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The Role of the Arctic Fox in the Breeding Success of the Snow Bunting

Master's thesis in Biology

Supervisor: Brage Bremset Hansen

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Kunnskap for en bedre verden

Abstract

The reproductive success of breeding birds can be determined by many different factors. One factor often associated with the failure of a brood is nest depredation. To avoid depredation, different bird species implement different adaptations. Some species have evolved a specific nesting-strategy, for example cavity-nesting. In addition to the top-down regulation by predators, breeding birds are also subjected to changing climatic conditions. Bird species which are breeding in the high Arctic, where the breeding season is short and the effects of Arctic warming have already led to changes in the local climate, can be very sensitive to those factors. In this thesis, I explore the role of the Arctic fox (*Vulpes lagopus*) and its top-down effect on the fledging success of a population of migratory snow buntings (*Plectrophenax nivalis*) on Svalbard. First, I investigated how the nest's accessibility influences the daily probability of snow bunting broods being depredated by the Arctic fox and how the predation pressure changes on snow bunting nests throughout the season. Then, I investigated the role of fox abundance in the reproduction of the snow bunting in comparison to weather factors, which have previously been found to impact the breeding success significantly. I used a 22-year long time series from 1998 to 2020 of monitored snow bunting nests in Adventdalen. My analysis revealed nest height to be the dominating factor influencing the daily probability of a nest being depredated. In addition, I found a tendency of broods that were started later in the season to be more depredated than earlier broods. Arctic fox abundance had a rather small effect on the snow buntings' fledging success in comparison to the local climate. The mean temperature had a strong impact on the fledging success, as well as the timing of breeding. This study shows the Arctic fox might not play an essential role in the snow bunting population's breeding success at present. However, there are implications that future warming will impact both the snow bunting and the Arctic fox and might therefore also alter their interactions with each other.

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Introduction

The predator-prey interaction of an ecosystem is an essential factor driving changes in communities, as well as changes in traits of the prey species. The presence of a predator can particularly impact birds in the breeding season. Nest predation is generally seen as the primary factor for nesting failure (Cox et al., 2013; Martin, 1993). Assessing the effect of a predator on a breeding bird species is of high importance since the nesting period is a very sensitive time, and its outcome affects the whole bird population (Martin, 1993). Birds have established different strategies to adapt to predation risk, like camouflage or morphological adaptations (Swaddle & Lockwood, 1998; Troscianko et al., 2016). The characteristics of the nest, like height or concealment, are often used to create a proxy for the accessibility of the nest to a predator, which is another decisive factor in nest depredation (Colombelli-Négrel & Kleindorfer, 2009). Cavity-nesting is often considered more protected than open-nesting and is seen as another form of adaptation to depredation (Martin, 1993; Wesolowski, 2021).

Besides depredation, climatic conditions influence the reproductive success of breeding birds. This could be dramatic in regions where warming is magnified. The Arctic experiences warming that is projected to be almost double the global warming rate (Lameris et al., 2017; Post et al., 2009). This process is called Arctic amplification (Førland et al., 2011). The Svalbard Archipelago experiences the fastest warming in the Arctic and the whole of Europe (Descamps et al., 2017; Førland et al., 2011; Nordli et al., 2020), and the rapid temperature increase has already taken effect in the form of warmer and wetter winters on Svalbard (Førland et al., 2011; Wickström et al., 2020). The consequences of this changing climate are predicted to be manifold. The most influential impact might be the advancement of spring onset, which influences abiotic and biotic factors alike, most notably the properties of the snow cover and the extent of the growing and reproduction season. Earlier and increased snowmelt leads to a decline in sea ice and terrestrial ice cover and a decrease in the depth of the snow (Descamps et al., 2017; Fossøy et al., 2014; Høye et al., 2007; Post et al., 2009). The Arctic vegetation already showed an advancement in flowering and increased productivity, as well as an encroachment in shrubs, called “Arctic greening” (Descamps et al., 2017; Fossøy et al., 2014; Høye et al., 2007; Layton-Matthews et al., 2020; Post et al., 2009). The fauna is affected as well. For example, insects emerge earlier and the egg-laying of several species has advanced in the season (Høye et al., 2007; Post et al., 2009). Several studies have found evidence that

temperature affects the breeding behavior of different bird species. Mainly, warmer and earlier springs are associated with an earlier migration and an earlier clutch initiation (Boelman et al., 2017; Both et al., 2005; Clausen & Clausen, 2013; Fossøy et al., 2014; Liebezeit et al., 2014; Smith, 2012).

The study subject of this project is the snow bunting (*Plectrophenax nivalis*), a small passerine bird which breeds in the Arctic, with a circumpolar breeding pattern around the North Pole (Espmark, 2016; Hoset, 2004). It is the only passerine species that breeds regularly in Svalbard (Espmark, 2016). During the spring migration, male snow buntings arrive in late March to early April on their breeding grounds, while females arrive three to four weeks later (Cramp & Perrins, 1994). Snow buntings are cavity-nesting birds. They build their nests preferably under boulders or in rock cervices (Hussell, 1972). In addition, they use nest boxes and other human-made structures (own observation). Females often start the brooding phase after the third or fourth egg is laid, and the average incubation and fledging period are 13 days long each (Cramp & Perrins, 1994; Espmark, 2016). The chicks' diet differs throughout the season but consists mainly of insects of the families Chironomidae, Scathophagidae, and Muscidae (Stolz, 2019). The breeding behavior of the snow bunting is potentially affected by Arctic warming. The snow bunting population in Fennoscandia has decreased which might be linked to changes in the climate (Lehikoinen et al., 2019; Lehikoinen et al., 2014). Fossøy et al. (2014) have shown that the breeding success of the snow bunting is affected by the local climate, with egg-laying advancing with a warmer climate in spring.

Research has been done on the effect of food abundance on the development of chicks of Arctic breeding birds, including passerine species like the snow bunting (Gravelsæther, 2021; McKinnon et al., 2012; Pérez et al., 2016; Samplonius et al., 2016; Schekkerman et al., 2003). However, the effect of higher trophic levels on the breeding snow bunting has been parameterized so far, even though predators play an important role with their top-down effects on High Arctic ecosystems (Legagneux et al., 2012). In a study on Arctic bird species in Alaska, nest predation by the Arctic fox (*Vulpes lagopus*) was found as the main reason for nest failure (Liebezeit et al., 2014). The Arctic fox is an opportunist whose diet can vary with the seasonality and availability of its prey (Fuglei et al., 2003b; Pedersen et al., 2017). The fox is an essential component in the very simple ecosystem on Svalbard, which lacks other prey items like lemmings and voles found in other Arctic food webs (Fuglei & Ims, 2008; Pedersen et al., 2017). While foxes that live in the inland tundra can rely on lemmings as their dominant prey item, coastal foxes include marine food resources in their diet. They hunt ringed seal pups (*Pusa*

hispida) and scavenges of polar bear (*Ursus maritimus*) kills (Fuglei & Ims, 2008). They prey heavily on the pink-footed goose (*Anser brachyrhynchus*) and the barnacle goose (*Branta leucopsis*) and on several seabirds and their eggs and young in the summer (Fuglei & Ims, 2008; Fuglei et al., 2003a; Layton-Matthews et al., 2020; Pedersen et al., 2017). In addition, evidence that snow buntings are part of the Arctic fox's diet has been found in fox scats (Eide et al., 2005).

Climate change may have many different effects on the Arctic fox. One source of influence on the Arctic fox population that has been highlighted over the past few years are so-called "rain on snow (ROS)" events (Descamps et al., 2017). Warmer and rainier winters result in thawing and subsequent freezing, which leads to the formation of an ice layer on the tundra and the encapsulation of the vegetation underneath. Consequently, the food sources of herbivores, like the Svalbard reindeer (*Rangifer tarandus platyrhynchus*), are harder to reach. This reduces their chance of survival and creates a higher abundance of reindeer carrion, one of the main food resources for the Arctic fox in winter and spring (Fuglei & Ims, 2008; Fuglei et al., 2003a; Hansen et al., 2013; Layton-Matthews et al., 2020; Pedersen et al., 2017). Another effect of climate warming is the retreat of sea ice. Years with a higher amount of sea ice were characterized by fewer dying foxes and a higher breeding rate (Nater, 2021). A decrease in sea ice would disrupt hunting and scavenging. Less sea ice limits access to additional food sources like polar bears' kills and marine resources (Nater, 2021). Moreover, it leads to less connectivity between islands and even isolation of the Arctic fox (Descamps et al., 2017). Due to these both positive and negative impacts of the changing climate, is it challenging to predict how Arctic fox populations will respond to climate change and how their interaction with other trophic levels will be affected. Studies on this issue have been mostly done in Arctic ecosystems which include lemmings in their food web (Gilg et al., 2009; Ims et al., 2017). For example, a study by Gilg et al. (2009) on the effect of changing climate on the predator-prey dynamics in Greenland has shown a disturbance of this dynamic and a decrease in the fox's breeding success under a modeled climate change scenario.

My study aims to investigate the role of the Arctic fox on the reproductive success of a Svalbard population of snow buntings. First, I explored the impact of the Arctic fox on the daily survival probability of accessible nests, and how nest characteristics influence the probability of being depredated. Daily survival probability means here the daily probability of not being depredated. I expected nest height to have a substantial influence on the survival probability, with higher nests being less depredated since they are harder to reach by the fox. In addition, I compared

the effect of the Arctic fox to weather variables that have been proven to affect the breeding outcome of the snow bunting population. I expected the increase of fox abundance to be negatively correlated with the fledging success. Since warmer temperatures are linked to an increase in arthropod abundance and a decrease in energy cost in the incubation stage, I predict that the local climate will have a stronger effect on the reproductive success of the snow buntings than the presence of the fox (Hoset, 2004; Weathers, 1992).

Methods

Study area

The fieldwork for this project was conducted in Adventdalen (78°13'N, 15°38'E; Fig. 1), a valley on the island of Spitsbergen, which belongs to the Svalbard archipelago in the High Arctic. Mountains, glaciers, and fjords dominate the island's landscape, and the main vegetation type is the Arctic tundra (Fuglei & Ims, 2008). The climate of Svalbard is cold and dry all year round, with an average summer temperature of 5.6 °C, an average winter temperature of -9.1 °C, and an average total annual precipitation of approx. 195 mm from 1998 to 2020, all recorded at the Svalbard airport by the Norsk Klimaservicesenter, Norway (<https://klimaservicesenter.no/>).

