., 2021c). Here the most important management actions are conservations of habitat, increased monitoring, securing reproduction, continued research, implementing restrictions on disturbance and cooperation with other countries (The Norwegian Directorate for Nature Management, 2009). Many of these activities are important for all alpine species and the most important actions for the horned lark now would be conservation of habitat and continued research.

Adaptive ecosystem management is important to keep the ecosystems we have today, and often it is easier to get funding and more straightforward to conserve habitats instead on focusing on single species. Therefore, managers should prioritize strategies that leads to more open habitats and minimizes the upslope shift of the tree line and shrub establishment (Chamberlain et al., 2013). This could be altered grazing strategies where the number of grazers is limited, and the grazing species are selected based on which species help the continuation of open alpine habitats. The grazing needed to limit tree and shrub establishment is severe and this would impact the horned lark negatively as seen in the habitat model. As an alternative to grazing, managers can restore alpine areas, if necessary, by removing tree saplings and shrubs that have moved upslope, or by mowing to keep the vegetation low. However, Bazzi et al. (2015) found that grazing should be prioritized over mowing when managing grasslands for alpine birds. To assess which areas are the most valuable for a stable population and thereby where it is most important to implement managing activities, bedrock mapping can be used for Norway as well as our 'hotspot' findings for the region of Dovre. Further, the population of horned lark in southern Norway should be monitored to assess further changes.

It should be considered to change the red list categorization for the horned lark based on our findings of elevational shifts and depletion of available habitats. This would make it easier to gain awareness of a possible decline of the species in the future, and to have active management of alpine habitats.

Further studies on alpine birds and their future should be considered, as well as an action plan for alpine birds and their habitat.

In conclusion we can now say that the horned lark prefers calcareous rich areas with minimal grazing, although it probably needs some grazing which should be managed to avoid a possible degradation of alpine habitats. Further, the horned lark has shifted its elevational occurrence, and this must be seen as the biggest threat towards the population right now. With the population size for Dovre showing a stable trend the last fourteen years, we did not find evidence for a population decrease the last decade, although we can conclude that there will be a decrease in available habitat because of the ongoing elevational shift for the horned lark. Therefore, the population should be monitored to detect temporal populational effects of climate change and changed land use.

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# Appendix

Table A1: Recorded values for each study site in 2022 that is included in habitat analyses.

