Master's thesis

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Norwegian University of Science and Technology
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Abstract

Climate and weather are major abiotic factors affecting organisms, especially in highly seasonal environments like the Arctic. How weather conditions influence the reproductive success of a bird breeding here is of particular interest when predicting the effects of anthropogenic climate change. I used time-series data from 1998 to 2018 to look at effects of local environmental variables on various stages of offspring production in natural nests versus nest boxes of the passerine bird snow bunting (*Plectrophenax nivalis*) at Spitsbergen.

Timing of breeding was earlier in nest boxes than in natural nests and came earlier in warmer springs, as well as when more snow fell in winter. Earlier breeding led to more fledglings per brood. Among years, the average number of eggs laid per brood (mean = 5.76, SD = 0.87), and the hatching probability per egg (mean 0.94, SD = 0.049), showed very little variation. Accordingly, a sensitivity analysis showed that fledging rates were a much more important determinant of annual variation in fledgling production.

In general, breeding was more successful in artificial than in natural nests. In natural nests, the probability of having fledglings decreased following springs with high local fox cub production, suggesting a direct negative effect of increased predator presence. Also, while more July rainfall reduced the probability of having fledglings, the probability increased in years with warm July temperatures, likely because of invertebrate (i.e. chick food) availability and lower energetic demands. In broods with fledglings, the same mechanisms probably led to higher numbers of fledglings, as July temperature also had a positive effect on this number. The same did increasing annual May snowfall, possibly by postponing arthropod emergence and countering trophic mismatch. Also, more snow fallen in the preceding winter had a negative effect in natural nests on the probability of having fledglings, but a positive effect in nest boxes, indicating contrasting mechanisms and implications of prolonged snow cover.

This study shows that the snow bunting is breeding successfully despite climate change. Even though there are warming trends in the spring temperature, fledgling numbers are stable, likely because warmer weather is beneficial during chick rearing. Also, with little variation among broods in clutch size and hatching probability, chick rearing is the key step for breeding. Fox predation plays a key role for explaining nest failure, while warming leads to earlier breeding and longer breeding seasons. In the Arctic where the fastest climate changes in the world are happening, the snow bunting shows that birds can take advantage of the milder climate, and that direct effects of climate change won’t necessarily be negative.

Sammendrag

Klima og vær er viktige abiotiske faktorer som påvirker organismer, spesielt i områder med store værforskjeller, som Arktis. Hvordan været påvirker reproduksjonssuksessen til en fugl som hekker der er spesielt interessant for å forutse effekter av menneskeskapte klimaendringer. Jeg har brukt tidsseriedata fra 1998 til 2018 for å se på effektene av lokale miljøvariabler på forskjellige stadier av avkomproduksjon i naturlige reder og fuglekasser hos snøspurv (*Plectrophenax nivalis*) på Spitsbergen.

Tidspunkt for hekking var tidligere i fuglekasser enn i naturlige reder og kom tidligere i varme vårer og når det hadde falt mer snø om vinteren. Tidligere hekking førte til at flere unger fløy ut av redet, men mellom år var det lite variasjon i antall egg lagt per rede (gjennomsnitt = 5.76, SD = 0.87), og klekkesannsynlighet per egg (gjennomsnitt = 0.94, SD = 0.049). Derfor utførte jeg en sensitivitetsanalyse som viste at raten for antallet unger som flyr ut påvirket årlig variasjon i ungeproduksjon mer.

Generelt gikk hekking bedre i fuglekasser enn i naturlige reder. I naturlige reder var sannsynligheten for å klare å oppdra unger mindre når det var mange revungekull i området, noe som peker på en direktevirkende negativ effekt av rovdyr. Regn i juli reduserte sannsynligheten for å oppdra unger, mens sannsynligheten økte i år hvor juli var varmere enn normalt, sannsynligvis på grunn av mere insekter å spise og mindre energi brukt på egenoppvarming. I kull med unger førte dette også til flere unger, da julitemperatur også hadde en positiv effekt på dette antallet. Det samme gjorde snøvær i mai, muligens ved å utsette aktiviteten til leddyrenes (mat for snøspurvungene) og dermed motvirke trofisk mismatch. Dessuten førte mer snø om vinteren til en sannsynlighet for å oppdra unger i naturlige reder, men høyere i fuglekasser, noe som tyder på kompleksitet og kontraster i effekten av lengre snødekke.

Denne studien viser at snøspurven har god hekkesuksess til tross for klimaendringer. Selv om våren blir varmere er antallet unger som flyr ut stabilt, sannsynligvis fordi varmere vær er positivt når ungene oppdras. Med lite varians mellom reder hva angår antall egg klekkesannsynlighet er det dessuten ungeoverlevelse som er viktigst. Likevel leder oppvarmingen til tidligere hekking og lengre hekkesesong, men rev er også viktig for å forklare hekkefiasko. I Arktis, hvor de raskeste klimaendringene i verden finner sted, viser snøspurven at fugler kan dra nytte av det varmere klimaet, og at direkte følger av klimaendringer ikke nødvendigvis er negative.

Introduction

The reproductive process in birds can be influenced by temporal variation in weather (Reid, Monaghan, and Ruxton 2000; Ringsby et al. 2002; Siikamäki 2008; Skinner et al. 1998). Temperature affects breeding success for example directly through effects on chicks' energetic demands (Weathers 1992), but weather can also have indirect effects. For instance, many birds eat arthropods (Kirk, Evenden, and Mineau 1996), and higher ambient temperatures increase arthropod abundance (Perrins 1991) and activity (Avery and Krebs 1984). Food abundance can also have an effect on incubation effort (Rauter and Reyer 1997), clutch size (Hussel and Quinney 1987), and number of breeding attempts (Rodenhouse and Holmes 1992). Temperature-dependent availability of food has an effect on both timing of breeding (Moreno 1989; Perrins 1991) and feeding rate (Avery and Krebs 1984; Hoset et al. 2004). Rainfall has also been found to be reduce breeding success (Becker, Finck, and Anlauf 1985; Moss, Oswald, and Baines 2001), and has been found to have an effect on reproductive timing (Fossøy et al. 2015).

Near the poles where seasonal variations in temperature are greater, the wildlife has adapted to different conditions in different seasons. A result of adaptation is the synchronized timing of breeding to best fit the different seasonal conditions (Lack 1950). Having young during the short, warmer summer half of the year, takes advantage of the moderate temperatures and peak in food abundance. For birds in seasonal environments, the main selection pressure on offspring timing is the food peak (Visser et al. 1998). In the Arctic, the short breeding season, which is constrained by the long winter represents an extra challenge (Forsman and Mönkkönen 2003). Arctic birds must therefore be well-timed and synchronized when breeding.

Because of anthropogenic effects, global climate is now changing. The atmosphere is getting warmer due to higher concentrations of CO_2 and other climate gasses (Allen et al. 2018). The warming has already had great ecological effects on ecosystems (Parmesan 2006). As the climate is expected to warm even more in the future (Allen et al. 2018), more ecological changes are expected. The Arctic is experiencing a warming at more than twice the rate of temperate areas, due to the phenomenon called *Arctic amplification* (Høye et al. 2007; Overpeck et al. 1997). Arctic amplification occurs mainly due to melting snow cover and sea ice, leading to less reflection of solar heat (Kirtman et al. 2013). One effect of climate change in the Arctic is warmer and shorter winters (Serreze and Barry 2011), leading to earlier snowmelt. The phenological effects of climate change are expected to be stronger close to the poles, because the combined effects of snowmelt and increasing temperatures regulate vegetation growth and arthropod emergence (Høye et al. 2007; Høye and Forchhammer 2008; Schekkerman et al. 2004). Snowmelt has also been found to influence bird breeding phenology (García-González et al. 2016; Madsen et al. 2007), and a snow free ground could lead to easier access to food and nesting places and earlier breeding (Martin and Wiebe 2004). Onset of breeding is usually plastic (Lack 1968), and in the northern temperate zone, most birds start egg laying earlier in warmer springs regardless of climate change (Dunn 2004; Torti and Dunn 2005; Weatherhead 2005). Still, their main cue for phenology is photoperiod (Dawson et al. 2001). The harsh and unpredictable Arctic weather (Walsh, Shapiro, and Shy 2005; Weatherhead, Gearheard, and Barry 2010) is expected to become more variable in the future as the climate changes come more into effect (Høye et al. 2007; Post et al. 2001; Walsh et al. 2011). Arctic birds need to be highly flexible, as harsh weather conditions can lead to complete nesting failure, forcing them to start over with a new brood (Walker et al. 2015). They also need to spend more energy than birds in other areas incubating, due to low ambient temperature (Piersma et al. 2003). However, with the end of winter progressing towards earlier dates, the longer breeding season could increase the opportunity for multiple broods.

The effects of changing temperatures from climate change also works through changes in biological processes and relationships. A potential problem caused by climate change is temporal mismatch, caused by earlier spring events (Parmesan 2006; Visser and Both 2005). Temporal mismatch is when biological relationships become disturbed by different rates of change on different trophic levels, for instance as predator reproduction becomes decoupled from peak food abundance (Parmesan 2006; Visser and Both 2005). The problem happens when consumers are unable to keep up with phenological changes in their food peak (Both and Visser 2005; Carey 2009; Visser and Gienapp 2019; Visser, te Marvelde, and Lof 2012), and can be detrimental because prey abundance at time of peak necessity has been shown to be important for reproductive success in birds (Lack 1968; McKinnon et al. 2012). Migratory birds that spend the winter away from their breeding grounds are particularly challenged by changing timing of spring events, as they cannot monitor the environment on their breeding ground from far away (Both and Visser 2001; Gwinner 1996; Sanderson et al. 2006).

In addition to food availability and energetic demands, there are other factors on the breeding grounds that can influence breeding success. One of these is predation, as predators can influence breeding success in birds by preying on young and parents (Baines, Moss, and

Dugan 2004; Tapper, Potts, and Brockless 1996). Predation pressure can sometimes vary due to *apparent competition*, which happens when a second prey species drives up predator abundance by contributing prey (Holt 1977).