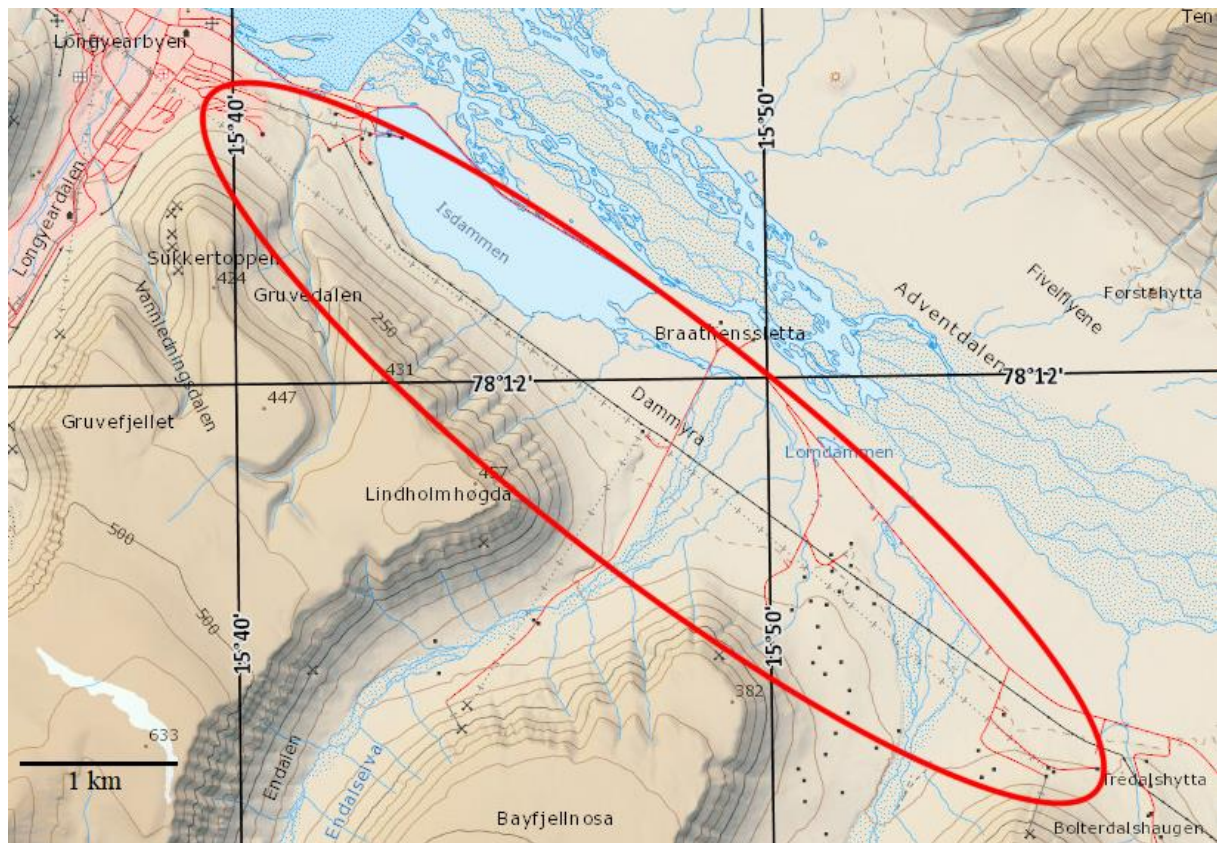


Figure 1: Topographical map of the study area in Adventdalen in Svalbard, marked by a red ellipse. The map was built on a base map from the Norwegian Polar Institute (2022). Coordinates are marked on the grid.

The food web of Svalbard in winter is very simple. It includes one big herbivore, the Svalbard reindeer, the sibling vole (*Microtus levis*), two predators, the polar bear and the Arctic fox, and only a single bird species, the Svalbard rock ptarmigan (*Lagopus muta hyperborean*). The food web's complexity increases in the summer due to the presence of several different migratory bird species, including the snow bunting (Ims et al., 2013).

Data collection

The data collected in this project was added to a long-term data set that was initiated in 1998. The monitoring process followed the established protocols of the preceding years. However, there is variation between years due to different lengths in the monitoring period, different numbers of participants in the fieldwork, and the number of nests found each year.

At the beginning of the monitoring process, the fieldwork took place predominantly along an abandoned cableway that was once used for transporting coal through the valley. The cableway follows a 7 km long transect, consisting of wooden posts placed 50 to 100 m apart from each other (Fig. 2). Approximately 90 wooden nest boxes had been



Figure 2: Part of the cableway in the Adventdalen valley. On the right: Wooden poles with artificial nest boxes.

installed on posts in the study area to facilitate the monitoring process (Fig. 3, Fig. 4). Nests in natural cavities or other human construction were located by observing the behavior of nearby snow buntings, like territorial behavior by the male, nest building, feeding of the partner or chicks, or warning calls by the parents. Every nest was visited, if possible, every second to third day until hatching to record the developmental stages of the brood. The recorded breeding data included the date of the first laid egg as the number of days since May 1st, called clutch initiation date, number of laid eggs, hatching date (the day when at least one egg has hatched), number of hatched eggs, and number and weight of the fledglings. If the nest was found in its incubation stage, the clutch initiation day was calculated by back-dating with the assumptions that a female lays one egg per day and the incubation period lasts for 11 days. This was often done with the

help of a floating test (Ackerman & Eagles-Smith, 2010). When a nest was found after all eggs had hatched, the hatching date was estimated by assessing the age of the oldest chick. We revisited the nests on day eight after the hatching date of the oldest chick. The nestlings were weighed individually using a spring scale and a cotton bag to place the chick inside. A chick was considered a fledgling if it weighed at least 15 g. Chicks smaller than 15 g were deemed too weak to fledge (Fossøy et al., 2014). The number of fledglings and the weight of each chick were noted down. Due to the logistic of this fieldwork, we had to weigh some chicks after day eight. After the weighing, the nests were not visited anymore to avoid premature leave of the nest. In addition, the possible access for Arctic foxes was noted down for each nest, assessed by the height above ground or its inaccessibility due to its placement inside a cavity. Nest boxes were initially considered inaccessible. However, there were two instances of depredated nest boxes. If a nest was found depredated, it was noted down as well. A fox attack is easy to identify, as the fox usually consumes all eggs or chicks and rips out the nest material, destroying the whole nest in the process. Interestingly, two natural nests were found depredated, but with two and one chicks having survived the attack, respectively.



Figure 3: Example of a nest box with an opened lid and with old nest material. Photo by: Iselin Helløy



Figure 4: Snow bunting nest in a nest box.

In addition to nest depredation, there are several other causes of nest failure. The parents can abandon the nests for various reasons, leaving intact nests with cold eggs. Another reason would be a mite infection, which almost always leads to the death of all chicks in a brood. Infected chicks can be easily identified due to their yellow skin with occasionally appearing red spots and their overall weak appearance (own field observation). We found that almost all infected broods did not survive until the fledging stage during the field season 2021. Chicks that die due to malnutrition or infection are transported far away from the nest by their parents. Other nests could only be made eye contact with and not reached. Therefore, we could not record the nestlings' weight. At last, some nests were found too late into the season with chicks too old to be weighed.

The proportion of fox dens with cubs per year in Adventdalen and Sassendalen, hereafter called fox dens proportion, was used as a proxy for the abundance of the Arctic fox. The data was obtained from the website of MOSJ (<https://www.mosj.no/en/fauna/terrestrial/Arctic-fox-population.html>). Since no data on fox abundance was available for 2021, I had to exclude the data for this year.

Environmental data

I used weather data that was recorded at a weather station at the Longyearbyen Airport (78° 15'N, 15° 30'E), located ca. 4 km away from the study site. All data was obtained from the

Norsk Klimaservicesenter (www.eklima.no). The data included the daily mean air temperature in °C and mean precipitation in mm from 1997 to 2020. I aggregated the data to the monthly mean for temperature and the monthly sum for precipitation. I then calculated the mean temperature for June and July, called “summer temperature”. I also calculated the total amount of fallen snow in May by summing the precipitation on days with mean temperatures under 1°C. The spring onset was defined as the first day (Julian day) of the first ten days each year with mean temperatures above 0 °C.

Statistical analysis

All analyses were done with R version 4.2.1(2021-11-01) (Team, 2022).

First, I decided to explore the weather predictors on interannual trends from 1998 to 2020. Summer temperature, spring onset, and the total amount of snowfall in May were tested by fitting a linear regression for each weather variable with year as the numerical explanatory variable. I also tested for interannual trends in fox abundance by fitting a linear regression to fox dens proportion with year as the numerical explanatory variable. In addition, I fitted a linear regression with the total count of predated nests and year as the numerical explanatory variable to test for a possible decrease or increase of predation events over the years. Finally, I wanted to know if the fox shows a preference for nests with eggs or chicks. I calculated the percentage of each developmental stage from the total number of depredated nests. I tested for an interannual trend in the timing of egg-laying by fitting a linear regression for the clutch initiation day with year as the numerical explanatory variable. To test for trends in the breeding success of snow buntings, I fitted a linear regression for the total number of fledglings with year as the numerical explanatory variable.

For the analysis on the daily depredation probability and fledging success of snow bunting nests, I filtered out all nests that had not been completely monitored, either due to abandonment, destruction of nests by other causes, possible fox depredation before the nest was found, or other causes of death like mite infections.

I created a correlation matrix with all continuous variables to explore potential multicollinearity (Fig. A2). Spring onset and summer temperature were negatively correlated ($r=-0.59$) and were therefore never used simultaneously in the same model. All models were fitted with the “glmer”-function from the “lme4”-package (Bates et al., 2014). The significance level was set to 0.05.

Model selection process

I used the dredge-function of the MuMIn-package to select the best-fitting models (Bartoń, 2013). This function creates models with all possible explanatory variables that are fed to it in a global model and ranks them according to their Akaike Information Criterion, corrected for small sample sizes (AIC_c) (Akaike, 1974). The model with the smallest AIC_c is considered the

best-fitting model. Generally, models with $\Delta AIC_c < 2$ are considered best fitting. All global models included year as the random effect. All categorical predictor variables had two levels: 0 and 1. All numerical variables were standardized by subtracting the mean and dividing by the standard deviation before being implemented into the global models.

I tested if nest accessibility was a better predictor as a numerical or categorical variable. For each research question, I created one model with the continuous nest height and one with nest placement which had two levels, on and above ground.

To investigate which factors affected the daily depredation probability of a nest, I fitted a generalized linear mixed model. The response variable, daily survival probability, was a categorical variable, where 0 equaled fully depredated, and 1 equaled survival of at least one chick until fledging. I included fox dens proportion as a proxy for fox abundance as a predictor. I also included the nest's accessibility as a predictor variable. Analysis showed that nests with a height of over 1.7 meters above the ground were never depredated (Fig. A1). Those nests were primarily located in nest boxes, cavities on pylons, or in human constructions and were deemed inaccessible to the fox. This meant that the influence of the Arctic fox only takes effect on nests with a height of 1.7 meters or less. Since this model aimed to answer which factors affect the daily survival of a nest that *can* be depredated, I chose to exclude all nests with a height over 1.7 m above ground for the survival model. The interaction between fox dens proportion and the proxy for nest accessibility was included. Finally, I included the clutch initiation day to explore if the predation pressure changes over the season. The survival model incorporated a log-exp-function created by Bolker (2019). This function is a modified logit-link-function, which is typically used for binomial error distributions. The log-exp-function allows accounting for the fact that individual nests were monitored in different time windows because they were found at different developmental stages like building, egg-laying, incubation, or hatched, which then led to different exposure times. I created a new variable which is the number of days each nest was monitored, from the clutch initiation day to the day of weighing or the possible day of depredation. To use this function properly, all nests with an exposure time of zero days need to be excluded from the analysis. A total of 1131 nests were included in this analysis.