Site	Min height	Max height	Territories	Time used	Distance	Area	Isolation	Bedrock richness	Observers	Sheep/km2	Municipality
Blåhøe	1000	1620	1	324	14.6	11.99	2.76	Rich	3	17	Dovre
Slethøe	1000	1555	9	314.4	11	11.29	4.22	Rich	3	24	Folldal
Vålåsjuhøe	1050	1407	5	334.8	14	11.67	4.55	Rich	3	12	Dovre
Hjerkinnhøe	1020	1298	0	180.6	8.91	3.33	4.84	Rich	3	24	Dovre
Storhøe (Dovre)	1000	1453	0	210	12.8	8.1	4.33	Rich	2	11	Dovre
Avsjøhøe	1000	1635	0	240	9.9	13.47	2.84	Rich	2	17	Dovre
Storhøe (Folldal)	1000	1605	2	250.2	11.2	8.09	5.65	Intermediate	2	12	Folldal
Tverrfjellet	1050	1240	0	33	2.2	1.49	4.78	Rich	2	NA	Dovre
Grisungknatten	1010	1449	3	240	13	14.43	2.93	Rich	2	12	Dovre/Lesja
Langhøe	1005	1490	4	271.2	12.8	8.98	3.14	Intermediate	2	12	Folldal
Pikhøe-Mehøe	1000	1510	1	180	7.5	9.24	2.59	Rich	2	11	Dovre
Råtåsjuhøe	1000	1583	2	247.8	10.7	11.05	4.15	Rich	2	24	Folldal
Nystugghøe	1000	1755	1	270	15	14.31	2.54	Poor	1	5	Oppdal
Nordre Knutshøe	1000	1684	7	268.8	13.6	12.15	2.29	Intermediate	1	32	Oppdal
Vesle Elgsjøtangen	1090	1450	4	246.6	11.4	7.99	4.38	Rich	1	32	Oppdal
Steinhøe	1200	1610	4	331.2	18.3	14.82	1.85	Rich	1	24	Folldal
Fokstugghøe-Storhøe	1000	1716	5	360	18.2	19.93	5	Intermediate	2	17	Dovre
Mesæterhøe	1021	1425	0	123	8	9.93	4.08	Intermediate	2	11	Dovre
Elgsjøtangen	1060	1494	0	240	13.5	17.73	4.38	Rich	2	39	Oppdal
Slethøe (Oppdal)	1260	1686	1	252	12	17.02	3.48	Poor	1	5	Oppdal
Finnsjøa (Oppdal)	1000	1438	3	144	9	8.7	3.79	Intermediate	1	32	Oppdal
Fatfjellet-Skardhøa	1025	1501	2	240	10.8	7.69	2.22	Intermediate	2	10	Folldal
Halvfarhøe	1000	1687	8	244.8	13.9	12.96	3.37	Intermediate	1	17	Dovre
Kattuglehøe	1000	1553	7	192	10.3	10.45	3.27	Rich	1	8	Dovre
Gygerhøe	1000	1388	1	61.2	3.4	2.46	3.57	Rich	1	8	Dovre
Storvassberget	1224	1406	1	61.2	3.33	2.25	2.20	Poor	1	4	Dovre
Hornsjøhøe	1280	1565	5	249.6	14.5	18.23	4.19	Intermediate	1	4	Dovre
Hornsjøkollen	1224	1355	0	66	5	5	2.77	Poor	1	4	Dovre
Gravhøe	1224	1488	0	207	14.9	18.15	3.3	Poor	1	NA	Dovre
Sæterberget	1200	1386	0	25.8	6	2.24	2.2	Poor	1	4	Dovre
Knutshøa	1000	1690	2	316.8	14.15	10.81	2.29	Intermediate	2	32	Oppdal
Streitkampen	1000	1214	0	70.2	5.15	2.55	6.14	Rich	1	11	Folldal
Olmflya	1000	1580	3	85.8	7.8	21.69	2.45	Rich	1	39	Oppdal
Brunkollen	1450	1665	1	142.2	9	6.54	3.28	Poor	2	5	Dovre
Veslhetta	1460	1669	0	81	5.6	4.86	3.28	Poor	2	NA	Dovre
Steinhø (Einunndalen)	1017	1348	3	85	3.09	2.23	2.08	Intermediate	1	10	Folldal
Finnsjø (Einunndalen)	1285	1523	10	249	10.06	7.96	2.08	Intermediate	1	10	Folldal
Marsjøfjellet	1117	1524	9	357	15.19	13.12	2.86	Intermediate	1	50	Folldal/Tynset
Lågegga	1117	1410	8	204	9.43	4.89	1.88	Intermediate	1	10	Folldal
Høgegga	1340	1512	7	132	4.31	4.05	1.88	Intermediate	1	10	Folldal
Fundberget	1095	1277	1	69	3.73	1.33	4.3	Intermediate	1	63	Folldal
Digerkampen	1180	1493	3	189	8.24	7.7	2.89	Intermediate	1	63	Folldal
Setalberget	1240	1370	2	120	5.65	5.57	2.89	Intermediate	1	63	Folldal
Fallfosshøe	1280	1343	2	60	4.5	3.96	2.59	Intermediate	2	11	Dovre

Table A2: Descriptive statistics of the variables used in the habitat analyses. Territories recorded are of the horned lark (*Eremophila alpestris*) in the region of Dovre, Norway.

Variable	N	Mean	SD	SE	95% confident interval	
					lower	upper
Territories per site	127	2.88	2.93	0.44	0.75	4.25
Max height (m a.s.l.)	44	1501	134.78	20.31	1407	1606
Time used (min)	44	194.8	96.14	14.49	111.5	250.7
Area (km <sup>2</sup> )	44	9.37	5.42	0.81	4.88	13
Isolation (km)	44	3.33	1.06	0.16	2.52	4.19
Sheep/km2 (log)	44	2.67	0.79	0.12	2.3	3.17
Mean height	33	1424	91.1	91.1	1357	1484
Livestock: 2	34					
Livestock: 3	10					
Bedrock: Poor	8					
Bedrock: Intermediate	19					
Bedrock: Rich	17					
Observers: 1	24					
Observers: 2	16					
Observers: 3	4					

Table A3: Descriptive statistics over observational variables on the horned lark (*Eremophila alpestris*) from field surveys in 2022.