A bird with reproductive success strongly influenced by weather is the passerine snow bunting (*Plectrophenax nivalis*), living in the high Arctic (Fossøy et al. 2015; Skøien 2015). It feeds its young mainly arthropods (Cramp and Perrins 1994; Hussel 1972). Higher ambient temperatures lead to increased parental feeding rates during incubation and chick rearing (Hoset et al. 2004), and higher breeding success (Fossøy et al. 2015; Hoset et al. 2004; Skøien 2015). The reproduction of the snow bunting is timed so that maximum energetic demand coincides with maximum arthropod emergence (Skjøstad 2008). In addition to controlling insect abundance, low ambient temperatures pose a challenge for offspring due to increased energetic demands (Dawson, Lawrie, and O'Brien 2005; McCarty and Winkler 1999; Starck and Ricklefs 1998), especially considering that snow bunting nests cool quickly when not incubated (Lyon, Montgomerie, and Hamilton 1987). The snow bunting has to cope with unpredictable weather conditions during and before breeding, which can affect its breeding success negatively (Walker et al. 2015). It times breeding with respect to food abundance (Skjøstad 2008), and its breeding success is higher in years with higher breeding synchrony (Skøien 2015). The breeding success in the snow bunting is also driven by regional climate, being linked with the index Arctic Oscillation (AO) (Fossøy et al. 2015). AO is an index that denotes the main trends in variations in sea-level air pressure, which predicts the weather in Northern Europe (Thompson and Wallace 2000). Due to warming climate, snow buntings have advanced their laying of the first egg (Fossøy et al. 2015; Skjøstad 2008). Also, temperature is a driver for extra-pair paternity among the snow buntings (Hoset et al. 2009).

Reproduction in the snow bunting consists of several steps. First, the birds need to find a mate and a suitable nest location. After they have mated, the eggs are laid and later incubated. When the chicks emerge from the eggs, they need to be cared for until they can leave the nest and fend for themselves, a process found to be particularly costly to some breeding birds (Moreno et al. 1995). How successful passerines are in these steps can depend on their quality as care givers as well as their experience (Amundsen and Stokland 1990; Wendeln and Becker 1999), in addition to the quality of their territory (Ens et al. 1992; Weatherhead and Robertson 1977). It is not well-known which steps are the most important for the total reproductive success in the snow bunting. It is necessary to analyse this process to understand what makes up a successful breeding season. While a lot of research is done on temporal mismatch and different influences on single steps in the breeding process, few studies are concerned with holistic views of the season. Therefore, the relative effect of mismatch and earlier breeding is not well documented. Knowing which criteria are involved in a successful breeding season is key to understanding how the environment plays a part. Especially considering how the steps might be influenced differently by the same parameters. In a changing climate these relationships are particularly interesting and could turn out to be useful for conservation.

In this thesis, using a study species that is one of few non-marine birds available for this kind of study in one of the most rapidly changing biomes on Earth, i.e. high Arctic Svalbard, I examine the relative importance of the different steps in the reproductive process for the snow bunting in a sensitivity analysis and use an extensive set of environmental variables to explain the annual variation in six components of fecundity. To achieve this, I use a two-decade long timeseries of snow bunting reproduction data to test for the effects of monthly aggregated local weather variables as well as predator abundance on different reproductive measures. I intend to investigate if and how warming temperatures are likely to affect terrestrial birds at these latitudes.

Methods

Study system

The fieldwork was conducted in Adventsdalen valley on Spitsbergen island (78˚13'N, 15 ˚38'E, Appendix 1 Figure A1) in the Svalbard archipelago. The landscape on the island is mainly Arctic tundra, with proximity to both coast and mountains. Svalbard belongs to the high arctic and has a cold and harsh climate. The temperature is low, but the climate is relatively dry, as seen by the fact that the average temperature between 1998 and 2018 was -3.3 ˚C, with an average annual rainfall of 198 mm. Modelling predicts warmer springs with more precipitation and longer breeding seasons on Svalbard (Førland et al. 2011). Svalbard is home to a breeding population of snow buntings (*Plectrophenax nivalis*), which has been monitored for over two decades since 1998. Here, my study population of snow buntings has been limited to the study site in Adventdalen, but the snow bunting is found elsewhere throughout the Svalbard archipelago (Espmark 2016). The total population at Svalbard is estimated to consist of between 1,000 and 10,000 breeding pairs (www.npolar.no/en/species/snow-bunting.html). However, mainland populations in the Scandinavian mountains are in decline (Lehikoinen et al. 2014).

The snow bunting is the only passerine to breed regularly at Svalbard. It is a small, cavity-nesting bird with a circumpolar distribution north of latitude 60˚ north. Due to the harsh climate on these latitudes, the snow bunting is well adapted to endure extreme conditions and a life in the Arctic (Snell et al. 2018). It nests in scree slopes and rock crevices well sheltered underground but will also use nest boxes. The Spitsbergen population migrates 4000 km to Central Asia in fall, and overwinters in steppe habitats of Kazakhstan and adjacent countries (Snell et al. 2018).

The male returns to the breeding ground around late March to early April, with the females typically following 3-4 weeks later (Cramp and Perrins 1994). The nesting season runs from the middle of May to the middle of July, depending on annual weather conditions (Hoset et al. 2009). Snow buntings typically lay six eggs (modal clutch size). They take 13 days of incubation (modal duration) by the female to hatch (Hussel 1972) , and the chicks hatch asynchronously (Espmark 2016). After hatching, a 13-day nestling period follows, before the chicks leave the nest (Espmark 2016). The male guards the female during her fertile period, feeds her while she is incubating, but also possibly searching for extra-pair copulations (Espmark 2016). He returns when the eggs hatch and helps with the raising of the chicks

(Espmark 2016), caring for the young with the female as in all passerines. The chicks hatch asynchronously and are born incapable of moving around on their own and nearly naked, which could be a challenge in the harsh Arctic environment. Typically, snow buntings lay one clutch per season, but re-nesting due to clutch failure and attempts at second broods happen in years with early start of breeding (Espmark 2016). The young are fed a diet of protein-rich arthropods, especially crane flies, but also other insects and spiders (Cramp and Perrins 1994; Hussel 1972).

Arctic fox (*Vulpes lagopus spitzbergensis*) is the only predator known to have a significant effect on snow bunting nest survival. However, also the Arctic skua (*Stercorarius parasiticus*), and possibly the glaucous gull (*Larus hyoperboreus*), are predators that prey on the snow buntings on Spitsbergen. Also, parasitic mites (e.g. *Isospora plectrophenaxia*) have been found to inhabit snow bunting nests during the breeding season (Dolnik and Loonen 2007). They are thought to eradicate entire broods when present. An infected nest can stay infected through the winter, becoming a problem for any individual inhabiting it in the following year (personal communication with F. Fossøy).

Snow bunting data

The long-term data set consists of observations from nest record schemes spanning from 1998 to 2018 and has been collected annually. The data contain the clutch initiation dates (defined as the day of laying of the first egg in the brood, where 1 = May 1st), number of eggs laid, number of eggs hatched, and the number of chicks fledged from 1591 broods (Appendix A1 Table A1). Some of the parameters are missing from some broods, which were checked every 2-3 days after breeding in the snow bunting was known to start.

The team collecting the data varied in its composition and size between years. Data have primarily been collected along an abandoned cableway previously used for coal transport from the mines in Adventdalen. Adventdalen is a valley that stretches south-eastwards from Longyearbyen city and the line of pylons that supported the cableway follows its orientation. The pylons are spaced out 50-100 meters apart. The part of the valley used for the study measures around 14 km (Appendix A1 Figure A1).

In the following is given a description of the field work of the summer 2018, the last year of the data included in this thesis and describe the field work in general terms for the entire study period. Any work done in preceding seasons is reported to have been identical. All pylons had not yet been given a nest box in the 2018 field season, but approximately 90 nest boxes were operative, with one nest box per pylon. During the study period, more nest boxes have been put in the field from time to time, meaning the number of available nest boxes has varied between years. In addition to nests in nest boxes, any brood found in natural nests was added to the study. In total, 657 broods were from nest boxes while 924 were from natural nests (Appendix A1 Table A2). The 10 remaining broods lacked data on their location. The natural nests were mainly found in the rocky slopes in the area around the cableway, but nests in Longyearbyen city and in crevices in and around cabins were also found and used. Usually the natural nests were found by observing parent behaviour such as feeding and territory defence.

The date of the first egg laid would be calculated by floating eggs (Ackerman and Eagles-Smith 2010) if the clutch was close to complete when found or by backtracking based on the number of eggs laid. If the eggs were already hatched their development was assessed to make an estimate of the hatching date and clutch initiation date.

On the eighth day after hatching, the chicks were ringed and weighted using a spring scale and a fabric bag. Young usually fledge at age of 13 days and the eight day is the last day the chicks can be weighed without risk of premature fledging due to disturbance. The age of the brood when weighing took place was noted, as counted in days after hatching, as it varied somewhat due to convenience. An effect of this was tested for, using a binomial generalized linear model with probability of fledging as the response variable. Chicks unable to fledge are expected to be considerably smaller than their more fit siblings, and usually far lighter than 15 grams (Personal communication with F. Fossøy). To obtain the most precise weighting possible, the chicks were allowed to defecate before weighting, but not all chicks did so.

When returning to find an empty nest that previously had held eggs or chicks, it was assumed that it had been taken by foxes. Checking for predation could also be done by addressing the state of the nests, as foxes often leave the nests destroyed. Some broods were found to have been killed by mite infestation, but information on this was not noted.

Many entries contained missing values and had to be excluded from analysis when containing missing data in parameters that were included in the analysis in question. Entries with missing data had to be removed because model selection based on Akaike Information Criteria (AIC) does not work with missing values, as all candidate models need to be based on the same number of data points (Akaike 1974). Therefore, the number of broods included in each model selection varied, based on which data columns were used. Only broods weighed and assessed for fledging on day seven, eight or nine after hatching, or broods that didn't produce fledglings were included when analysing fledging measures. This discrimination was done to avoid any effect of weighting day on the fledging probability, as the decision of fledging was based on weighting the chicks and checking if they had passed a weight of 15 grams or not. Broods not producing any fledglings usually had no information on weighting day but were still included to compare parameters relating to fledgling success.

Broods from 2004 had to be excluded from the analyses because the field season was cut short and could have introduced bias. A total of 27 entries marked as containing second broods from all years were removed, as keeping these might have introduced noise into the analyses from pseudoreplication. It is, however, likely that several broods that were second for the season were included in the analyses because of lack of marking of the parents and broods. This lack of parent identity may have caused pseudoreplication by allowing the same parents to occur several times in the data set. There were also no data on parent identity, so pseudoreplication with the same parents occurring several times in the data set is likely to have occurred, especially considering that the birds often return to the same breeding grounds year after year (Espmark 2016). Coordinates or other data on brood placement and ID also lacked and could have been introduced to see if the different broods reacted differently to the explanatory variables.