Secondly, I created a generalized linear mixed effect model to investigate the importance of the fox on the fledging success of snow buntings. Here, I chose to use the `cbind()`-function in R to include both the number of fledged and the number of non-fledged chicks to account for the

numbers of successfully fledged chicks and the fledging proportion at the same time. This is, because the nests were of varying sizes, and smaller broods would therefore have a higher fledging proportion than larger broods with the same number of fledglings. For the predictors, I included the weather variables summer temperature or Julian day of spring onset and total snowfall in May into the models. The selection of these weather variables was based on previous studies on the effect of weather on breeding snow buntings, where summer temperature and the snowfall of May in the same year were shown to be strong weather factors affecting the fledging success (Fossøy et al., 2014; Lillehaug, 2019). Here, I included all nests to explore the role of the Arctic fox on the snow bunting at the population level. Nest accessibility and the clutch initiation day were included to account for their ecological effects on the broods. I also included the fox dens proportion and its interaction with nest accessibility. In total, 1121 nests were included in this analysis.

Results

Temporal variation and trends

The first day of spring has significantly moved to an earlier date from 1998 to 2021 ($\beta=-0.73$, $SE=0.32$, $p=0.03$; Fig. 5A). The amount of snow that had fallen in May has increased over the study's time from 5.5 mm in 1998 to 9.6 mm in 2020, with peaks in 2012 and 2018 of 18.6 mm and 20.3 mm, respectively ($\beta=0.25$, $SE=0.16$, $p=0.124$; fig. 5B). The mean summer temperature from June to July has increased from a mean temperature of 5.49 °C in 1998 to 7.18 °C in 2020 ($\beta=0.08$, $SE=0.02$, $p=0.0005$; Fig. 5C).

Fox dens proportion has increased over time ($\beta=0.38$, $SE=0.36$, $p=0.301$, Fig. 6A), while the number of nests per year that were depredated by the Arctic fox shows a significant decline ($\beta=-0.39$, $SE=0.14$, $p=0.014$; Fig. 6B). In summer 2021, 11 out of 69 completely monitored nests were depredated. This data was not used in further analysis due to the lack of fox abundance data for this year. Around 56.4% of all depredated broods were already in the chick stage of their development.

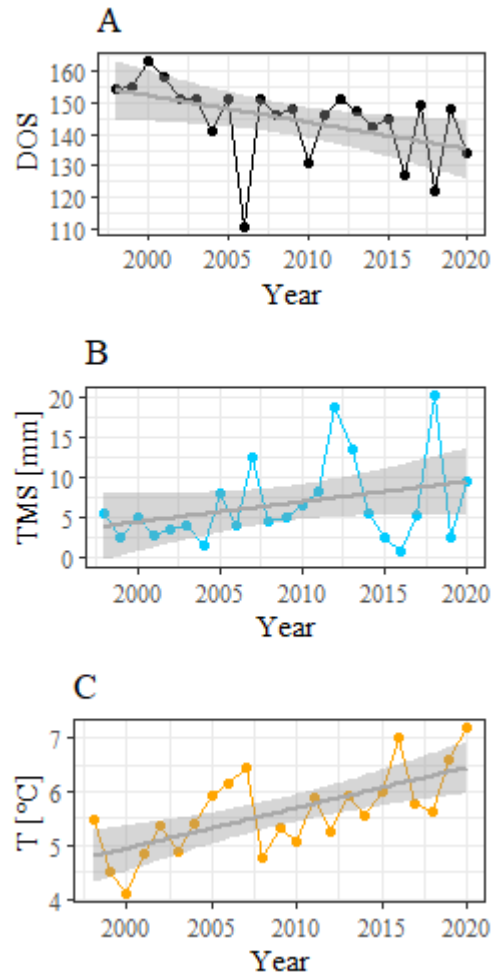


Figure 5: Interannual trends of all weather predictors from 1998 to 2020. T = mean temperature from June to July (A), TMS = total May snowfall (B), DOS = Julian day of spring onset (C).

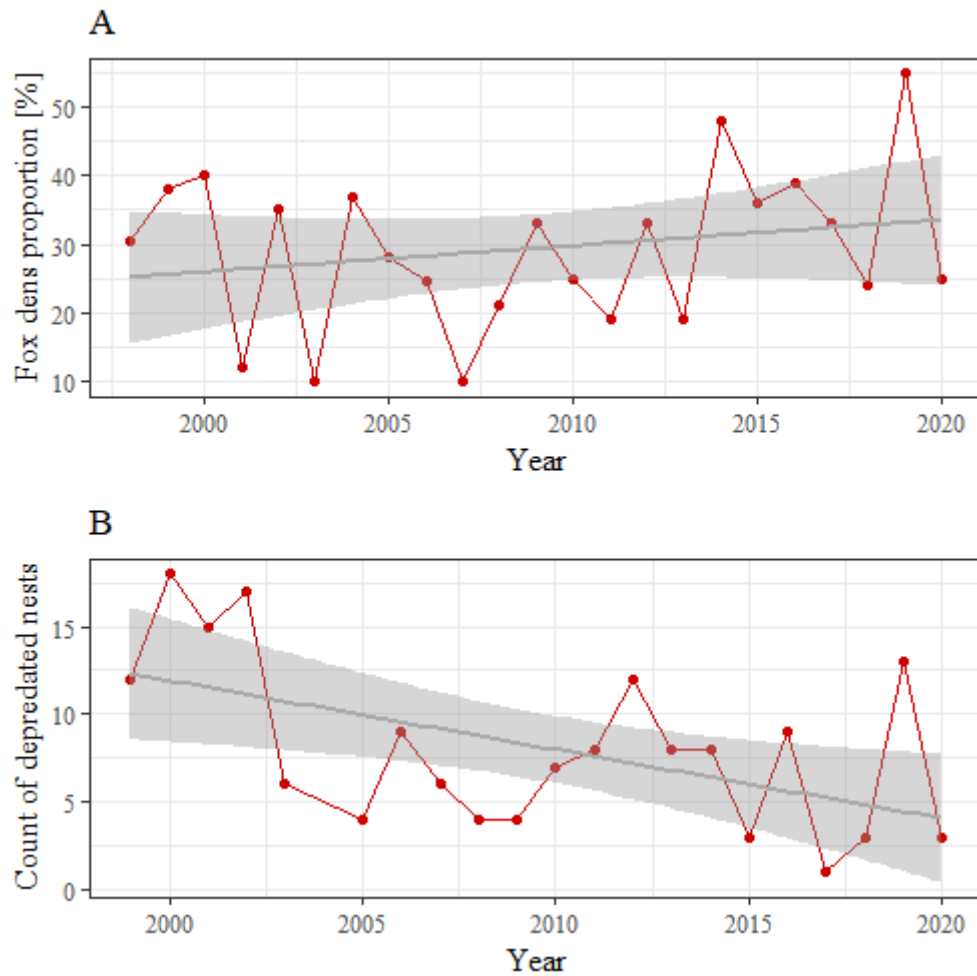


Figure 6: Interannual trend of fox abundance (as the proportion of occupied dens with cubs) (A) and the total count of depredated nests per year (B) from 1998 to 2020.

The median clutch initiation day has decreased from 43 in 1998 to 35.5 days after May 1st in 2020 ($\beta=-0.16$, $SE=0.13$, $p=0.237$; Fig. 7A). The total number of fledglings per year has increased from 1998 to 2020 ($\beta=0.02$, $SE=0.01$, $p=0.001$, Fig. 7B).

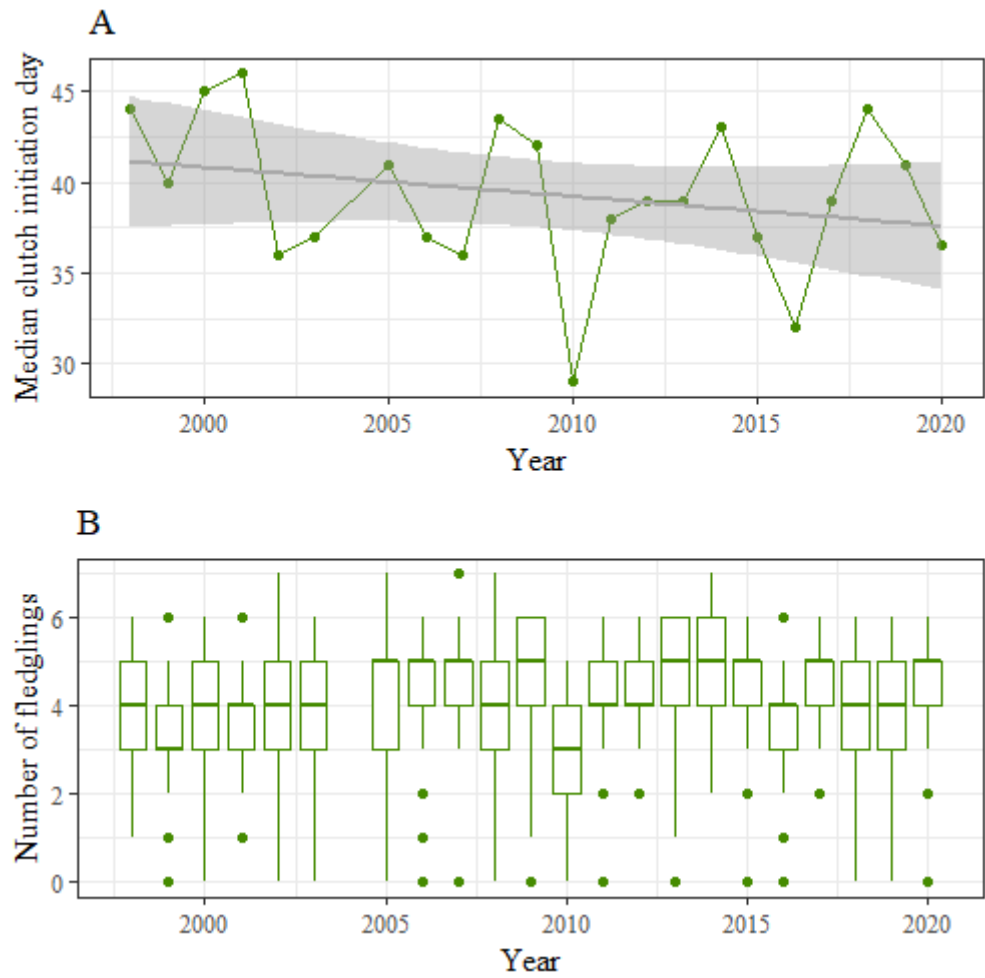


Figure 7: Interannual trend of median clutch initiation as the number of days since May 1st (A), and the total number of fledglings (B) per year from 1998 to 2020.

Model selection

For clarity, I chose the best fitting model that included fox dens proportion out of all models with $\Delta AIC_c < 2$. According to the AIC_c -tables, daily survival probability was better explained by a model including nest height, while for the fledging success model, both predictors were almost equally strong (see Appendix, Tab. A1 – A4). To be consistent, I decided to present the fledging success model with nest height in the results.