Variable	N	Mean	SD	SE	95% confident interval	
					lower	upper
Height of observations (m a.s.l.)	138	1430	87.22	7.42	1374	1490
Aspect of observations	138	172°	76.93	6.54	115°	218°

Table A4: AIC values from the different GLM with Poisson distribution conducted to describe habitat preferences. Bold model is created by StepAIC from all the available variables because this combination has the lowest AIC and describes habitat preferences the best, therefore it is also selected for the analyses.

Model	AIC	$\Delta$ AIC
<b>Time used + Bedrock richness + Observers + log (Sheep/km<sup>2</sup>)</b>	<b>157.39</b>	<b>0</b>
Time used + Bedrock richness + Observers	161.96	4.57
All variables	162.65	5.26
Time used + Isolation + Bedrock richness + Observers + Sheep/km <sup>2</sup>	168.95	11.56
Time used + Bedrock richness + Observers + Sheep/km <sup>2</sup>	169.16	11.77
Time used + Isolation + Bedrock richness + Observers + log (Sheep/km <sup>2</sup> )	169.24	11.85
Time used + log (Isolation) + Bedrock richness + Observers + log (Sheep/km <sup>2</sup> )	169.63	12.24
Time used + Isolation + Bedrock richness	179.13	21.74
All variables (without sheep/km <sup>2</sup> )	180.51	23.12
All variables (without Observers and Sheep/km <sup>2</sup> )	184.51	27
Time used + Area + Bedrock richness	186.21	28.82
Distance + Isolation + Bedrock richness	186.44	29.05
Log (Isolation) + Bedrock richness + log (Sheep/km <sup>2</sup> )	192.44	35.05
Livestock + Bedrock richness	200.28	42.89
Area + Isolation + Bedrock richness	211.48	54.09
Area + Isolation + Livestock	215.57	58.18
Isolation + Livestock	219.95	63
Area + Isolation + Max height	226.82	69.43

Table A5: Best fitting GLM including the interaction between grazing density (Sheep/km2) and observed heights (Mean\_height) of horned lark (*Eremophila alpestris*) to check if grazing is height dependent. AIC: 137.52

Predictors	Estimate	SE	Z-value	P-value
Intercept	10.51	6.97	1.50	0.13
Time used	0.004	0.001	2.94	<b>0.003</b>
2 observers	-0.92	0.24	-3.83	<b>&lt;0.001</b>
3 observers	-0.29	0.36	-0.81	0.41
Bedrock richness (poor)	-1.54	0.57	-2.69	<b>0.007</b>
Bedrock richness (rich)	-0.37	0.23	-1.6	0.1
Sheep/km2	-2.89	2.28	-1.26	0.2
Mean height	-0.006	0.004	-1.29	0.19
Sheep/km2:Mean_height	0.001	0.001	1.16	0.24

Table A6: Available habitat in square kilometres for each height contour and intervals for our study sites. Calculated using a DEM in QGIS 3.8.

Height (m a.s.l.)	Area (km <sup>2</sup> )	Contour interval	Area (km <sup>2</sup> )
1200	392.88	1200-1250	65.15
1250	327.73	1250-1300	74.55
1300	253.18	1300-1350	71.22
1350	181.96	1350-1400	51.49
1400	130.47	1400-1450	42.41
1450	88.06	1450-1500	31.26
1500	56.8	1500-1550	25.58
1550	31.22	1550-1600	17.98
1600	13.24	1600-1650	9.87
1650	3.37	1650-1700	3.06
1700	0.31	1700-	0.31