Environmental data

Weather data were acquired from www.eklima.no. The data stem from a weather station at Longyearbyen Airport (78˚ 15’N, 15˚ 30’E) approximately 4 km from the study site. This station is operated by the Norwegian Meteorological Institute and the data are available through their website (www.eklima.no). The data included mean daily temperature and total daily precipitation from 1998 to 2018, aggregated into mean monthly values for temperatures and sum of monthly values for precipitation. The variables included in the analyses were April, May and June precipitation and temperature, and precipitation and temperature of the first 15 days of July (hereafter referred to as “July temperature” and “July precipitation”, respectively). Only the first 15 days from July were used because most chicks have been assessed for fledging by July 15th. May precipitation was divided into rain and snow by looking at the temperature from the previous day (whether it was above or below 1˚C, respectively) (Hansen et al. 2013).

In addition, averages across April and May temperature, May and June temperature and June and July temperature as well as an average temperature from April 1st to July 15th, were calculated. This aggregation allowed testing for effects of temperature during two or more months without creating problems due to multicollinearity.

Data on regional Arctic Oscillation indices were obtained from the National Weather Service Climate Prediction Centre, USA (www.cpc.ncep.noaa.gov). The mean value from December to March from the preceding winter was used as an index of AO.

A yearly index of day of winter end was calculated as the first of the first ten days with an average temperature of above 0 ˚C (Le Moullec et al. 2019). A measure of the amount of snow fallen in the preceding winter was also included, as this could influence the time it takes for the ground to become snow free. Total winter snowfall was calculated as the total precipitation on days following days with average temperature of less than 1˚C from November to April (Hansen et al. 2013).

Data on the percentage of known fox dens with litters per year (hereafter “fox litter percentage”) in Adventdalen and Sassendalen were obtained from “Miljøovervåkning Svalbard og Jan Mayen”, from the website http://www.mosj.no/no/fauna/land/fjellrev-bestand.html. Fox data were included because foxes are the main predator preying on snow bunting chicks (Personal communication with F. Fossøy).

For each year, the median clutch initiation day and coefficient of variance for clutch initiation day, average number of eggs laid per brood and average hatching success were calculated. These calculated variables were to be included as explanatory variables when conducting subsequent analyses and are referred to as “intrinsic covariates”. They were included to check whether one step could influence another occurring later in the breeding process. The coefficient of variance was included to see if years with higher breeding synchrony yielded better breeding success, as this was reported by Skøien (2015). All numerical explanatory covariates were standardized prior to inclusion in models.

Statistical analyses

Testing for trends

May, April, June and July temperatures and precipitation were tested for long-term trends in the 21-year study period by fitting linear regressions with year as explanatory variable. Also, fox litter percentage, winter end day and total winter snowfall were tested in this way. When testing for trends in these explanatory variables, 2004-data were also used.

The clutch initiation day, number of eggs laid per clutch and the number of fledged chicks per clutch were tested for trends using a linear mixed effects model with year as explanatory variable and year as a random effect. Trends in hatching probability, probability of having at least one fledgling per brood and probability of fledgling for each chick already emerged from an egg were tested for using binomial generalized linear models, with year as the only explanatory variable (Figure 1). All available records for the dependent variables were used in analyses testing for trends. All mixed-effects models were fitted in R using function “lmer” from package ‘nlme’ for linear mixed models (Pinheiro et al. 2015) and function ‘glmer’ in package ‘lme4’ for generalized mixed models (Bates et al. 2014). P-values smaller than 0.05 were considered statistically significant.

Effect of Arctic Oscillation

Linear mixed effect models were fitted for the effect of winter AO on clutch initiation, number of eggs, and number of fledglings. Year was included as a random factor.

Sensitivity analysis

To find out what stages in the process relating to the raising of young were the most important in deciding the number of fledglings, a sensitivity analysis was performed in three steps. See Appendix A2 for methodology.

Model selection

Statistical analyses were conducted for six components of reproductive effort: clutch initiation, number of eggs laid per clutch, hatching probability for each egg per clutch, probability of having at least one fledging (both with all covariates except fox and with all extrinsic covariates plus nesting category), probability of fledging given that at least one chick from the brood fledged and the number of fledglings per brood given that at least one chick from the brood fledged (Figure 1). Year was included as a random effect. Best fit models were based on the tools of model selection in an information theory framework. Generally in model selection, the model with the lowest Akaike Information Criterion (AIC) (Akaike 1974) corrected for small sample sizes (AIC_c) score is the best one and the one chosen for fitting for interpretation, based on the theorem of maximum parsimony. The model with the lowest AIC_c score is the one said to have $\Delta AIC_c = 0$ and is here considered the “top model”. A general rule says that any model with $\Delta AIC_c < 2$ has good support from the data, given the data and the candidate models. AIC also aims to reduce the number of explanatory variables, leading to the most parsimonious model being selected (Burnham and Anderson 2002).

The dredge-function from the MumIn-package (Barton 2018) was used to perform the model ranking in R. This function ranks all possible allowed combinations of covariates based on AIC_c. The use of the dredge function assumes that all the possible tested models made with the included parameters would make biological sense. Different temperature covariates were excluded from being in the model at the same time, as well as temperature covariates and day winter end due to generally high correlation between these (Appendix A1 Table A3). Also, for the same reason, May snow and May rain were not allowed into the same model, and winter snowfall and April precipitation. To avoid undesirable combinations of correlated covariates, the subset parameter for the dredge function was used. Having correlating covariates in a statistical analysis can lead to biased estimates (Graham 2003). Model selection for linear models was done with maximum likelihood (ML). After finding the top model according to AIC_c, the linear models were fit using restricted maximum likelihood (REML). REML ensures unbiased estimators of the variance components, so the likelihood is maximized on the set of parameters while excluding the fixed effects (Searle and Corbeil 1976).

Nesting category was divided into two levels: One category consisted of all nests found on pylons plus all other nest boxes (hereafter “Nest boxes”), the second one everything else (hereafter “Natural nests”). The effect of the factor as response variable was tested in the model selection to see if it had any effect on the response variables. Also, interaction effects between nest category and weather variables were included in the analyses, to check whether the weather variables had different effects on natural nests and nest boxes. The terrain could influence how exposed the nests are to weather and predation.

For each analysis, a different selection of data from the data set was performed, based on what columns were used for the analysis, because model selection based on AIC needs all candidate models to be based on the same amount of observations. Therefore, missing values cannot be present in any of the possible covariates, nor in columns used to calculate the response variable. Missing information led to the number of broods to vary between analyses.

After choosing the top best explanatory variables for the different count data based on AIC_c, linear models and Poisson models were tested to check the fit to the data. After using the histograms of the residuals and qq-plots for comparison, linear models were deemed to fit the data better and were chosen as the preferred model in these cases. All data preparation and analyses were done using R (R Core Team 2019).

Timing of clutch initiation. First, it was investigated which factors influenced date of first egg laid in each brood. All the weather variables, nesting category, winter end day and winter snowfall, but not weather variables including July measures, were included as explanatory variables in a linear mixed model. Warm temperatures, early springs and heavy snowfall were expected to increase soil moisture and the availability of arthropods for nesting females. Nest boxes were on raised poles and might be available earlier than sites for natural nests. July measures were not included because clutch initiation usually happens in June (Figure 1). Interaction effects between nesting category and the other covariates were also tested for. A total of 1530 broods were used in this analysis.

Number of eggs per clutch. Then, a linear mixed model was fit to test the effects of the environmental variables on the number of eggs laid per clutch. In this analysis 1419 broods were included. Here, median clutch initiation and clutch initiation coefficient of variance were included as possible explanatory variables, in addition to weather variables until June, snowfall and winter end. Nesting category was also included, as well as interactions between nesting category and all extrinsic covariates (Figure 1). Most egg laying happens by the end of June, which is why July-measures were excluded.

Probability of hatching. In the next step, a binomial generalized mixed model was fitted for hatching probability per egg. All the same covariates as in the previous step were here included, in addition to yearly average number of eggs laid per clutch. Nesting placement and interactions between nesting placement and all included extrinsic covariates were also included. Any brood that was marked as taken by fox was removed before this analysis (Figure 1). For this analysis, n = 1097 broods were used. Most egg hatching happens before the end of June, so July-measures were excluded.

Probability of having at least one fledgling (No fox data). Thereafter, a binomial generalized mixed model was fitted for binary fledging success, i.e. whether any chick fledged from the nest or not. Broods where no eggs had hatched and lines that were marked as taken by foxes were excluded. A total of 958 broods were included in the analysis: 56 failures and 902 successes. The yearly average hatching success was also included as explanatory variable, in addition to all extrinsic covariates except fox litter percentage (Figure 1). Nesting category and possible interaction effects between nesting placement and included extrinsic explanatory variables were also included.

Probability of having at least one fledgling (Fox data included). Then, a binomial generalized mixed model was fitted for binary fledging success with all the extrinsic explanatory variables, and nesting placement as possible explanatory variables. Also, interaction effects between nesting category and all other included explanatory covariates were tested for. Interaction between the fox litter percentage and nesting category was included because it was thought that foxes can get to the natural nests on the ground but are unable to get to the nest boxes on pylons. In this analysis, broods taken by fox and broods where no eggs had hatched were also included (Figure 1). Therefore, this model would describe the whole breeding process as completely as possible. For this analysis, 1214 broods were included. Of these, 312 had failed completely, while 902 had had at least one fledging chick.

Fledglings per hatched egg in broods with fledging success. With the same covariates, a binomial generalized mixed model was fitted to find the fledging probability of each nestling, from broods leading to at least one fledgling. Brood fledging success proportion weighted for number of trials was used as response variable. The nests with reproductive success of zero were removed to test whether different covariates influenced steps in the reproductive process. All explanatory variables except fox litter percentage were included, as well as interaction effects between included explanatory covariates and nesting placement (Figure 1). An effect of nesting category was tested for but not found, meaning entries with missing values in this column could be included. A dataset of 831 broods was used for this analysis.

Fledglings per brood with fledging success. Finally, a linear mixed model for fledged chicks was fitted with the data from nests that had had at least one fledged chick. All extrinsic covariates were included in this analysis, in addition to nesting placement and interaction effects between nesting placement and the extrinsic covariates (Figure 1). The data set included in this analysis contained 902 broods.

The different models, their data selection and included covariates are shown in Figure 1. After model selection had identified models that in each case suited the data best based on AIC_c, these models were fitted for inspection and plotted.