Factors influencing the daily survival of snow bunting nests

The daily chance of chick survival was best described by a model with clutch initiation day, fox dens proportion and nest height included as predictors, as well as the interaction between fox dens proportion and nest height, and with year as a random effect (see Appendix, Tab. A1). Nest height had the strongest effect, with the survival probability increasing approx. 26.49 % for broods that were located 0.5 over the ground compared to nests that were located on the ground. Fox dens proportion had a negative effect on the probability of daily survival. For example, the survival probability of broods in the year 2002, which was marked by 35 % occupied fox dens with cubs, was approx. 1.6 % higher than in 2000, where the fox dens proportion was 40%. The negative interaction term of fox dens proportion and nest height indicates that an increasing fox abundance had a stronger negative effect on the survival probability of higher located broods, while the general survival probability is higher than in lower positioned broods (Fig. 8A). The clutch initiation day had a negative effect, meaning that there is a tendency for later broods to be more likely to be depredated. For example, a retreat of the clutch initiation day by ten days, from day 50 to day 40, led to an increase in survival probability by approx. 1.97 % (Tab. 1, Fig. 8B).

Table 1: Output of the model explaining the daily survival probability of a snow bunting brood from the start of egg laying until the end of monitoring. The model includes the clutch initiation day, the interaction between height and fox dens proportion, and year as a random effect. Number of observations = 1131.

Fixed effects	<i>Estimates</i>	<i>SE</i>	<i>p</i>
<i>Intercept</i>	5.45	0.15	<0.001
<i>Clutch initiation day</i>	-0.14	0.09	0.101
<i>Fox dens proportion</i>	-0.29	0.14	0.039
<i>Nest height</i>	1.04	0.14	<0.001
<i>Fox dens proportion * nest height</i>	-0.26	0.12	0.032
Random effect	<i>Variance</i>	N_{Year}	
<i>Year</i>	0.16	22	

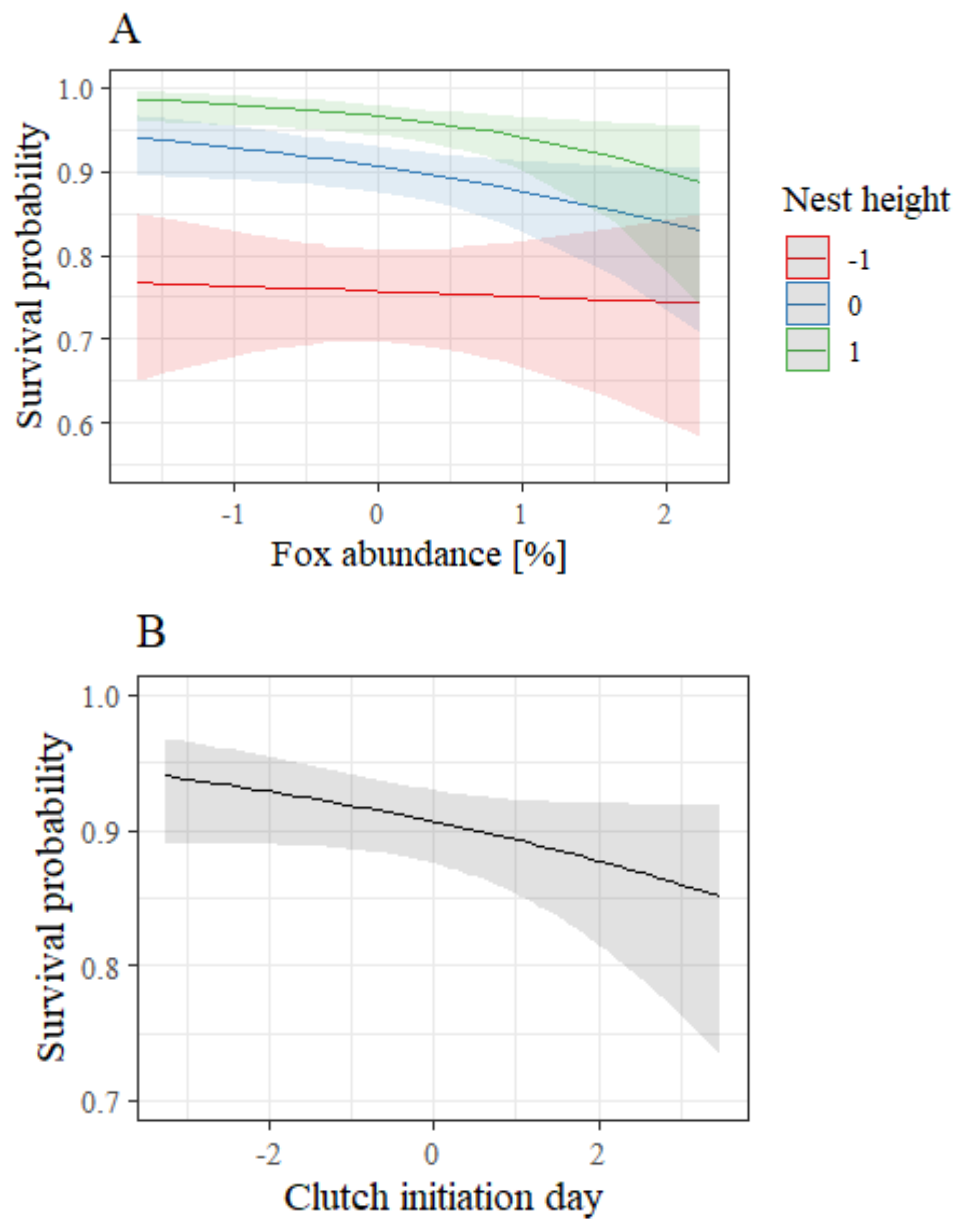


Figure 8: Effect plots of the estimates from the highest-ranked model including fox dens proportion from Appendix Table A1. The plots show the effect of the interaction between nest height and fox dens proportion, with the mean of the standardized nest height, and the mean \pm SD as reference (A), and clutch initiation day (B) on the daily survival probability of snow bunting chicks between 1998 and 2020.

The role of fox abundance on the fledging success of the snow bunting

When including fox dens proportion, the fledging success was best described by a model with clutch initiation day, fox dens proportion, nest height, and summer temperature as fixed effects, and year as a random effect (see Appendix, Tab. A3). The clutch initiation day had the strongest effect of all predictors, with later broods being more successful than earlier broods in the season. For example, broods that were started on day 40 were approx. 12.57 % less successful than broods started on day 50. The second strongest predictor was the summer temperature. An increase from only approx. 1.0 °C from 5.01 to 6.0 °C coincided with an increase in fledging success of approx. 19.86 %. Nest height and fox abundance were similar in their effect sizes. Higher located nests were more successful, with an increase of 0.5 m from the ground leading to an increase in fledging success of approx. 1.27 %. Fox dens proportion had a small negative effect. A decrease from 40 to 35 % in occupied fox dens with cubs would lead to an increase in approx. 2.2 % of fledging success (Tab. 2, Fig. 9).

Table 2: Output of the model explaining fledging success of snow bunting chicks. The model includes the clutch initiation day, fox dens proportion, nest height, summer temperature, and year as a random effect. Number of observations = 1121.

<i>Fixed effects</i>	<i>Estimates</i>	<i>SE</i>	<i>p</i>
<i>Intercept</i>	1.09	0.07	<0.001
<i>Clutch initiation day</i>	0.30	0.04	<0.001
<i>Fox dens proportion</i>	-0.06	0.07	0.441
<i>Nest height</i>	0.07	0.03	0.031
<i>Summer temperature</i>	0.20	0.08	0.009
<i>Random effect</i>	<i>Variance</i>	N_{Year}	
<i>Year</i>	0.09	22	

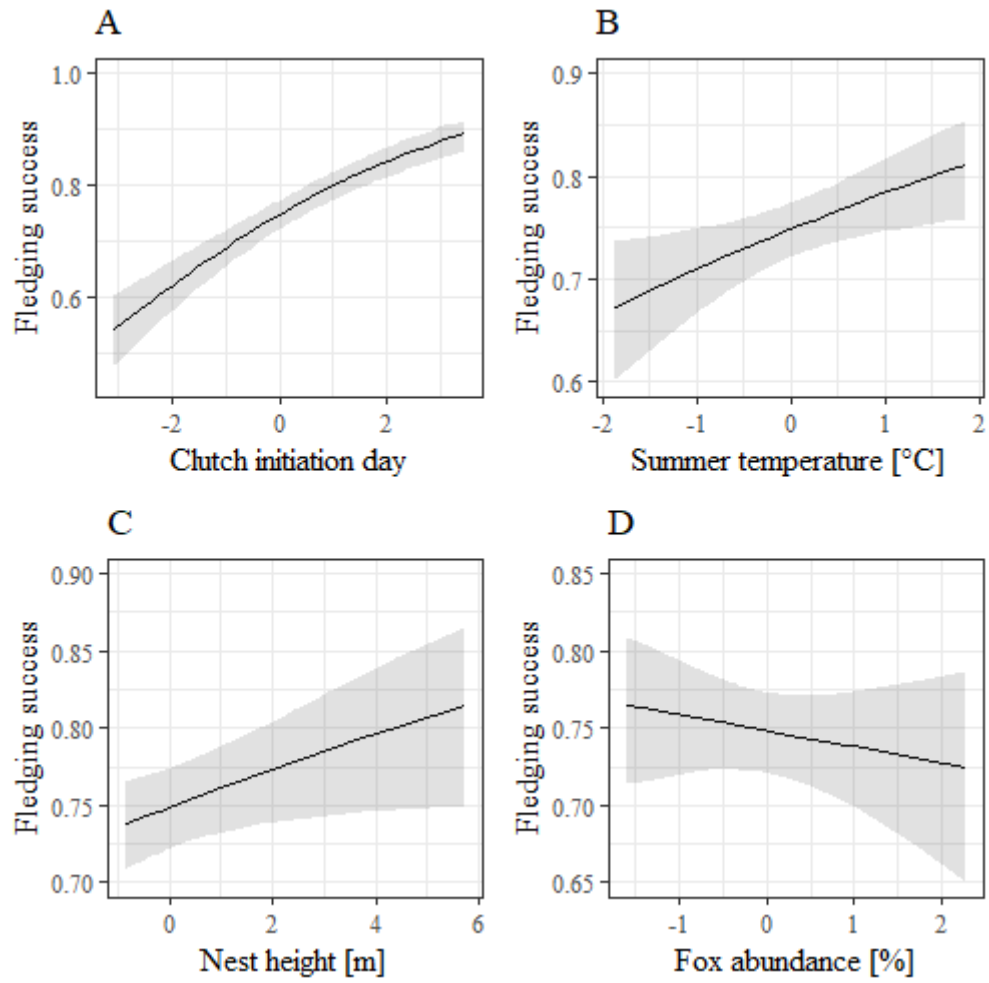


Figure 9: Effect plots of the estimates from the highest-ranked model, including fox dens proportion from Appendix Table A3. The plots show the effect of the clutch initiation day (A), mean temperature in June and July (B), nest height (C), and fox dens proportion (D) on the fledging success of snow bunting chicks between 1998 and 2020.