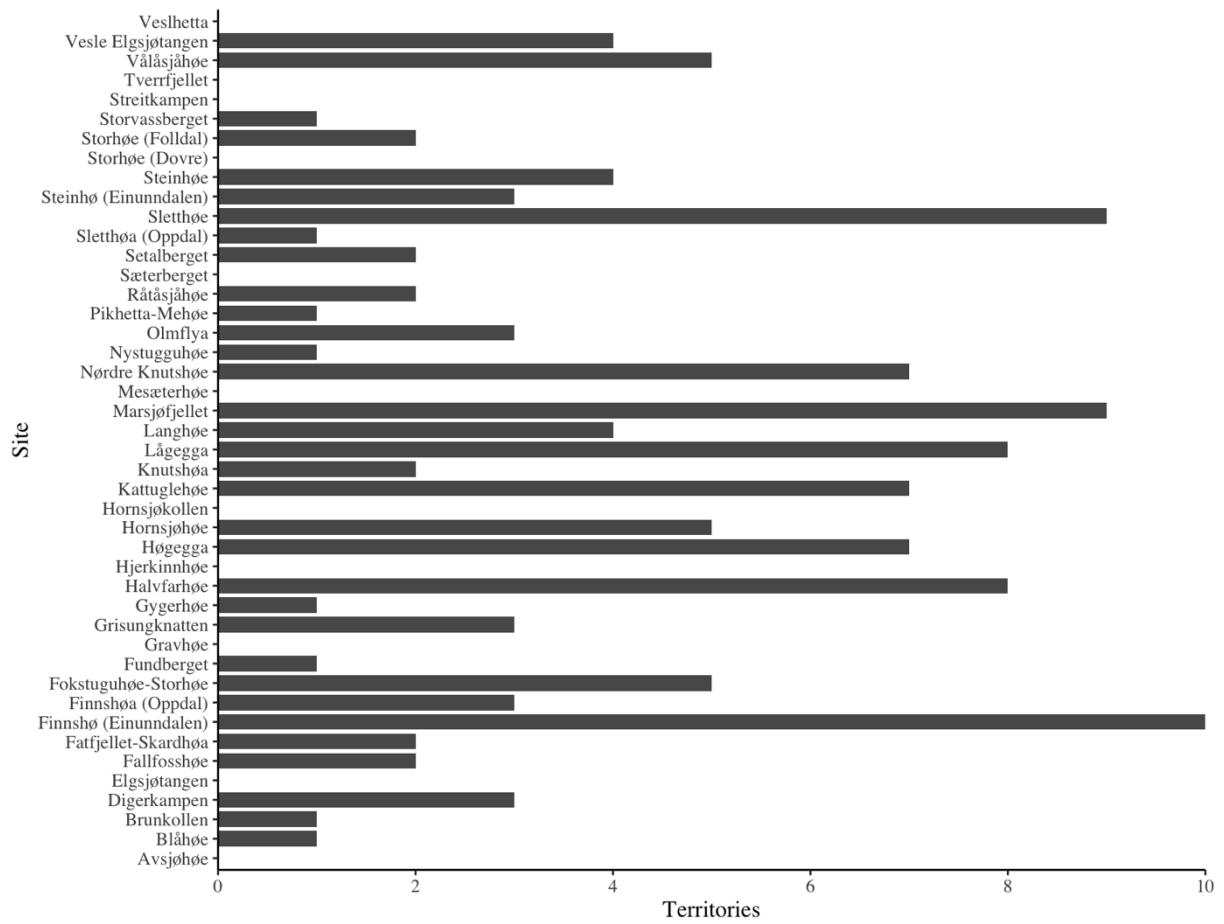


Figure A1: Number of horned lark (*Eremophila alpestris*) territories (x-axis) recorded per study site (y-axis) in Dovre during field surveys in 2022.