Results

Temporal variation and trends

Analysing the explanatory variables for long-term trends showed that mean air temperatures registered at Longyearbyen Airport for May and June increased from respectively -3.41 ˚C and 2.91˚C in 1998 to -0.21˚C and 4.69˚C in 2018. Mean temperatures in April and in July showed no significant trends. The amount of May precipitation also increased from 3.77 mm in 1998 to 11.38 mm in 2018, while the other monthly precipitation measures showed no significant trends. Winter end day showed a significant progression towards earlier dates from 37.90 (38 = June 7th) in 1998 to 18.50 (19 = May 19th) in 2018, while total winter snowfall and fox litter percentage showed no significant trends (Figure 2, Appendix A1 Table A4).

In analyses of trends in the response variables, there were no significant long-term trends in clutch initiation time, the number of eggs laid per brood or the number of fledglings per brood. The probability of eggs hatching showed a decline 0.94 in 1998 to 0.92 in 2018 ($P = 0.0085$). The probability of having at least one fledgling and the probability of fledging for a chick from a brood with at least one fledgling showed no trend (Figure 2, Appendix A1 Table A4)

Effects of AO

None of the linear mixed models with winter AO as an explanatory variable came up with significant estimates at significance level $p < 0.05$ (Appendix A1 Table A5).

Sensitivity analysis

The sensitivity analysis showed that the average number of fledglings expected was 3.26 young per nest per year, the value obtained by multiplying the average for each step. The addition of one standard deviation to the average number of eggs laid changed the average number of fledglings by 0.12 (Figure 3). A change in one standard deviation in the number of eggs laid changed the expected number of fledglings by 0.17. A change in one standard deviation in the probability of having at least one successful fledgling changed the number of fledglings by 0.28, while a change of one standard deviation in the probability of fledging in broods with at least one fledgling changed the number of fledglings by 0.29.

Step-wise analysis of reproduction stages

Timing of clutch initiation. Clutch initiation date was best described as a function of nesting placement, average April and May temperature and total snowfall during winter (See model selection table in Appendix A1 Table A6). Laying eggs in a natural nest had a positive coefficient for clutch initiation day, indicating that birds nesting in natural nests started their egg laying on average 2.52 days later than individuals using nest boxes (SE = 0.39, P << 0.001, Figure 4). The effect of April and May temperature was negative, and nests were initiated 1.34 days earlier per ˚C increase in annual average April/May temperatures (SE = 0.39, P < 0.001, Figure 4a). The effect of total winter snowfall was also negative, indicating that for each millimetre snow falling in the preceding winter, clutch initiation day came 0.051 days earlier (SE = 0.038, P = 0.19, Figure 4b).

Number of eggs laid per clutch. The number of eggs laid was best described by a linear model with effects of the brood being in a nest box versus in a natural nest, May temperature, median clutch initiation per year, May rainfall and a two-way interaction between nesting placement and May rainfall (See model selection table in appendix A1 Table A7). Laying eggs in a nest box versus laying in a natural nest increased the number of eggs laid by 0.067 (SE = 0.060, P = 0.27, Appendix A1 Figure A2). Increased temperature in May had a negative effect on the number of eggs laid, meaning that for each ˚C warmer May was, the birds laid 0.057 fewer eggs (SE = 0.023, P = 0.027). Median clutch initiation had a negative effect on the number of eggs laid, so for each day the median date was postponed, the birds laid 0.028 fewer eggs (SE = 0.0099, P = 0.011). May rainfall had an effect close to zero on the number of eggs laid in nest boxes so that for each millimetre of rain in May the birds in nest boxes laid 0.018 eggs more (SE = 0.022, P =0.41), but the negative interaction effect with nesting placement meant that individuals in natural nests laid 0.035 fewer eggs per millimetre rain in May (SE = 0.021, P = 0.11) .

Probability of hatching. Hatching probability was best described by a model containing effects of nesting placement, April temperature, May snowfall, June precipitation and a two-way interaction effect between June precipitation and nesting category, and winter snow fall and a two-way interaction between winter snowfall and nesting category (See model selection table in appendix A1 Table A8). The effect of nesting category meant that eggs laid in a natural nest had lower probability of hatching than eggs in nest boxes (β = -1.34, SE = 0.48, P = 0.051, Appendix A1 Figure A3). The effect of April temperature was positive, ergo when temperatures were high, the probability of eggs hatching increased (β = 0.062, SE = 0.024, P = 0.011). The effect of May snowfall being positive meant that in years when there was higher snowfall in May, the probability of eggs hatching increased (β = 0.072, SE = 0.023, P = 0.0020). June precipitation had a negative effect in nest boxes (β =-0.054 , SE = 0.015, P < 0.001), so in years with more precipitation in June, there was a smaller chance of hatching. The interaction effect between June precipitation and natural nest means that the negative effect was weaker there (β = 0.014, SE = 0.014, P = 0.35). Snowfall had a negative effect on eggs laid in nest boxes, indicating that these eggs were less likely to hatch in years with more snow in the preceding winter (β = -0.011, SE = 0.0055, P = 0.038). The interaction effect between snowfall and nesting category shows that in natural nests, the effect was virtually zero (β = -0.00095, SE = 0.0048, P = 0.84).

Probability of having at least one fledgling (No fox data). The probability of having at least one fledgling when excluding predation was best described by a binomial model containing effects of nesting category, June precipitation and winter end day (Appendix A1 Table A9). The negative effect of nesting in a nest box indicated that broods raised in a natural nest had greater chance of leading to at least one fledging chick than those in nest boxes (β = 0.71, SE = 0.29, P = 0.014, Appendix A1 Figure A4). The positive effect of June precipitation means that broods were more likely to lead to at least one fledgling when there was more precipitation in June (β = 0.079, SE = 0.045, P = 0.079). The effect of day of winter end was also positive, meaning that when the winter was longer, the probability that a brood would lead to at least one fledgling was higher (β = 0.041, SE = 0.011, P = 0.023).

Probability of having at least one fledgling (Fox data included). The probability of broods having at least one fledging when only extrinsic covariates and nesting placement were included was best explained by a model containing effects of nesting category, July temperature, July precipitation and a two-way interaction between July precipitation and nesting category, fox litter percentage and a two-way interaction effect between fox litter percentage and nesting category, and total winter snowfall and a two-way interaction effect between total winter snowfall and nesting category (Appendix A1 Table A10). The effect of the brood being in a nest box versus a natural nest was positive, meaning that the probability was higher in the nest boxes than in the natural nests (β = 2.31, SE = 0.89, P = 0.0092, Figure 5). July temperature had a positive effect, so when it is hotter in July, the probability increases (β = 0.34, SE = 0.11, P = 0.0016). Fox litter percentage had a slightly positive effect on broods in nest boxes (β = 0.88, SE = 1.14, P = 0.44), but it had a negative effect on broods in natural nests (β = -2.84, SE = 0.94, P = 0.0026) as the model included an interaction effect.

The negative coefficient means that the probability of raising at least one chick to fledging decreases in natural nests when there are more fox litters. July precipitation had a negative effect on the probability of raising at least one fledgling in nest boxes ($\beta = -0.042$, SE = 0.015, P = 0.0045), and a less negative effect on broods in natural nests due to the interaction effect ($\beta = -0.012$, SE = 0.012, P = 0.34). Total snowfall during the preceding winter had a positive effect on the probability of raising at least one fledgling in nest boxes ($\beta = 0.020$, SE = 0.0066, P = 0.0028). A positive coefficient means that in years following winters with more snowfall, the probability of raising fledglings increased in nest boxes. The relationship was opposite in natural nests, as the presence of an interaction effect meant that the effect of snowfall was slightly negative here ($\beta = -0.0084$, SE = 0.0052, P = 0.14).

Fledglings per hatched egg in broods with fledging success. The probability of fledging for each chick from broods with at least one fledgling was best described by a model with effects of July temperature, May snowfall and median day of clutch initiation (See model selection table in appendix A1 Table A11). All the effects were positive, meaning that each of: Higher temperature in the first 15 days of July ($\beta = 0.24$, SE = 0.065, $P < 0.001$, Appendix A1 Figure A5), more May snowfall ($\beta = 0.044$, SE = 0.013, P = 0.0011) and later annual median clutch initiation ($\beta = 0.047$, SE = 0.011, $P << 0.001$), lead to higher probability of chicks fledging.

Fledglings per brood with fledging success. The number of fledglings emerging for each brood with at least one fledgling was best described by linear model with effects of nesting category, July temperature and May snowfall (See model selection table in Appendix A1 Table A12). The effect of nest box was positive, meaning broods in nest boxes had 0.21 more fledging chicks than those in natural nests (SE = 0.074, P = 0.0046, Figure 6). The effect of July temperature was also positive, indicating that for each ˚C warmer July temperatures got, 0.17 more fledglings emerged per brood (SE = 0.09, P = 0.10). The positive effect of snowfall during May means that for each millimetre of snow fallen in May, 0.086 more chicks fledge per brood (SE = 0.020, $P < 0.001$).

Discussion

This 21-year study of annual variation in the reproductive output of an Arctic population of snow buntings (*Plectrophenax nivalis*) resulted in three major findings. First, the result from the sensitivity analysis suggests that the breeding success of snow buntings on Spitsbergen is mainly determined after eggs hatch (Figure 3). Three components of the environment determine the success in this final step: First**,** extrinsic factors influenced because higher temperatures increase the number of fledglings per brood (Figure 6a), as well as leading to earlier timing of clutch initiation (Figure 4a). Furthermore, increased snowfall in preceding winters surprisingly also leads to earlier clutch initiation (Figure 4b) and increases the probability of having at least one fledgling in nesting boxes (Figure 5d). The amount of precipitation during the chick rearing period also has a negative effect on the probability of having fledglings (Figure 5c). Also, in natural nests, fox abundance is a strong predictor for whether clutches fail completely or not (Figure 5b). Second, timing is important because years with later time of clutch initiation have higher fledging percentage (Appendix A1 Figure A5) and longer breeding seasons. Third, nest placement also plays a role because broods in nest boxes had more fledglings (Figure 6) and initiated breeding earlier than broods in natural nests (Figure 4), and nest placement interacted with several extrinsic effects.

The results of the sensitivity analysis could reflect that the chick rearing is the hardest step to complete, also seen by the fact that there is more interannual variance in this step than egg number and hatching success (Figure 3). The observed pattern could mean that nestling care is a bigger strain on the parents than egg laying or incubation (Moreno et al. 1995). However, it was somewhat surprising that so little variation existed in the number of eggs and hatching success, as this indicates that parent quality and food availability does not strongly influence success in these steps. Links between parental quality and number of eggs laid have been found in for instance kittiwake (*Rissa dactyla*) (Coulson and Porter 1985), and in the passerine marsh tit (*Parus palustris*) food availability has been shown to influence the number of eggs laid per female (Nilsson 1991). A factor that was not controlled for in my study is the fact that snow bunting eggs are known to vary in size (Espmark 2016). Hatching rates has also been found to vary greatly among different bird species, and the overall common rate of infertile eggs has been reported to be around 13 % from several studies (Morrow, Arnqvist, and Pitcher 2002). In this study hatching rate was 93 % both counting infertile eggs and eggs not hatching for other reasons, indicating that snow bunting eggs have a very high hatching success.