Discussion

It is still not fully understood, how changes in the local climate can affect interactions between different trophic levels in the High Arctic. This project lays the foundation for such research by assessing the role of the Arctic fox in the reproductive success of the snow bunting, which can be built on in future research.

After analyzing the influence of the Arctic fox on the breeding success of the snow bunting in a 22-yearlong study, I am able to make the following statements: The results of my analysis show that the Arctic fox has no significant effect on the fledging success all the whole population, but that it has an impact on the daily depredation probability of accessible nests. Nest accessibility was a very strong predictor of depredation probability. Furthermore, the probability of depredation increased throughout the season. Later clutch initiation and warmer summer temperatures were very beneficial for the fledging success of a brood, while the Arctic fox only had a weak effect on the nests' fledging success.

I. The effect of fox abundance on the reproductive success of the snow bunting

Fox abundance has a significant effect on the survival probability during the breeding process of accessible nests, but not on the final fledging success of the population. The effect of fox abundance on the fledging success should be interpreted with care. The diagnostics of the model showed that it did not predict very well for low and high extremes in the fledging success (Fig. A3). This is most likely because of outliers in the fledging success due to the low number of nests with zero fledglings. Nevertheless, the observation that the fox has no strong impact on the reproduction of the population is already hinted at with the contradicting trends of increasing fox abundance and decreasing number of recorded depredations on snow bunting nests, and the increasing fledging success from 1998 to 2020 (Fig. 6, Fig. 7B). Both the survival probability and the fledging success model revealed a negative effect of fox abundance, indicating that even though the fox does not affect the snow bunting at the population level, there is still an effect on the individual nest level. The annual depredation rate varies from approx. 4 to 22 %.

The Arctic fox seems very resilient, partly due to its nature as an opportunist feeding on different prey items (Frafjord, 1993; Nater, 2021), and its behavior of scavenging and storing

food for fall and winter (Fuglei & Ims, 2008). Due to those factors, the fox might be less affected by climatic conditions, which allows the fox to preserve a stable population and litter size (Fuglei & Ims, 2008; Fuglei et al., 2003a). The increase in fox abundance and the simultaneous decrease in recorded depredations might be connected to the “alternative prey hypothesis”, where the predation pressure of one prey is negatively correlated with the abundance of another prey (McKinnon et al., 2014; Murdoch, 1969). This could be connected to the ROS events. An increase in reindeer carrion abundance leads to a lagged increase in the Arctic fox population size (Hansen et al., 2013). Angerbjörn et al. (1991) had shown that experimentally added reindeer carrion in the proximity of Arctic fox dens led to a higher occupation of those. ROS events are a phenomenon that is promoted by warming and might therefore occur more often in the future, leading to a higher amount of reindeer carrion as a consequence. They thus might also promote the growth of the Arctic fox population. Over the past decades, the populations of barnacle geese and pink-footed geese on Svalbard have both dramatically increased. This increase is attributed to a warmer climate at breeding grounds and stopover sites (Fox & Madsen, 2017; Hessen et al., 2017). Therefore, one could predict the geese populations in Svalbard to continue growing with the climate becoming more beneficial. A study on the effect of geese abundance on the predation risk of less-abundant prey species showed that a higher geese abundance led to a lower predation rate of the latter (Pedersen et al., 2017). Geese breed on the ground and their nests might require less energy to access than the natural nests of snow buntings which are often located in cavities under stone piles. Additionally, goose eggs are larger than snow bunting eggs. Thus, preying on goose eggs is more profitable than preying on snow bunting nests. This supports my findings that the effect of the fox is very small on the less-preferred snow bunting. Even though the mentioned study could only analyze one year of data -which leads me to conclude that those findings can only be judged as preliminary-, I still theorize that an increase in goose population decreased the predation pressure on the snow bunting over the study’s period and will continue to do so in the future. This might explain the decrease in predated nests while the fox population increased simultaneously. I would like to suggest that it could be worthwhile to look at both goose nest depredation rates and snow bunting depredation rates in one study to explore a possible correlation between high depredation rates on geese and low depredation rates on snow buntings.

II. Factors determining the daily survival probability of a snow bunting brood

The location of the nest is a fundamental predictor of the probability of depredation by the fox. The height of the nest above ground, as well as its placement on or above the ground, were very strong predictors of the daily survival probability, while nest height was a better predictor according to the model selection process (see Appendix, Table A1 and Table A2). This result fits our prediction that the nest's location has a strong influence on whether a brood will be depredated or not. Around 78% of all depredated nests – with recorded height – were located on the ground, making them easier to access for the fox (Fig. A4). Many studies have been done on different bird taxa on the role of nest characteristics on the predation risk. The results are vastly different, with some studies showing a decrease in depredation risk with an increasing nest height (Holcomb & Twiest, 1968; Nilsson, 1984), some showing the opposite (Colombelli-Négrel & Kleindorfer, 2009; Guan et al., 2018; Holcomb, 1972), and some showing no correlation at all (Christman & Dhondt, 1997; Colombelli-Négrel & Kleindorfer, 2009; Ortega et al., 1998). Interestingly, while the general daily survival probability is higher in higher located nests, the effect of an increasing fox abundance is stronger on higher than on lower nests. One possible explanation could be the competitive pressure to find food resources in years of high fox abundance. The competition might lead some foxes to depredate nests that are more difficult to access and require more energy to reach. This result could moreover be a statistical artifact due to the low sample size for nests over 0 meters. Most depredated nests above ground were nest boxes on stone piles and cavities on pylons. The fox can reach those nests by climbing. 14 of the 15 depredated nest boxes on pylons had been depredated between 2018 and 2020. This indicated that these depredations were done by a single fox that learned how to climb up the pylons.

The timing of breeding may also play a role in the depredation probability of the brood. We can see that nests that are started later in the season have a higher daily risk of depredation. The Arctic fox has its pups between March and July, which coincides with the breeding season of the snow bunting (Cramp & Perrins, 1994; Prestrud, 1991). I theorize that with the progressing development of the pups, the parents are under more pressure to find food resources and will choose to prey on snow bunting nests, even though there are less profitable than goose nests. Another reason for such a result could be the vanishing snow in June. That could facilitate the detection of the snow bunting parents, whose plumage camouflages them well on a white background but makes them jump out from the greening vegetation in the summer. This hypothesis had been tested before by Byrkjedal (1980) on the shorebird the golden plover

(*Pluvialis apricaria*) in southern Norway. Byrkjedal (1980) theorized that nests on small-free patches would be more vulnerable to depredation by the red fox (*Vulpes vulpes*), which affects the timing of clutch initiation. However, the golden plover is an open-nesting bird, which might be more affected by long-lasting snow than cavity-breeders like the snow bunting (Byrkjelda, 1980). Therefore, the snow-patch hypothesis might not apply to the snow bunting. A study on the possible linkage between higher predation rate of bird nests and primary production due to increasing predator abundance showed an increase in predation risk with an increase in Arctic greening (Ims et al., 2019). However, this study did not only focus on the Arctic fox, so its role in this phenomenon is difficult to decipher. It must be mentioned that most studies on the depredation by the Arctic fox focus solely on open-nesting birds like geese. Since the snow bunting breeds in cavities, the role of snow on the ground might not be of particular importance. 622 out of 1131 accessible nests are located above ground and are likely not affected by snow cover. To conclude, more research is needed to explore the reason for such a trend.

III. Comparing the effect of the Arctic fox and the local climate on the reproductive success of the snow bunting

The local climate has a stronger influence on the reproductive success of snow buntings than the Arctic fox. Even though the first day of spring has moved to an earlier date, it did not play a significant role in the fledging success of the snow bunting. On the contrary, summer temperature seems to be a dominant climatic factor in the success of the breeding snow buntings. The results of the model selection process for the fledging success model suggest that warmer summers are beneficial for the brood. Similar results had been found previously in other studies (Fossøy et al., 2014; Hoset, 2004; Lillehaug, 2019). One reason for this is a higher insect abundance, which is the main food source of snow bunting chicks (Hoset, 2004). Another reason is that Arctic bird species are subjected to generally lower ambient temperatures and have higher thermoregulation costs than bird species of other latitudes (Weathers, 1992). The incubation process is less energy consuming if the temperature around the nests is higher, which had been shown in an experimental study on starlings (Reid et al., 2000). From there, we can theorize that warmer temperatures would decrease energy costs for both the young and the adults, and fledging would be less energy demanding. Additionally, nestlings in nests with a warmer ambient temperature have a higher fitness, according to an experimental study (Dawson et al., 2005). Snowfall in May had no effect in the chosen top models. However, may snowfall has been proven before to affect the final number of fledglings (Lillehaug, 2019). This could

be connected to a later arthropod emergence due to extended periods of snow-covered grounds (Høye et al., 2007). A later peak of the snow bunting's food source would help the snow buntings to avoid a potential mismatch due to an early arthropod emergence (Visser & Gienapp, 2019). Only the timing of clutch initiation had a stronger effect than the local climate. Reasons for this had been discussed elsewhere. A higher arthropod abundance later in the season or a higher investment in later broods by the parents have been mentioned before as possible explanations for later broods being more successful (Lillehaug, 2019).

Conclusion and outlook

This long-term study gave a novel insight into the intraspecific interaction between the snow bunting and the Arctic fox and the role of the Arctic fox in the reproductive success of the bunting. The location of the nests plays a major role in the survival probability of chicks, especially the height of nests, since the depredation rate decreased with increasing height. Broods that were started later in the season had a higher probability of being depredated than earlier nests, which might have to do with the increase in food requirement for foxes with pups, or the vanishing snow cover that makes nests and snow bunting easier to detect and should be more explored in the future. The increase in fox abundance had led me to predict an increase in depredation over the study's time, which was not the case. The opportunistic nature of the Arctic fox might play a role in this observation. An increase in the population size of their preferred prey, the goose, may decrease the predation pressure on less profitable prey like the snow bunting. It would be interesting to investigate a possible linkage between the depredation rate of snow buntings and geese. The model selection revealed fox abundance to be a poor predictor of the fledging success compared to temperature and during the rearing phase until fledging. Generally, the reproductive output of the snow bunting has increased over the years. With the positive effects of warmer temperatures, together with the small effect of the Arctic fox on the reproductive success of the bunting, the outlook for the snow bunting is positive. However, due to the projected increase in ROS events and, therefore, the possible increase in reindeer carrion, the number of cubs and the number of reproducing foxes per season may also increase (Angerbjörn et al., 1991). This could potentially lead to higher predation pressure on all of the fox's prey items, including the snow bunting.