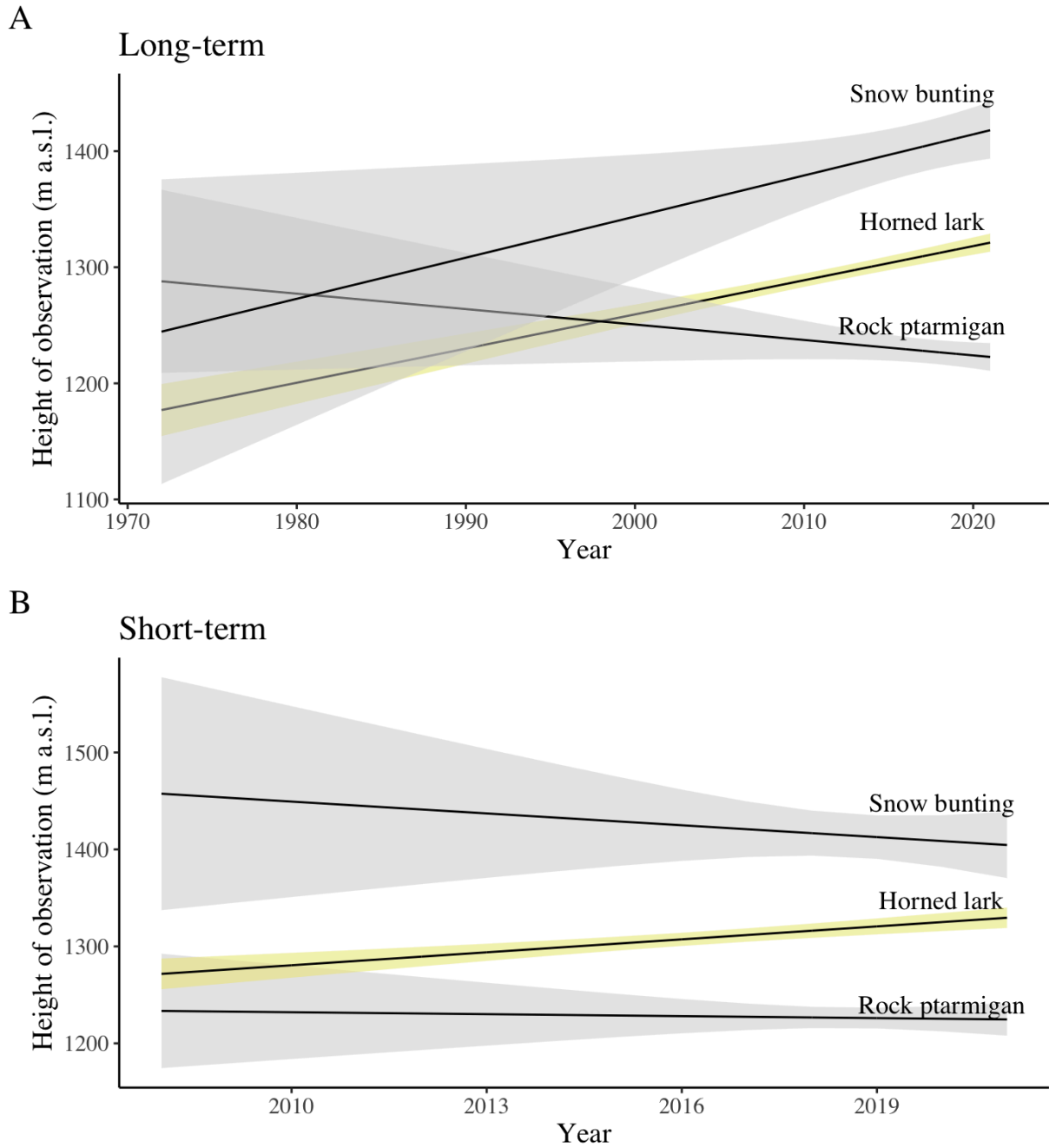


Figure A2: Plot with linear regression lines over the height of observations across years. A. Long-term distribution of observed heights of snow bunting (*Plectrophenax nivalis*), horned lark (*Eremophila alpestris*), and rock ptarmigan (*Lagopus muta*) in Southern Norway. B. Short-term observed heights of the same species in the same areas, divided into long- and short-term because of a higher number of observations after 2008. Since the same trend (slope) does not occur for all species, we can conclude that the elevational shift observed for the horned lark is accurate and not a result of a change in observer behaviour.