Annual variation in environmental drivers

Regarding the environmental variables, the increasing trends found for temperature in May (1.6 ˚C per decade) and June (0.91˚C per decade) and advancing winter end day (9.7 days per decade) show that temperatures at the study site are warming (See Appendix A1 Table A4) , which is in line with the current scientific consensus of a warming climate (Allen et al. 2018). Advancing of winter end day means that the stage could be set for mismatch (Parmesan 2006; Visser and Both 2005; Visser and Gienapp 2019). While there was no warming found in April and July, the trends were positive (1.3˚C per decade and 0.33˚C per decade, respectively) and would probably become significant using longer time series.

Annual variation was minimal in two of six reproduction response variables. While chick fledging rates varied between year (Fledging probability per chick from broods with breeding success: coefficient of variance (CV) = 0.087, probability of having at least one fledgling: CV = 0.090), the number of eggs laid and the hatching probability per egg showed very little variance (Number of eggs: CV = 0.036 and hatching probability: CV = 0.052) among years (Figure 2), and between nests (Appendix A1 Table A1). The low variance is probably the reason why the models for number of eggs and hatching probability showed support for many of the covariates tested (Appendix A1 Table A7, Figure A2, Table A8 and Figure A3). However, using the same nest boxes in several years and a philopatric study species such as the snow bunting (Espmark 2016) means that the brood observations are probably not as independent as the mixed effect models assumes them to be. Therefore, it is possible that the observed effect has become inflated, and even very small effect sizes have become significant. The results from model selection for clutch size and hatching probability are therefore not interesting for further discussion.

Interestingly, the only reproductive measure to show a significant trend was the hatching probability, but since the hatching probability showed so little variance between years this effect seems to not impact the breeding success in the snow bunting particularly. More interesting is the fact that the number of fledglings per brood and fledging probability per chick showed no significant decrease from 1998 to 2018 (Appendix A1 Table A4). Especially considering that climate change is often mentioned as a serious of extinctions (Crombie 2015), the lack of trends could be cause for optimism.

Annual variation in six components of reproductive effort

For clutch initiation day, a negative effect of warmer temperatures, in line with previous findings of how northern-temperate birds start egg-laying earlier in warmer springs (Dunn 2004; Torti and Dunn 2005; Weatherhead 2005), was found (Figure 4). The observed relationship could mean that the snow bunting will advance its timing of clutch initiation in the future, leading to a longer breeding season and more time for second broods. The mechanism for earlier breeding in warmer springs is probably that higher spring and early summer temperatures make it easier to find nesting spots due to earlier snowmelt (Høye and Forchhammer 2008), and that the higher abundance (Perrins 1991) and activity (Avery and Krebs 1984) of surface dwelling arthropods allows the parents to prepare for earlier breeding as food availability has been shown to lead to earlier breeding due to earlier preparation, for instance in Florida scrub jays (*Aphelocoma coerulescens*) (Schoech 1996). Furthermore, the finding that breeding was initiated earlier in nest boxes than in natural nests (Figure 4) can be explained by the fact that nest boxes are easily available before the snow has disappeared. It could also mean that the earliest arriving males prefer the nest boxes, as the pylons are safe from foxes and provide good singing posts. The negative effect of winter snow meaning that more snow leads to earlier clutch initiation (Figure 4b) is surprising. I predicted the opposite due to how other studies have found that, in general, earlier snowmelt leads to earlier breeding in birds, for instance (García-González et al. 2016; Høye et al. 2007; Madsen et al. 2007). However, the effect of snowfall was not significantly different from zero (P = 0.19), and the same model except for lacking this effect was within $\Delta AIC_c < 2$ (Appendix A1 Table A6). The found effect of snowfall on day of clutch initiation day could well be from fallacy in the data.

When analyzing timing of clutch initiation, the fact that also second broods are likely to be in the data set may affect the analysis, even though the known proportion of second-broods is low. Espmark (2016) reported that only 2.3 % of the snow bunting broods observed between 1998 and 2005 on Svalbard were second broods. If day of first breeding in the population now advances, the average day of clutch initiation could remain unchanged if the snow bunting uses the longer breeding season for a second brood, canceling out the advance for average clutch initiation day. Therefore, it is important to distinguish first and second broods when investigating timing of clutch initiation. The possibility of a longer breeding season is underlined by the fact that the timing of the last brood varied less than the timing of the first one (standard deviation last brood = 3.78, standard deviation first brood = 6.56), and that these two measures were not found to be correlated (correlation = -0.16, analysis not shown). This explanation is also in line with Skøien's (2015) findings that later start of breeding in the population means more breeding synchrony. The fact that years where the population's first brood came earlier had a slight trend of more broods included (correlation = -0.33, analysis not shown) also supports this. However, variation in number of broods included could also be influenced by observer effort, which I could not account for in my analyses due to no data on this.

As for the success in breeding, fox predation seems to be key for explaining complete breeding failures. The model for probability of having at least one fledgling with all covariates except fox litter percentage covariates probably suffered from too few failures (Number of failures = 56, number of successes = 902), as the effects in this model were illogical (Appendix A1 Figure A4). The model is therefore not discussed further. The effects it showed were also very different (several even directly opposite) from the effects from model selection with the same response variable when only extrinsic covariates and including fox litter percentage was conducted (See Figure 5 and Appendix A1 Figure A4). The model including fox predation included many more failures (N = 313) as predated nests were also included.

The importance of fox numbers is emphasized by the fact that in natural nests, a strong effect on the probability of raising at least one fledgling (with only extrinsic covariates) was a negative effect of fox numbers (Figure 5b). This result indicates that predation has a major influence on the breeding success of the snow bunting on Svalbard population. Fox predation had no significant effect in nest boxes (P = 0.44), as nest boxes were a safe nesting environment because they are usually placed high up on pylons and unavailable to foxes. The effect of predation was not unexpected, as effects of predation on breeding success have been previously reported, for instance, by Baines, Moss and Dugan (2004) for capercaille (*Tetrao urogallus*) in Scotland, and Tapper, Potts and Brockles (1996) for grey partridges (*Perdix perdix*) in England. Overall, 162 out of 316 broods with complete breeding failure were taken by fox, making up a total of 10% of the 1591 broods in the study.

However, not only fox decided the breeding success; the probability of raising at least one fledgling (using only extrinsic covariates) (Figure 5), and the number of fledglings in broods where at least one chick fledged (Figure 6) were both higher in nest boxes than in natural nests. As there were no data on the parent ID and nest ID, it is impossible to know if this was influenced by repeated breeding by certain individuals in specific nests. However, it could be that more experienced, better quality individuals choose to breed in nest boxes. The fact that breeding starts earlier in nest boxes (Figure 4) could also mean that the best-placed nest boxes are occupied early by high quality individuals, leading to earlier breeding and better success in the nest boxes. Nest sites are a limited resource, and nest boxes in proximity to good areas for foraging would facilitate chick feeding. Territory quality has been shown to be important for breeding success for instance in the oystercatcher (*Haematopus ostralegus*) (Ens et al. 1992).

In the nest boxes, however, there was a negative effect of rainfall on the probability of having at least one fledgling (Figure 5c) that did not exist in natural nests. This result probably reflects that the nest boxes are more exposed in the terrain as they are high up in the terrain. Especially if wind and rain work together to create horizontal rain, the nest boxes could be exposed. Natural nests are often beneath rocks and should be less troubled.

As for temperature, the weather covariate with the strongest trends (Appendix A1 Table A4), the findings that higher July temperatures increased the probability of raising at least one fledgling (Figure 5a) and the number of chicks to fledge from broods with at least one fledgling (6a) are in line with snow bunting-results from Hoset et al. (2004) and Fossøy et al. (2015). These studies used many of the same data as in this study. Their studies found that summer temperatures increased breeding success. The relationship is probably due to how higher temperatures lead to more insects (Perrins 1991) and insect activity (Avery and Krebs 1984), and possibly lower energetic demands (Weathers 1992). It is interesting how only temperature and rainfall late in the season were included in the best models of breeding success, even though the duration of timings of clutch initiation spanned 55 days (Appendix A1 Table A1). This result indicates that most chicks are being raised in the start of July, supported by the finding that the median clutch initiation date was June 8th, leading to a 13-day chick rearing period starting on June 26th if assuming 6 days for hatching and 13 for incubation (Hussel 1972). However, it should be kept in mind that the clutch initiation dates varied a lot between years (Figure 2), and therefore the time periods of relevance could vary between years. The relevant period could be progressing as the clutch initiation times are progressing (Appendix A1 Table A4). Even though no statistically significant trends were found in the July temperature during this study, the climate is warming (Allen et al. 2018), meaning that the snow bunting population could be positively affected by increasing summer temperatures under continued warming.

Regarding snow cover, the unexpected apparently positive effect winter snowfall had on the probability of having at least one fledgling in the nest boxes (Figure 5d) could be an indicator of higher-quality individuals using nest boxes when there is more snowfall, because this makes the natural nesting places harder to find. The increased snowfall could also lead to increased competition for the nest boxes, only allowing early arriving high-quality males to occupy them. If so, the snow is not advantageous *per se* but leads to higher breeding success by concentrating high-quality breeders in the nest boxes. Since the total Svalbard population is obviously much larger than the part included in the study, the fact that no negative effect is seen in the natural nests is understandable. The fact that 20-50 high-quality pairs move to nest boxes should not drain the rest of the population of breeding quality and decrease breeding success. Since nest boxes are artificial while natural nests are the norm, the statistically insignificant negative trend in the natural nests is the “natural” effect on the snow bunting population on Svalbard.

The average probability of fledging for the hatched chicks from successful broods increased when the median clutch initiation day was delayed (Appendix A1 Figure A5). An explanation for this could be that early nests are rushed to make time for a second brood, at the cost of probability of fledging for the chicks. Another explanation is that insect abundance increases later in the season (Skjøstad 2008). The positive effect of later clutch initiation could indicate that even though later first-time breeding means less time for second broods, later broods should be less susceptible to harsh weather in late spring. If so, the parents will only have time for one brood and invest more into this one in years with later onset of breeding. I tested for a direct effect of clutch synchrony, but never found one, in contrast with the findings from Skøien (2015) (who used a different measure of synchrony). Further analysis on second broods’ effect on breeding success would be beneficial to understand these processes better.