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Bibliography

- Ackerman, J. T., & Eagles-Smith, C. (2010). Accuracy of egg flotation throughout incubation to determine embryo age and incubation day in waterbird nests. *The Condor*, *112*(3), 438-446.
- Akaike, H. (1974). Akaike, H. (1974). A new look at the statistical model identification. *IEEE transactions on automatic control*, *19*(6), 716-723.
- Angerbjörn, A., Arvidson, B., Norén, E., & Strömberg, L. (1991). The effect of winter food on reproduction in the arctic fox, *Alopex lagopus*: a field experiment. *The Journal of Animal Ecology*, 705-714.
- Bartoń, K. (2013). MuMIn: Multi-model inference.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv*, 1406.5823.
- Boelman, N. T., Krause, J. S., Sweet, S. K., Chmura, H. E., Perez, J. H., Gough, L., & Wingfield, J. C. (2017). Extreme spring conditions in the Arctic delay spring phenology of long-distance migratory songbirds. *Oecologia*, *185*(1), 69-80.
- Bolker, B. (2019, 30.09.2014). *Logistic regression, accounting for differences in exposure*. Retrieved 11.04.2022 from
- Both, C., Piersma, T., & Roodbergen, S. P. (2005). Climatic change explains much of the 20th century advance in laying date of Northern. *Ardrea*, *93*(1), 79-88.
- Byrkjelda, I. (1980). Nest Predation in Relation to Snow-Cover A Possible Factor Influencing the Start of Breeding in Shorebirds. *Ornis Scandinavica*, *11*(3), 249-252.
- Christman, B. J., & Dhondt, A. A. (1997). Nest predation in Black-capped Chickadees: How safe are cavity nests? *The Auk*, *114*(4), 769-773.
- Clausen, K. K., & Clausen, P. (2013). Earlier Arctic springs cause phenological mismatch in long-distance migrants. *Oecologia*, *173*(3), 1101-1112.
- Colombelli-Négrel, D., & Kleindorfer, S. (2009). Nest height, nest concealment, and predator type predict nest predation in superb fairy-wrens (*Malurus cyaneus*). *Ecological Research*, *24*(4), 921-928.
- Cox, W. A., III, T., R., F., & Reidy, J. L. (2013). The effects of temperature on nest predation by mammals, birds, and snakes. *The Auk*, *130*(4), 784-790.
- Cramp, S., & Perrins, C. (1994). Buntings and new world warblers. In *The birds of the Western Palearctic* (Vol. 9). Oxford University Press.

- Dawson, R. D., Lawrie, C. C., & O'Brien, E. L. (2005). The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. *Oecologia*, *144*(3), 499-507.
- Descamps, S., Aars, J., Fuglei, E., Kovacs, K. M., Lydersen, C., Pavlova, O., . . . Strom, H. (2017). Climate change impacts on wildlife in a High Arctic archipelago - Svalbard, Norway. *Global Change Biology*, *23*(2), 490-502.
- Eide, N. E., Eid, P. M., Prestrud, P., & Swenson, J. E. (2005). Dietary responses of arctic foxes *Alopex lagopus* to changing prey availability across an Arctic landscape. *Wildlife Biology*, *11*(2), 109-121.
- Espmark, Y. (2016). Breeding biology of snow buntings (*Plectrophenax nivalis*) in Svalbard. *Royal Norwegian Society of Sciences and Letters*.
- Fossøy, F., Stokke, B. G., Kåsi, T. K., Dyrset, K., Espmark, Y., Hoset, K. S., . . . Moksnes, A. (2014). Reproductive success is strongly related to local and regional climate in the Arctic snow bunting (*Plectrophenax nivalis*). *Polar Biology*, *38*(3), 393-400.
- Fox, A. D., & Madsen, J. (2017). Threatened species to super-abundance: The unexpected international implications of successful goose conservation. *Ambio*, *46*(2), 179-187.
- Frafjord, K. (1993). Food habits of arctic foxes (*Alopex lagopus*) on the western coast of Svalbard. *Arctic*, 49-54.
- Fuglei, E., & Ims, R. A. (2008). Global warming and effects on the Arctic fox. *Sci Prog*, *91*(Pt 2), 175-191.
- Fuglei, E., Øritsland, N. A., & Prestrud, P. (2003a). Local variation in arctic fox abundance on Svalbard, Norway. *Polar Biology*, *26*(2), 93-98.
- Fuglei, E., Øritsland, N. A., & Prestrud, P. (2003b). Local variation in arctic fox abundance on Svalbard, Norway. *Polar Biology*, *26*(2), 93-98.
- Førland, E. J., Benestad, R., Hanssen-Bauer, I., Haugen, J. E., & Skaugen, T. E. (2011). Temperature and Precipitation Development at Svalbard 1900–2100. *Advances in Meteorology*, *2011*, 1-14.
- Gilg, O., Sittler, B. T., & Hanski, I. (2009). Climate change and cyclic predator–prey population dynamics in the high Arctic. *Global Change Biology*, *15*(11), 2634-2652.
- Gravelsæther, M. (2021). *Effects of arthropod abundance on reproductive success in Svalbard snow bunting (Plectrophenax nivalis)* Norwegian University of Science and Technology].

- Guan, H., Wen, Y., Wang, P., Lv, L., Xu, J., & Li, J. (2018). Seasonal increase of nest height of the Silver-throated Tit (*Aegithalos glaucogularis*): can it reduce predation risk? *Avian Research*, 9(1), 1-8.
- Hansen, B. B., Grotan, V., Aanes, R., Saether, B. E., Stien, A., Fuglei, E., . . . Pedersen, A. O. (2013). Climate events synchronize the dynamics of a resident vertebrate community in the high Arctic. *Science*, 339(6117), 313-315.
- Hessen, D. O., Tombre, I. M., van Geest, G., & Alfsnes, K. (2017). Global change and ecosystem connectivity: How geese link fields of central Europe to eutrophication of Arctic freshwaters. *Ambio*, 46(1), 40-47.
- Holcomb, L. C. (1972). Nest success and age-specific mortality in Traill's Flycatchers. *The Auk*, 89(4), 837-841.
- Holcomb, L. C., & Twiest, G. (1968). Ecological factors affecting nest building in Red-winged Blackbirds. *Bird-banding*, 14-22.
- Hoset, K. S., Espmark, Y. N. G. V. E., Moksnes, A. R. N. E., Haugan, T., Ingebrigtsen, M., & Lier, M. (2004). Effect of ambient temperature on food provisioning and reproductive success in snow buntings *Plectrophenax nivalis* in the high arctic. *Ardea*, 92(2), 239-246.
- Hussell, D. J. T. (1972). Factors that affect breeding success. *Ecological Monographs*, 42(3), 317-364.
- Høyve, T. T., Post, E., Meltofte, H., Schmidt, N. M., & Forchhammer, M. C. (2007). Rapid advancement of spring in the High Arctic. *Curr Biol*, 17(12), R449-451.
- Ims, R. A., Henden, J. A., Strømeng, M. A., Thingnes, A. V., Garmo, M. J., & Jepsen, J. U. (2019). Arctic greening and bird nest predation risk across tundra ecotones. *Nature Climate Change*, 9(8), 607-610.
- Ims, R. A., Jepsen, J. U., Stien, A., & Yoccoz, N. G. (2013). *Science plan for COAT: climate-ecological observatory for Arctic Tundra* (Fram Centre report series, Issue.
- Ims, R. A., Killengreen, S. T., Ehrich, D., Flagstad, Ø., Hamel, S., Henden, J.-A., . . . Yoccoz, N. G. (2017). Ecosystem drivers of an Arctic fox population at the western fringe of the Eurasian Arctic. *Polar Research*, 36(sup1).
- Lameris, T. K., Scholten, I., Bauer, S., Cobben, M. M. P., Ens, B. J., & Nolet, B. A. (2017). Potential for an Arctic-breeding migratory bird to adjust spring migration phenology to Arctic amplification. *Global Change Biology*, 23(10), 4058-4067.
- Layton-Matthews, K., Hansen, B. B., Grotan, V., Fuglei, E., & Loonen, M. (2020). Contrasting consequences of climate change for migratory geese: Predation, density

- dependence and carryover effects offset benefits of high-arctic warming. *Global Change Biology*, 26(2), 642-657.
- Legagneux, P., Gauthier, G., Berteaux, D., Bêty, J., Cadieux, M.-C., Bilodeau, F., . . . Krebs, C. J. (2012). Disentangling trophic relationships in a High Arctic tundra ecosystem through food web modeling. *Ecology*, 93(7), 1707–1716.
- Lehikoinen, A., Brotons, L., Calladine, J., Campedelli, T., Escandell, V., Flousek, J., . . . Trautmann, S. (2019). Declining population trends of European mountain birds. *Global Change Biology*, 25(2), 577-588.
- Lehikoinen, A., Green, M., Husby, M., Kålås, J. A., & Lindström, Å. (2014). Common montane birds are declining in northern Europe. *Journal of Avian Biology*, 45(1), 3-14.
- Liebezeit, J. R., Gurney, K. E. B., Budde, M., Zack, S., & Ward, D. (2014). Phenological advancement in arctic bird species: relative importance of snow melt and ecological factors. *Polar Biology*, 37(9), 1309-1320.
- Lillehaug, E. (2019). *Environmental correlates of variation in a holistic analysis of annual offspring production in the high Arctic songbird snow bunting (Plectrophenax nivalis) on Spitsbergen* [Master's thesis, NTNU].
- Martin, T. E. (1993). Nest predation and nest sites. *BioScience*, 43(8), 523-532.
- McKinnon, L., Berteaux, D., & Bêty, J. (2014). Predator-mediated interactions between lemmings and shorebirds: A test of the alternative prey hypothesis. *The Auk: Ornithological Advances*, 131(4), 619-628.
- McKinnon, L., Picotin, M., Bolduc, E., Juillet, C., & Bêty, J. (2012). Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic. *Canadian Journal of Zoology*, 90(8), 961-971.
- Murdoch, W. W. (1969). Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological monographs*, 39(4), 335-354.
- Nater, C. R., Eide, N. E., Pedersen, Å. Ø., Yoccoz, N. G., & Fuglei, E. (2021). Contributions from terrestrial and marine resources stabilize predator populations in a rapidly changing climate. *Ecosphere*, 12(6).
- Nilsson, S. G. (1984). The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. *Ornis Scandinavica*, 167-175.
- Nordli, Ø., Wyszynski, P., Gjeltén, H. M., Isaksen, K., Łupikasza, E., Niedźwiedz, T., & Przybylak, R. (2020). Revisiting the extended Svalbard Airport monthly temperature series, and the compiled corresponding daily series 1898–2018. *Polar Research*, 39(0).