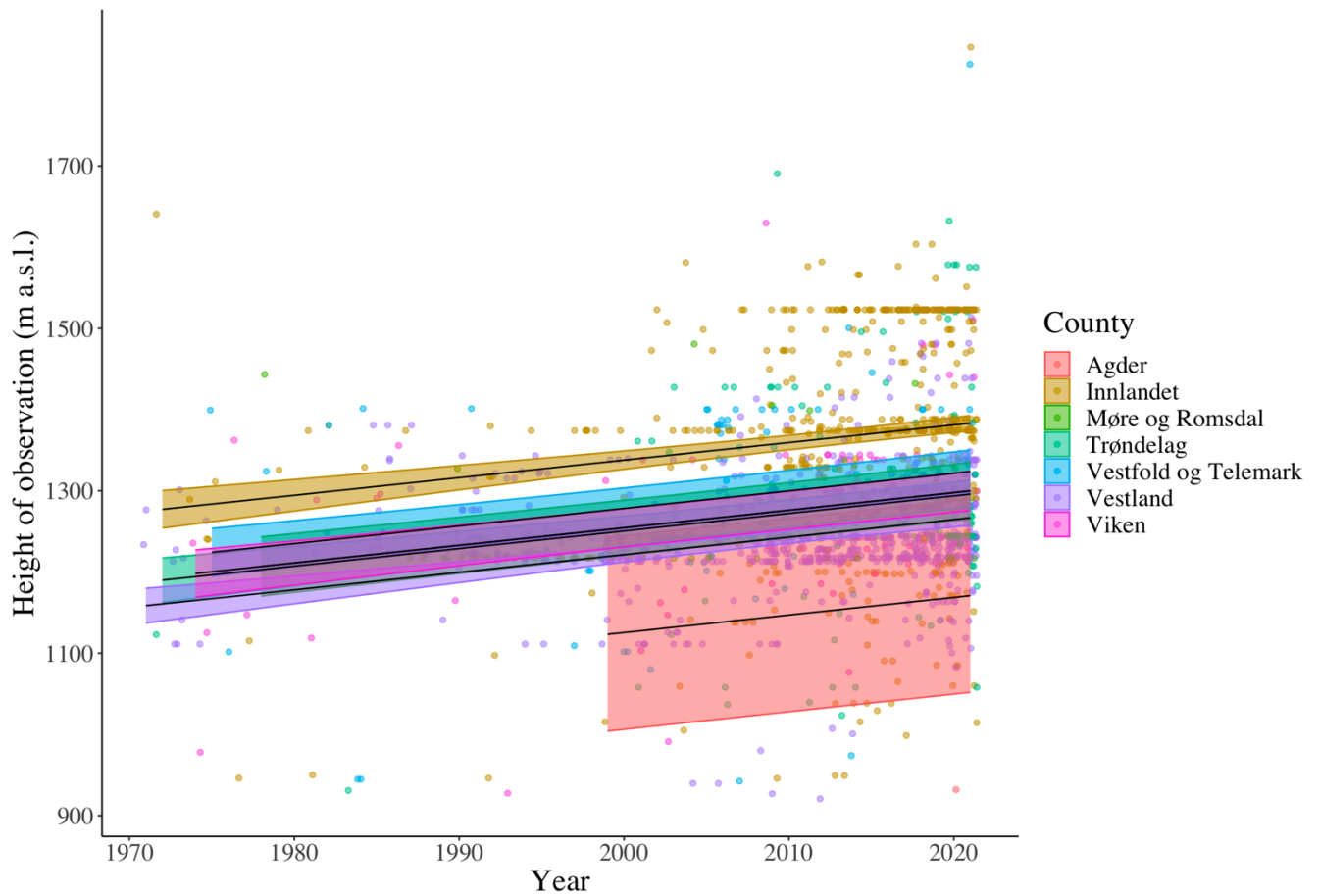


Figure A3: The historical elevational occurrence of horned lark (*Eremophila alpestris*) in southern Norway. The colour represents the different counties and their linear regression line with 95% confidence intervals. As seen in the figure the slope and elevational shift is the same for each county and therefore county has no effect on the analyses.