Snowfall in May seemed to have a positive effect on both the probability that a hatched chick would fledge (Appendix A1 Figure A5b) and the number of fledged from broods with at least one fledgling (Figure 6b). The observed effect could be due to how later snowmelt leads to later emergence of arthropods (Høye et al. 2007; Høye and Forchhammer 2008; Schekkerman et al. 2004), which could have positive effects for the snow bunting should it be struggling with mismatch. The positive effect would appear because the postponement of the food peak would help the snow bunting lay its eggs in time. This explanation would have been even more reasonable if an interaction effect was found so the effect of May snow was stronger in nest boxes, as timing of breeding starts sooner there (Figure 4). Still, an indication that mismatch happens is that in years with later time of clutch initiation there is a higher number of fledglings per successful brood. Another possible mechanism explaining the positive effect of snowfall is that arthropod abundance could be positively influenced by more snow cover due to higher winter survival (Bale and Hayward 2010), but then again how much snowfall as late as May influences this is uncertain.

The fact that no effect of timing of day of winter end or early spring temperatures on breeding success was found indicates that the breeding success won't necessarily change in the near future even if spring comes earlier or gets warmer. However, day of winter end was correlated with July temperature and was therefore excluded from appearing in the same model (Appendix A1 Table A3). As such, it could have had an effect that was not as important as the effect of July temperature. This claim is also supported by the fact that some models within delta 2 indicated that the number of fledglings from broods with at least one fledgling was higher in years with early day of winter end (Appendix A1 Table A12). Moreover, since all these models are on brood-level, effects on the number of broods could change without being captured here.

Effect of climate change

Even though the Norwegian Red List worries about the future for the snow bunting (https://artsdatabanken.no/Rodliste2015/rodliste2015/Norge/4217), my results give reason for careful optimism. Warmer summer temperatures appear to be advantageous for the breeding success (Figure 5a, Appendix A1 Figure A5a, Figure 6a), and not a challenge as the Red List speculates. However, with clutch initiation dates advancing due to warmer springs (Figure 4a), the average number of fledglings per brood is likely to decrease. The negative effect on breeding success could, however, be evened out by more opportunity for second broods due to longer breeding seasons. If total winter snowfall decreases due to shortening of winter and less cold weather, the results are not conclusive on how the snow bunting will be affected. All in all, there doesn't seem to be too much negative effect of increasing climate change, even though earlier clutch initiation leads to less fledglings and the effect of May snow could be an indicator of mismatch. Still, this study leaves out weather variance, which is expected to increase in the Arctic due to climate changes (Høye et al. 2007; Post et al. 2001; Walsh et al. 2011). Even though no detrimental trends were found in the fledging probability or fledgling numbers (Appendix A1 Table A4), this does not account for increased competition should other species become able to immigrate to Svalbard. Apparent competition could also lead to more predation pressure, as the herbivore community on Svalbard might be changing (Hansen et al. 2013).

Conclusion

In this long-term study I found that the most important step for breeding success in snow bunting broods on Svalbard is raising hatched chicks to fledging, conducting one of few studies investigating a breeding season in a holistic view. Little variation exists in clutch sizes and hatching probability. Temperature determines timing of broods and fledging success. Environmental covariates played parts in explaining differences in fledging success, both predation and weather in the winter to summer. How the weather influences the snow bunting breeding success cannot be fully understood from these results directly, as several mechanisms that are not distinguishable with these data are plausible. The effect of May snowfall indicates that trophic mismatch could be a problem, but this indication is far from certain. Studies using both environmental data as well as data on food abundance would be the logical next step in this studying these relationships, as well as proper timeseries data on snow cover, which are currently lacking at the weather station. The results show that breeding success in the snow bunting is not declining, allowing for optimism when predicting more effects of climate change in the Arctic.

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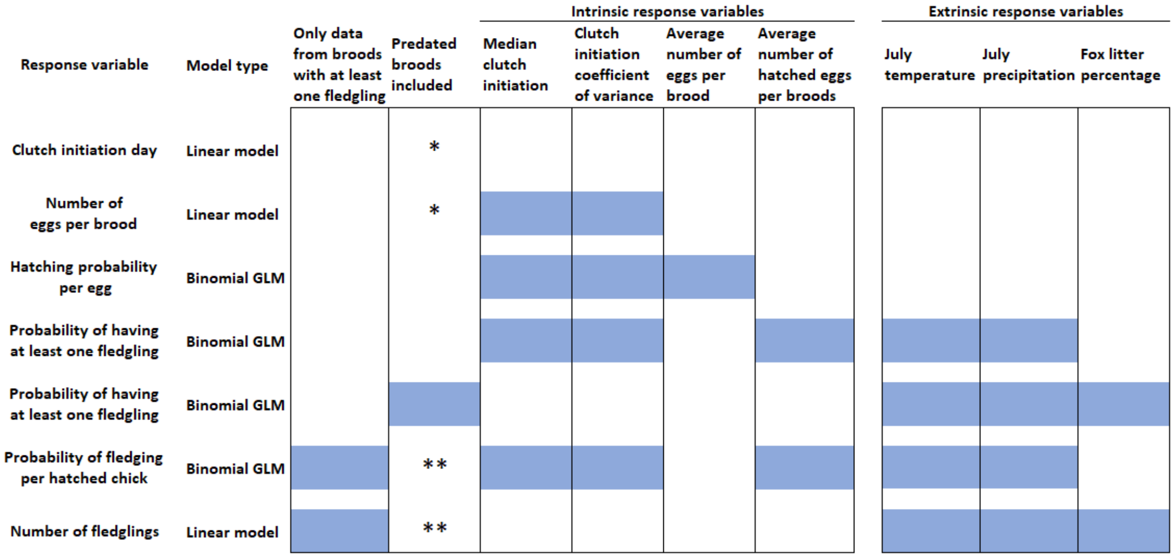
Figures



				Intrinsic response variables				Extrinsic response variables		
Response variable	Model type	Only data from broods with at least one fledgling	Predated broods included	Median clutch initiation	Clutch initiation coefficient of variance	Average number of eggs per brood	Average number of hatched eggs per broods	July temperature	July precipitation	Fox litter percentage
Clutch initiation day	Linear model		*							
Number of eggs per brood	Linear model		*	🟦	🟦					
Hatching probability per egg	Binomial GLM			🟦	🟦	🟦				
Probability of having at least one fledgling	Binomial GLM			🟦	🟦		🟦	🟦	🟦	
Probability of having at least one fledgling	Binomial GLM		🟦					🟦	🟦	🟦
Probability of fledging per hatched chick	Binomial GLM	🟦	**	🟦	🟦		🟦	🟦	🟦	
Number of fledglings	Linear model	🟦	**					🟦	🟦	🟦

Figure 1: Models fitted to the different response variables. Blue colour means “checked off”. * = not relevant as brood predation happens after clutch initiation/egg laying, ** = not relevant because all predated broods are already removed due to brood failure. Fox litter percentage is still controlled for in “Number of fledglings”. Note that nesting category and all explanatory covariates not shown are tested for in all models, plus interaction effects between nest category and all included extrinsic covariates. See Methods for all explanatory covariates. Shown intrinsic and extrinsic variables are tested for but not necessarily included in top ranked model.

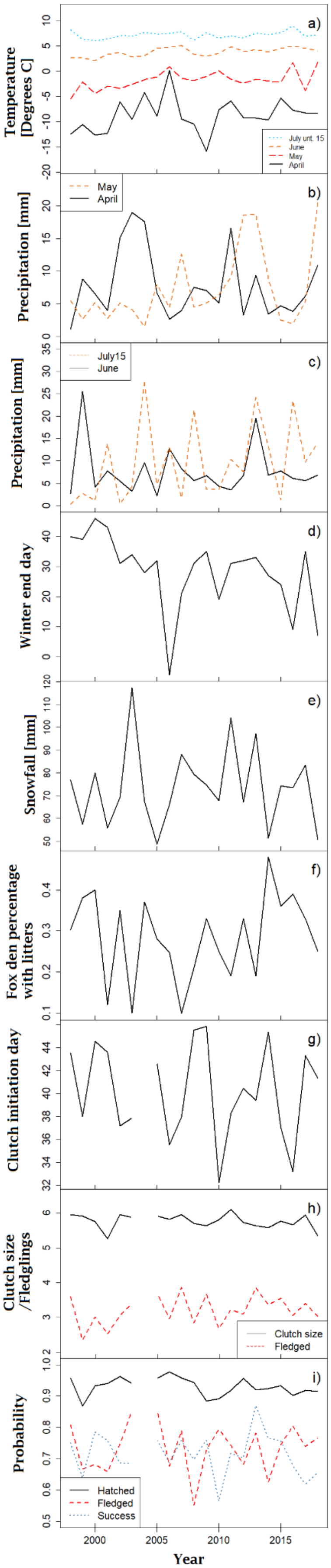

a)
Temperature [Degrees C]
10
5
0
-5
-10
-15
-20
July unt. 15
June
May
April
b)
Precipitation [mm]
May
April
20
15
10
5
0
c)
Precipitation [mm]
July15
June
35
30
25
20
15
10
5
0
d)
Winter end day
40
30
20
10
0
e)
Snowfall [mm]
120
110
100
90
80
70
60
50
f)
Fox den percentage with litters
0.4
0.3
0.2
0.1
g)
Clutch initiation day
44
42
40
38
36
34
32
h)
Clutch size /Fledglings
6
5
4
3
2
Clutch size
Fledged
i)
Probability
1.0
0.9
0.8
0.7
0.6
0.5
Hatched
Fledged
Success
2000
2005
2010
2015
Year

Figure 2: (Previous page) Time series (1998-2018) with annual values from Svalbard Weather Station of a) April, May, June, July (until the 15th) mean temperature, b) April and May total precipitation, c) June and July (until the 15th) total precipitation, d) Day of winter end where 1 = May 1st, e) snowfall in preceding winter from November to March, f) fox dens known to have litters, g) mean clutch initiation day where 1 = May 1st, h) number of eggs and number of fledglings, i) probability of hatching per egg, fledging per hatched egg and having at least one fledgling per snow bunting brood on Svalbard.