- Ortega, C. P., Ortega, J. C., Rapp, C. A., & Backensto, S. A. (1998). Validating the use of artificial nests in predation experiments. *The Journal of wildlife management*, 925-932.
- Pedersen, Å. Ø., Stien, J., Eidesen, P. B., Ims, R. A., Jepsen, J. U., Stien, A., . . . Fuglei, E. (2017). High goose abundance reduces nest predation risk in a simple rodent-free high-Arctic ecosystem. *Polar Biology*, 41(4), 619-627.
- Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., . . . Aastrup, P. (2009). Ecological Dynamics across the Arctic Associated with Recent Climate Change. *Scienc*e, 3252(325), 1355-1358.
- Prestrud, P. (1991). Prestrud, P. (1991). Adaptations by the arctic fox (*Alopex lagopus*) to the polar winter. *Arctic*, 132-138.
- Pérez, J. H., Krause, J. S., Chmura, H. E., Bowman, S., McGuigan, M., Asmus, A. L., & Wingfield, J. C. (2016). Nestling growth rates in relation to food abundance and weather in the Arctic. *The Auk: Ornithological Advances*, 133(2), 261-272.
- Reid, J. M., Monaghan, P., & Ruxton, G. D. (2000). Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267(1438), 37-41.
- Samplonius, J. M., Kappers, E. F., Brands, S., & Both, C. (2016). Phenological mismatch and ontogenetic diet shifts interactively affect offspring condition in a passerine. *Journal of Animal Ecology*, 85(5), 1255-1264.
- Schekkerman, H., Tulp, I., Piersma, T., & Visser, G. H. (2003). Mechanisms promoting higher growth rate in arctic than in temperate shorebirds. *Oecologia*, 134(3), 332-342.
- Smith, B. D., Hagmeier, K. R., Boyd, W. S., Dawe, N. K., Martin, T. D., & Monty, G. L. (2012). Trends in volume migration chronology in spring staging Pacific black brant. *The Journal of Wildlife Management*, 76(3), 593-599.
- Stolz, C. (2019). *Stolz, C. (2019). The nestling diet of Svalbard snow buntings identified by DNA metabarcoding* [Master's thesis, UiT Norges arktiske universitet].
- Swaddle, J. P., & Lockwood, R. (1998). Morphological adaptations to predation risk in passerines. 1998, *Journal of Avian Biology*, 172-176.
- Team, R. S. (2022). *RStudio: Integrated Development Environment for R*. In RStudio, PBC.
- Troscianko, J., Wilson-Aggarwal, J., Stevens, M., & Spottiswoode, C. N. (2016). Camouflage predicts survival in ground-nesting birds. *Scientific reports*, 6(1), 1-8.

- Visser, M. E., & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nat Ecol Evol*, 3(6), 879-885.
- Weathers, W. W. (1992). Scaling nestling energy requirements. *Ibis*, 134(2), 142-153.
- Wesołowski, T. (2021). Wesołowski, T. (2021). Natural nest sites of the European Starling *Sturnus vulgaris* in a primeval temperate forest. *Bird Study*, 68(2), 145-156.
- Wickström, S., Jonassen, M. O., Cassano, J. J., & Vihma, T. (2020). Present Temperature, Precipitation, and Rain-on-Snow Climate in Svalbard. *Journal of Geophysical Research: Atmospheres*, 125(14).

Appendix

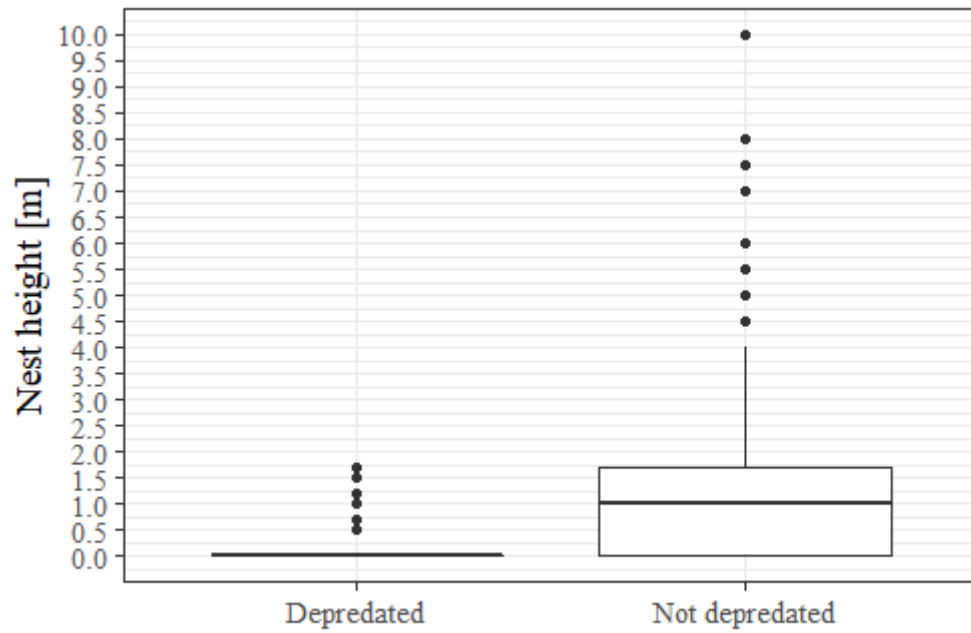


Figure A1: Boxplot of the height of depredated and not depredated nests.

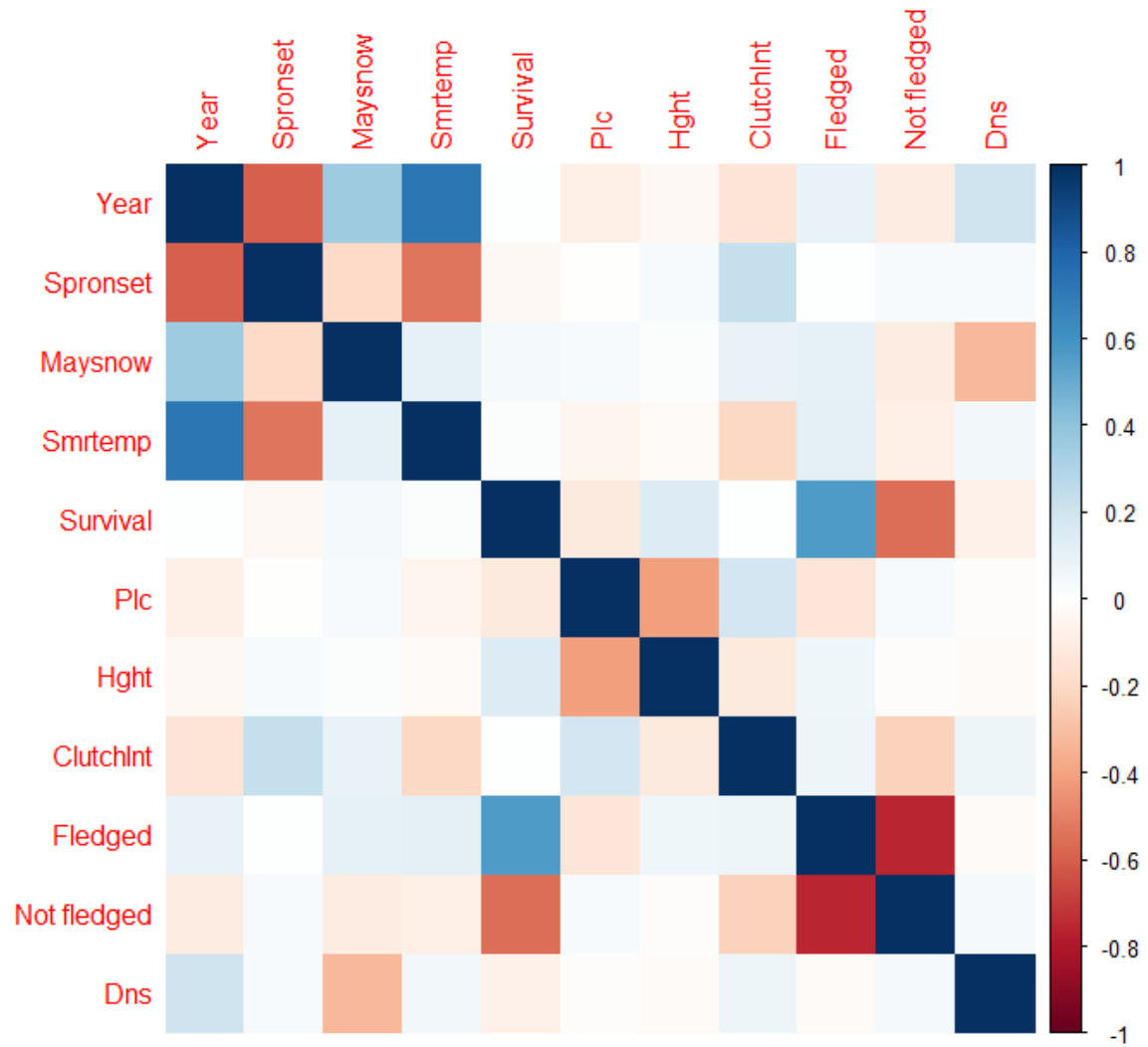


Figure A2: Correlation matrix of all variables. *Spronset* – Julian day of spring onset, *Maysnow* – total snowfall in May [mm], *Smrtemp* – mean temperatures in June and July [°C], *Survival* – rate of depredation *Plc* – nest placement, *Hght* – nest height [m], *ClutchInt* – day of clutch initiation from May 1st, *Fledged* – number of fledged chicks per brood, *Not fledged* – number of chicks per brood that failed fledging, *Dns* – fox dens proportion [%]

Model selection tables

Table A1: The first ten models from the model selection with survival probability as the response variable and including nest height. *ClutchInt* - clutch initiation day, *Dns* - fox dens proportion, *Hght* – nest height. All numerical variables are standardized.

Model rank	<i>Int</i>	<i>ClutchInt</i>	<i>Dns</i>	<i>Hght</i>	<i>Dens:Hght</i>	<i>AICc</i>	ΔAIC	weight
1	5.45	-0.14	-0.29	1.05	-0.26	947.7	0.00	0.34
2	5.45		-0.30	1.07	-0.26	948.3	0.62	0.25
3	5.39	-0.14		0.97		949.3	1.67	0.15
4	5.39			0.99		950.0	2.33	0.11
5	5.39	-0.14	-0.13	0.96		950.2	2.59	0.09
6	5.39		-0.13	0.99		950.8	3.16	0.07
7	5.10	-0.25				1034.5	86.79	0.00
8	5.09	-0.24	-0.14			1035.2	87.55	0.00
9	5.08					1041.4	93.76	0.00
10	5.08		-0.15			1042.0	94.39	0.00

Table A2: The first ten models from the model selection with survival probability as the response variable and including nest placement. *Plc* – nest placement, *ClutchInt* - clutch initiation day, *Dns* - fox dens proportion. All numerical variables are standardized.

Model rank	<i>Int</i>	<i>Plc</i>	<i>ClutchInt</i>	<i>Dns</i>	<i>Dens:Plc</i>	<i>AICc</i>	ΔAIC	weight
1	5.61	+	-0.17			1002.5	0.00	0.39
2	5.60	+	-0.17	-0.13		1003.4	0.91	0.25
3	5.63	+				1004.6	2.12	0.13
4	5.60	+	-0.17	-0.07	+	1005.1	2.57	0.11
5	5.62	+		-0.13		1005.4	2.95	0.09
6	5.62	+		-0.08	+	1007.1	4.64	0.04
7	5.10		-0.25			1034.5	31.97	0.00
8	5.09		-0.24	-0.14		1035.2	32.73	0.00
9	5.08					1041.4	38.94	0.00
10	5.08			-0.15		1042.0	39.56	0.00

Table A3: The first ten models from the model selection with fledging success as the response variable and including nest height. *ClutchInt* – clutch initiation day, *Dns* - fox dens proportion, *Mys* – snowfall in May, *Hght* - nest height, *Smr* – summer temperature. All numerical variables are standardized.