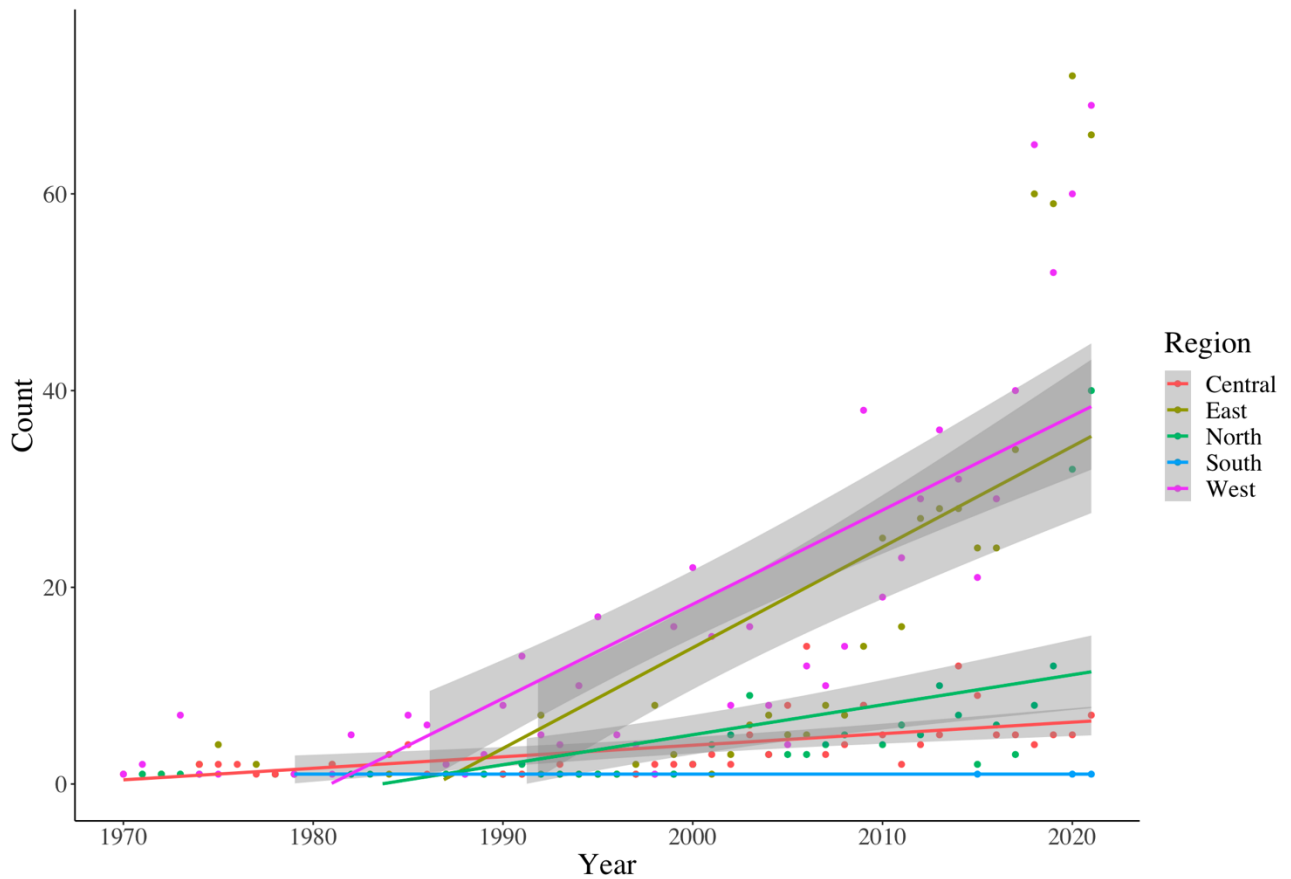


Figure A4: Linear regression lines for each region with the number of registrations as count over each year (x-axis). To check for regional differences in observers' behaviour, a linear regression was conducted with the number of registrations of horned lark (*Eremophila alpestris*) as response variable. The regions where: Central (Viken, Vestfold and Telemark), East (Innlandet), North (Trøndelag, Møre and Romsdal), South (Agder and Rogaland) and West (Vestland). As seen in the figure, no region had a negative trend, but West ( $E=0.84$ ,  $SE=0.14$ ,  $P=<0.001$ ) and East ( $E=0.90$ ,  $SE=0.14$ ,  $P=<0.001$ ) had significant higher visits from birders than the other regions.