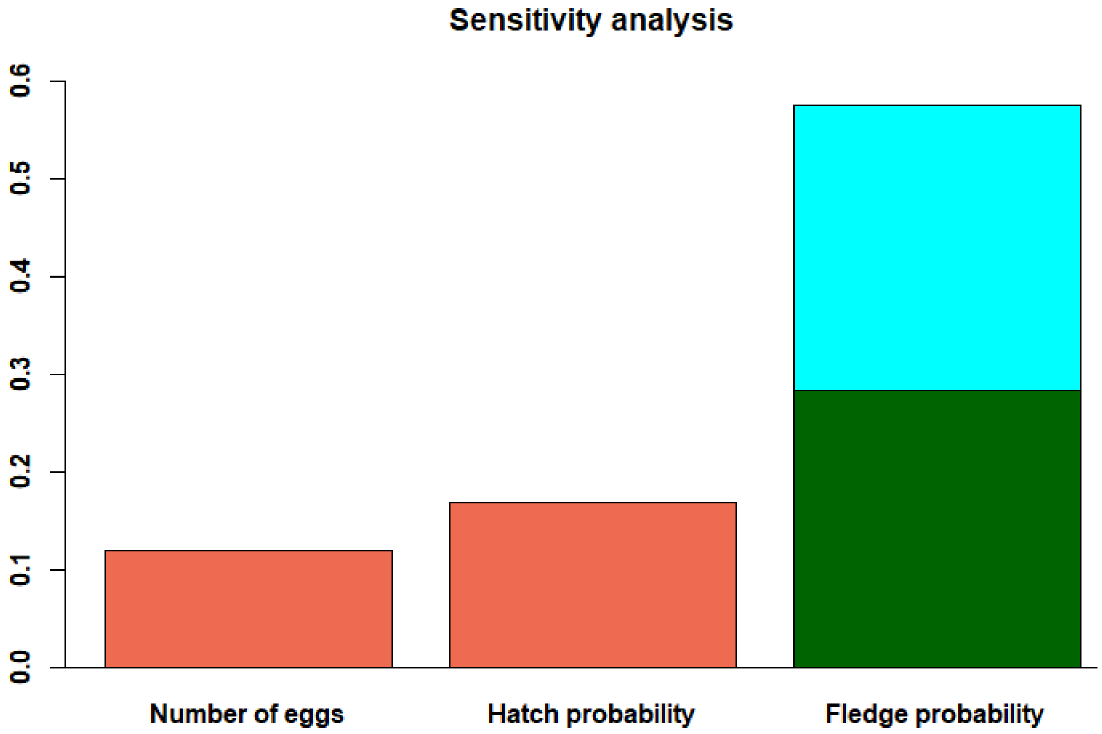


Figure 3: Change in expected average number of fledglings for snow buntings on Svalbard resulting from adding 1 standard deviation to the number of eggs, hatching probability and probability of having at least one fledgling (cyan) plus probability of fledging for hatched chicks from broods with at least one fledgling (green) .

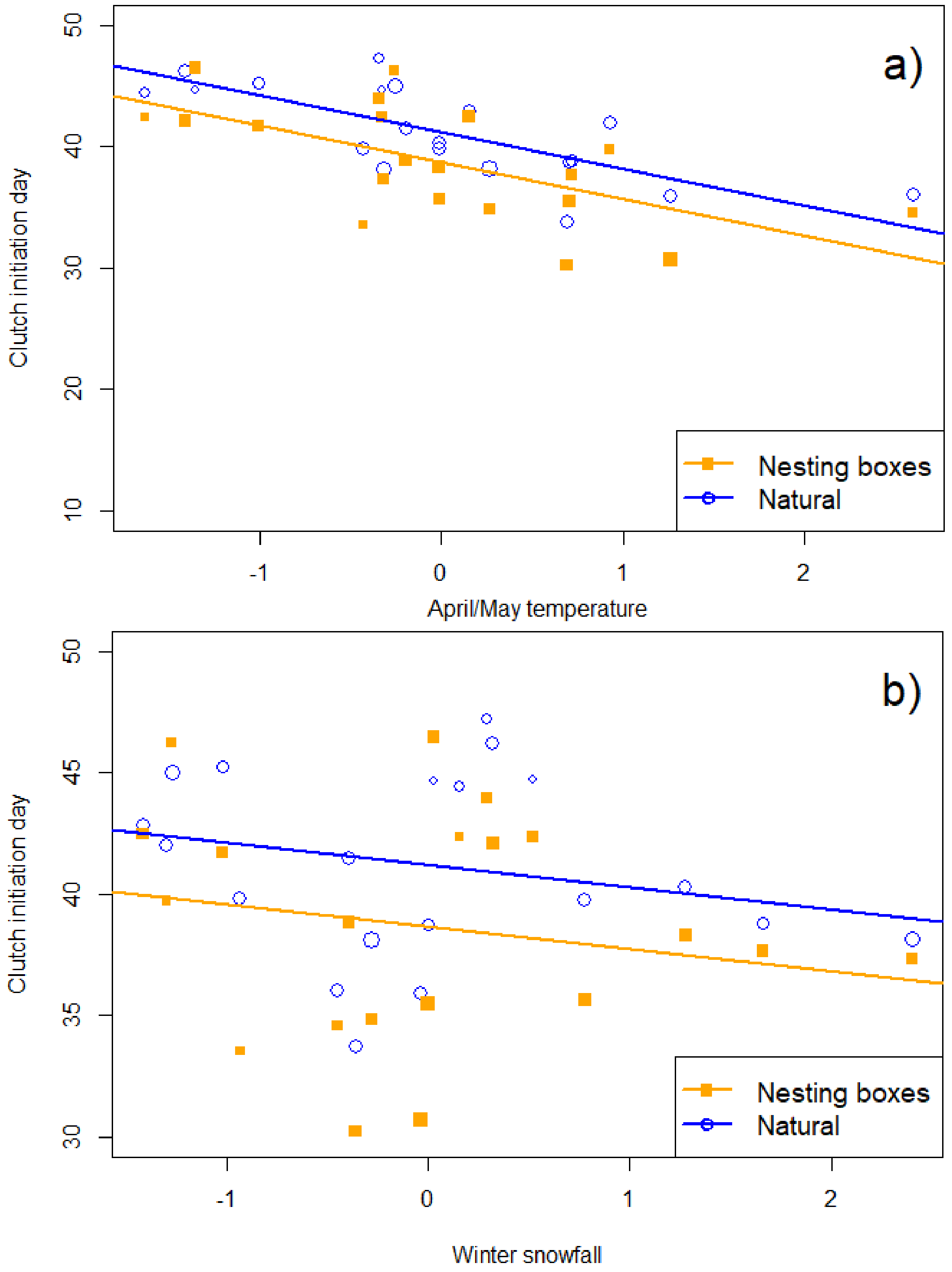


Figure 4: Effect plots of estimates from top ranked model from Appendix A1 Table A6 showing effect on snow bunting clutch initiation at Svalbard in 1998-2018 of a) mean temperature in April-May and b) winter snowfall. 1 on y-axis = May 1st. X-axes are standardized. Point sizes are proportional to the number of observations they contain.

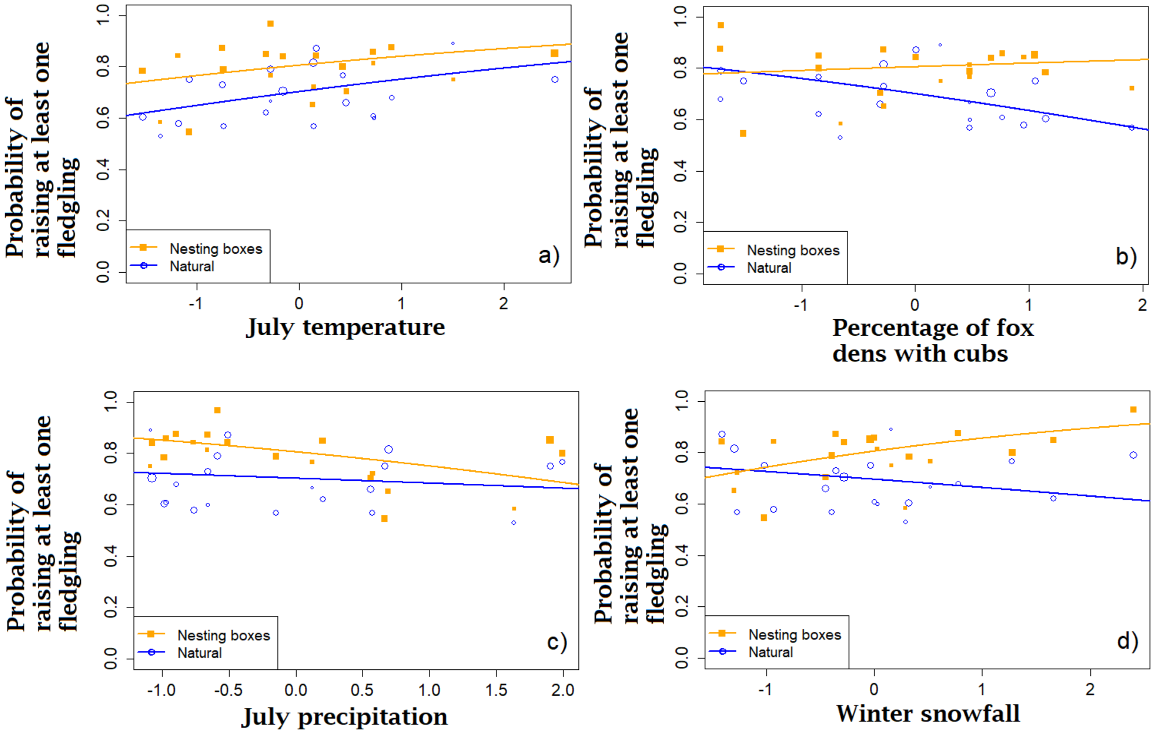


Figure 5: Effect plots of estimates from top ranked model in Appendix A1 Table A10, showing effect on probability of snow bunting broods having at least one fledgling on Svalbard in 1998-2018 of a) July mean temperature, b) fox litter percentage, c) July precipitation, d) Winter snowfall. X-axes are standardized. Point sizes are proportional to the number of observations they contain.