<i>Model rank</i>	<i>Int</i>	<i>ClutchInt</i>	<i>Dns</i>	<i>Mys</i>	<i>Hght</i>	<i>Smr</i>	<i>Dns:Hght</i>	<i>AIC</i>	Δ <i>AIC</i>	<i>weight</i>
1	1.09	0.30			0.07	0.19		3585.1	0.00	0.24
2	1.09	0.29		0.09	0.07	0.18		3585.6	0.54	0.18
3	1.09	0.30	-0.06		0.07	0.20		3585.5	1.44	0.12
4	1.09	0.30	-0.03	0.08	0.07	0.19		3587.5	2.40	0.07
5	1.09	0.28				0.19		3587.8	2.72	0.06
6	1.09	0.30	-0.06		0.07	0.20	0.02	3588.2	3.14	0.05
7	1.09	0.28		0.09		0.18		3588.3	3.23	0.05
8	1.09	0.29			0.07			3588.5	3.40	0.04
9	1.09	0.29		0.11	0.07			3589.9	3.83	0.04
10	1.09	0.30	-0.03	0.08	0.07	0.19	0.02	3589.2	4.10	0.03

Table A4: The first ten models from the model selection with fledging success as the response variable and including nest placement. *Dns* - fox abundance, *Mys* – Snowfall in May, *Plc* - nest placement, *Smr* – summer temperature. All numerical variables are standardized.

<i>Model rank</i>	<i>Int</i>	<i>Plc</i>	<i>ClutchInt</i>	<i>Dns</i>	<i>Mys</i>	<i>Smr</i>	<i>Plc:Dns</i>	<i>AIC</i>	Δ <i>AIC</i>	<i>weight</i>
1	1.14	+	0.30			0.19		3584.0	0.00	0.26
2	1.14	+	0.30		0.09	0.18		3584.4	0.42	0.21
3	1.14	+	0.30	-0.06		0.20		3585.5	1.43	0.13
4	1.14	+	0.30	-0.08		0.18		3586.0	1.95	0.097
5	1.14	+	0.30	-0.03	0.08	0.19	+	3586.3	2.29	0.08
6	1.14	+	0.30	-0.05	0.08			3586.8	2.77	0.07
7	1.14	+	0.29				+	3587.3	3.24	0.05
8	1.14	+	0.29		0.11	0.19		3587.6	3.56	0.04
9	1.09		0.28			0.18		3587.8	3.79	0.04
10	1.09		0.28		0.09			3588.3	4.30	0.03

Model outputs with nest placement

Table A5: Output of the model explaining the daily survival probability of a snow bunting brood from the start of egg-laying until the end of monitoring. The model includes the clutch initiation day, nest placement, fox abundance, and year as a random effect. “Nest placement on ground” refers to the category of nests that were recorded as being located directly on the ground. Number of observations = 1131.

Fixed effects	Estimates	CI	p
<i>Intercept</i>	5.60	0.17	<0.001
<i>Nest placement on ground</i>	-0.96	0.17	<0.001
<i>Clutch initiation day</i>	-0.17	0.08	0.041
<i>Fox dens proportion</i>	-0.13	0.12	0.28
Random effect	Variance	N_{Year}	
<i>Year</i>	0.17	22	

Table A6: Output of the model explaining fledging success of snow bunting chicks. The model includes the clutch initiation day, fox abundance, nest placement, the mean summer temperature (June-July), and year as a random effect. “Nest placement on ground” refers to the category of nests that were recorded as being located directly on the ground. Number of observations = 1121.

Fixed effects	Estimates	CI	p
<i>Intercept</i>	1.14	0.07	<0.001
<i>Nest placement on the ground</i>	-0.16	0.07	0.015
<i>Clutch initiation day</i>	0.30	0.04	<0.001
<i>Fox dens proportion</i>	-0.06	0.07	0.437
<i>Summer temperature</i>	0.20	0.08	0.011
Random effects	Variance	N_{Year}	
<i>Year</i>	0.09	22	

Fledging model with day of spring onset

Table A7: The first ten models from the model selection with fledging success as the response variable and including nest height. *ClutchInt* – clutch initiation day, *Dns* - fox dens proportion, *Mys* – snowfall in May, *Hght* - nest height, *Spr* – Julian day of spring onset. All numerical variables are standardized.

<i>Model rank</i>	<i>Int</i>	<i>ClutchInt</i>	<i>Dns</i>	<i>Mys</i>	<i>Hght</i>	<i>Spr</i>	<i>AIC</i>	Δ <i>AIC</i>	<i>weight</i>
1	1.09	0.29			0.07		3588.5	0.00	0.19
2	1.09	0.29			0.07	-0.11	3588.7	0.18	0.17
3	1.09	0.29		0.11	0.07		3588.9	0.42	0.15
4	1.09	0.29		0.09	0.07	-0.10	3589.5	0.96	0.114
5	1.09	0.29	-0.04		0.07		3590.3	1.83	0.07
6	1.09	0.29	-0.03	0.10	0.07	-0.11	3590.5	2.44	0.06
7	1.09	0.28					3590.9	2.44	0.06
8	1.09	0.29	-0.00		0.07		3590.9	2.44	0.06
9	1.09	0.28				-0.11	3591.3	2.81	0.05
10	1.09	0.27		0.11			3591.3	2.83	0.05

Table A8: The first ten models from the model selection with fledging success as the response variable and including nest placement. *ClutchInt* – clutch initiation day, *Dns* - fox abundance, *Mys* – Snowfall in May, *Plc* - nest placement, *Spr* – Julian day of spring onset. All numerical variables are standardized.

<i>Model rank</i>	<i>Int</i>	<i>ClutchInt</i>	<i>Dns</i>	<i>Mys</i>	<i>Plc</i>	<i>Spr</i>	<i>Plc:Dns</i>	<i>AIC</i>	Δ <i>AIC</i>	<i>weight</i>
1	1.14	0.30			+			3587.3	0.00	0.18
2	1.14	0.30			+	-0.11		3587.4	0.11	0.17
3	1.14	0.29		0.11	+			3587.6	0.31	0.15
4	1.14	0.30		0.10	+	-0.10		3588.1	1.80	0.072
5	1.14	0.29	-0.04		+			3589.1	1.82	0.07
6	1.14	0.30	-0.03		+	-0.11		3589.2	1.95	0.07
7	1.14	0.29	-0.00		+			3589.6	2.33	0.06
8	1.14	0.29	-0.06		+		+	3589.6	2.50	0.05
9	1.14	0.30	-0.06		+	-0.10	+	3589.8	2.58	0.05
10	1.14	0.29	-0.03	0.11	+			3590.1	2.82	0.04

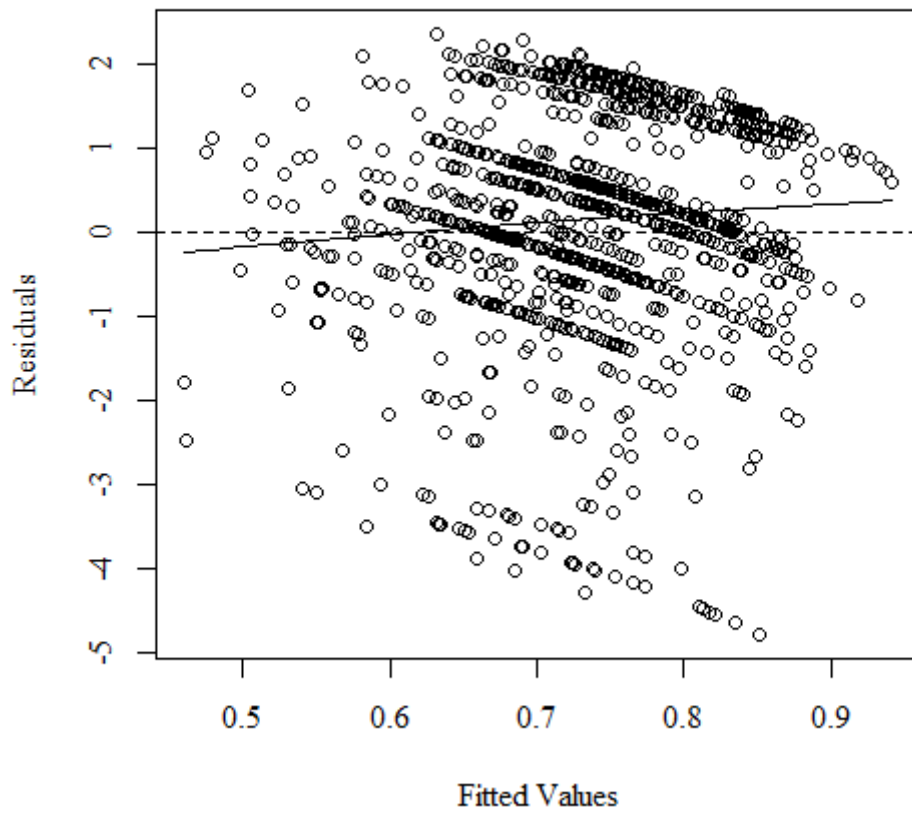


Figure A3: Residual plot of the top ranked model from table A3.

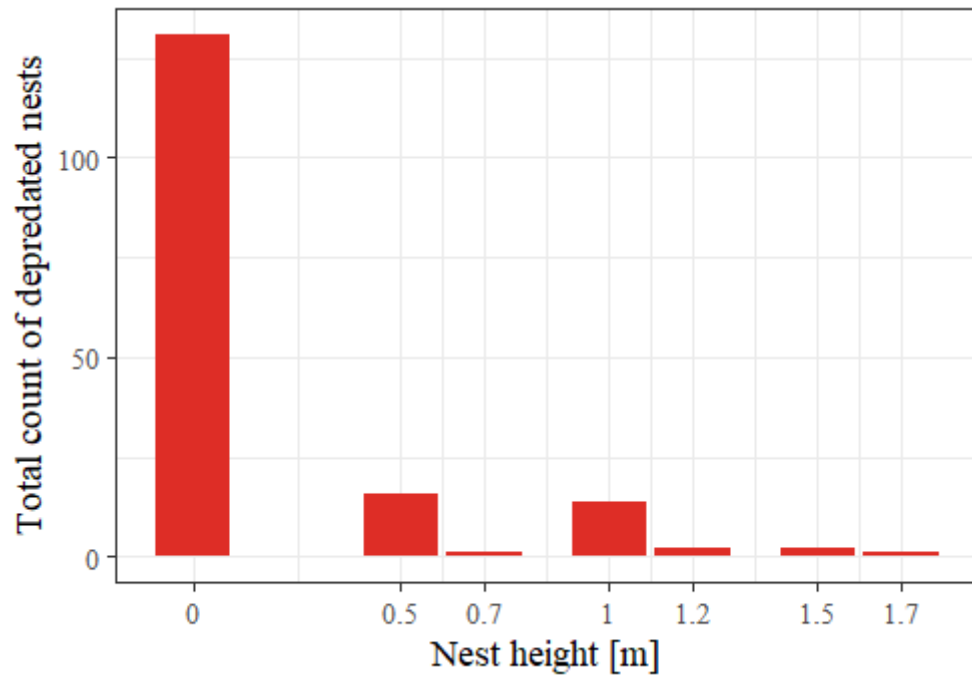


Figure A4: The total number of depredated nests per nest height.