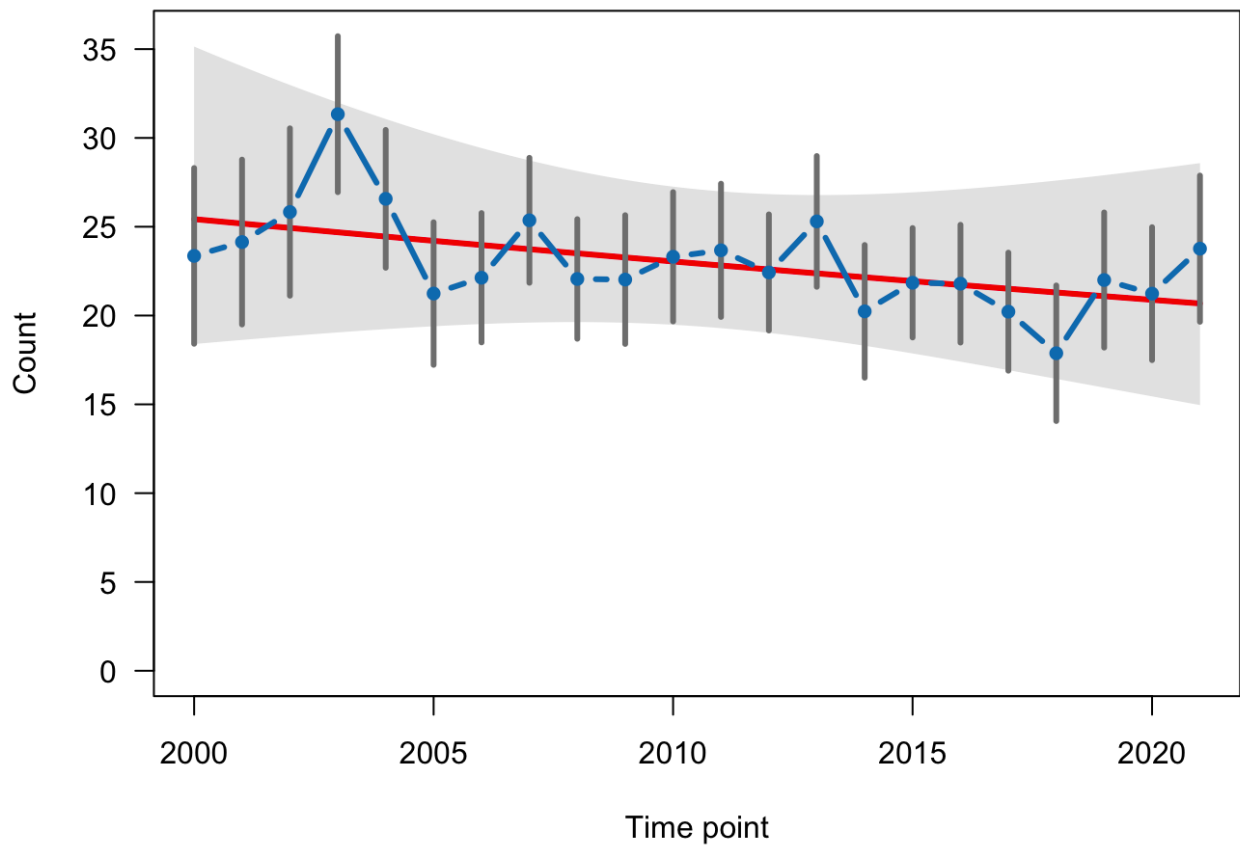


Figure A5: TRIM analysis of historical observational data of horned lark (*Eremophila alpestris*) from Dovrefjell in the period 2000-2021, showing a stable population trend with signs of decline (Slope = -0.009, SE = 0.012, P = 0.44). Wald test for slope significance: Wald = 0.61, df = 1, P = 0.43.



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