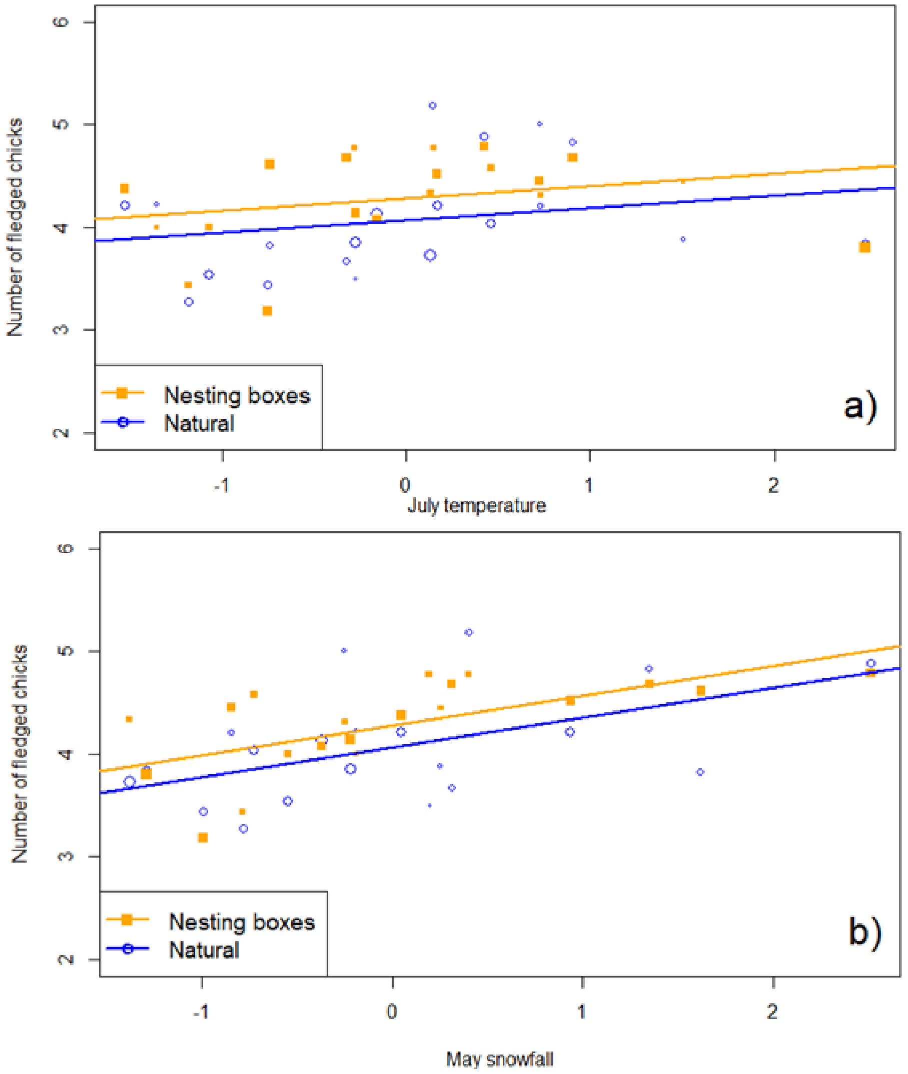


Figure 6: Effect plots of estimates from top ranked model from Appendix A1 Table A12, showing effect on number of snow bunting fledglings from broods producing at least one fledgling on Svalbard from 1998 to 2018 of a) July mean temperature, b) May snowfall. X-axes are standardized. Point sizes are proportional to the number of observations they contain.

Appendix A1

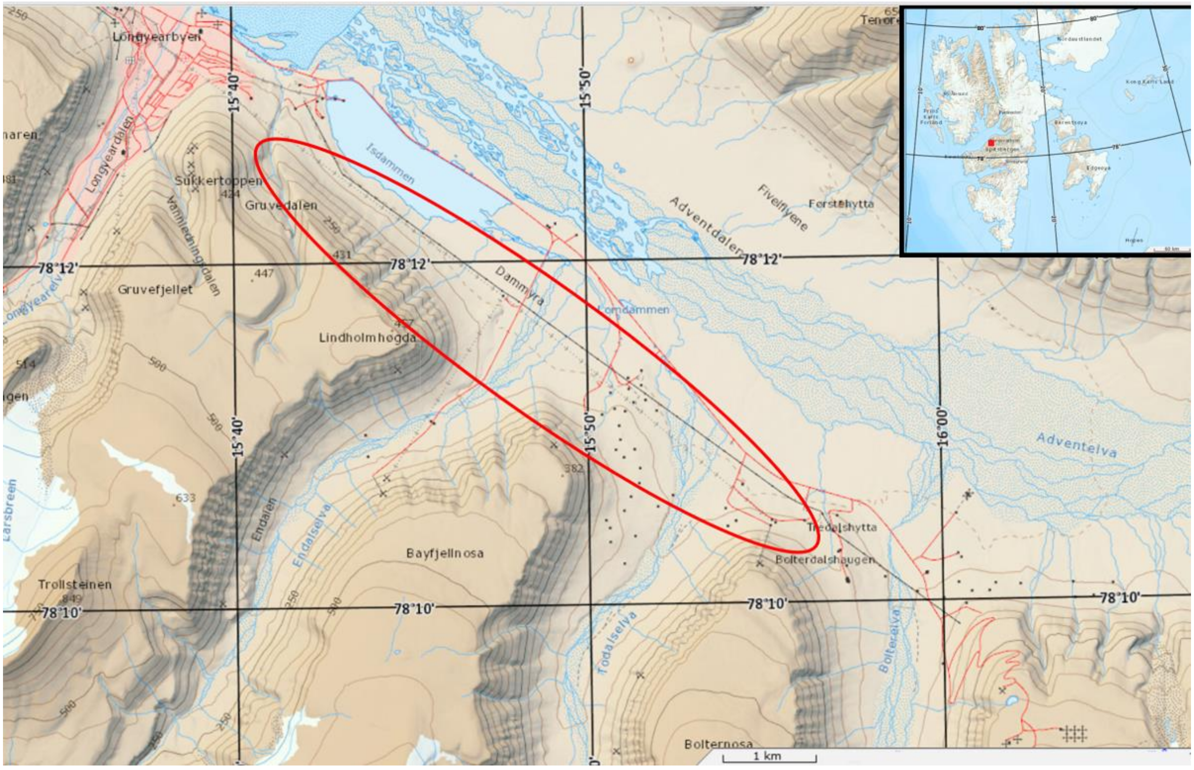


Figure A1: Geographical location of the study site in the Adventdalen valley, Spitsbergen, Svalbard (78° 13`N, 15°38`E), with nesting site of the study population of snow buntings indicated with red ellipse. The map was made expanding on a map from the Norwegian Polar institute. Coordinates are marked on the grid.

Table A1: Snow bunting fecundity data collected on Svalbard from 1998-2018, N = number of observations, Min = minimum value, Max = maximum value, SD = standard deviation, SD/mean = standard deviation divided by mean. For clutch initiation day; 1 = May 1st, meaning that 13 = May 13th, 68 = July 6th, 39 = June 8th.

Measure	**N**	**Min**	**Max**	**Mean**	**Median**	**SD**	**SD/mean**
Clutch initiation day	1539	13	68	39.7	39	8.44	0.21
Number of eggs	1427	2	8	5.76	6	0.87	0.15
Number of hatched eggs	1114	0	8	5.37	6	1.19	0.22
Number of fledged chicks	1395	0	7	3.19	4	2.01	0.63

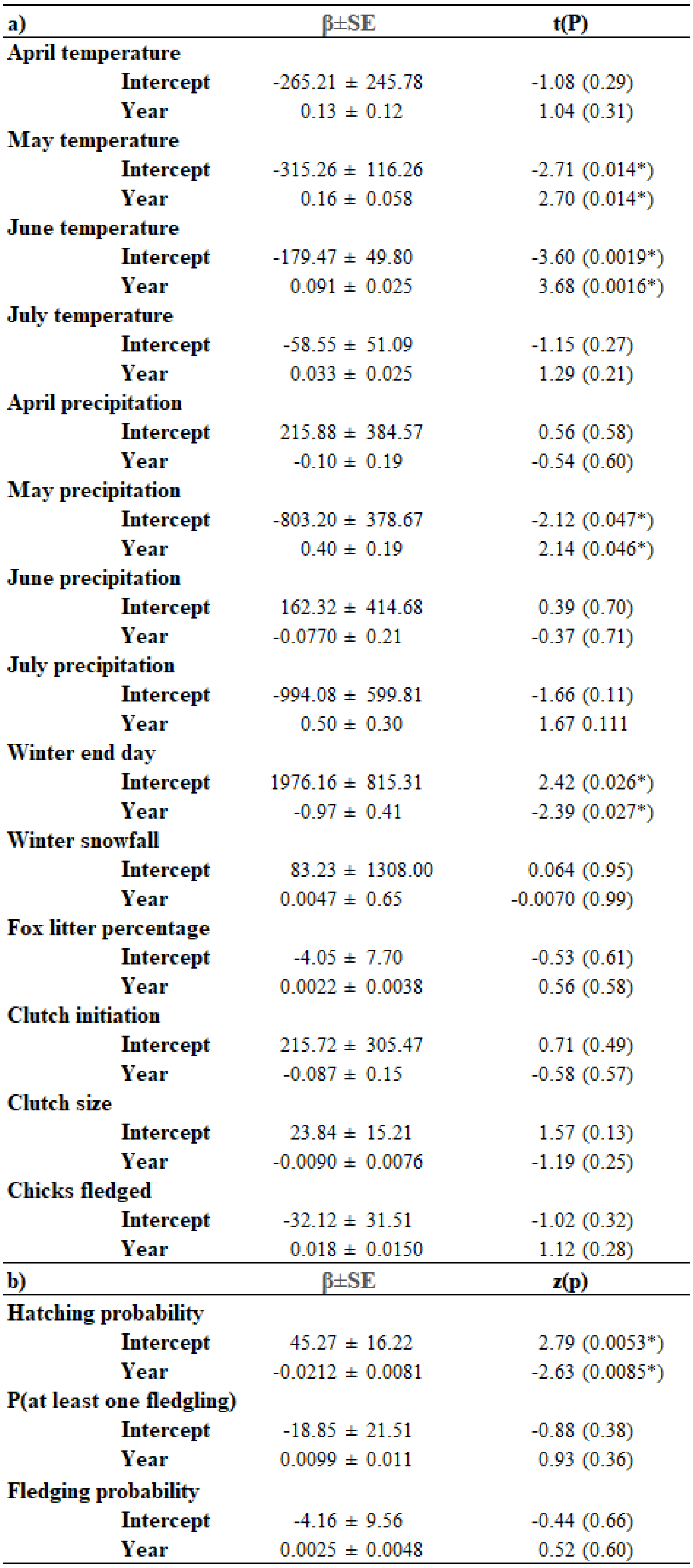
Table A2: Number of observations of snow bunting broods on Svalbard from nest boxes and natural nests per year from Svalbard. (All observations from 2004 were removed, see Methoods).

Year	Nesting boxes	Natural nests
1998	17	30
1999	20	48
2000	37	57
2001	33	43
2002	31	72
2003	31	62
2004	0	0
2005	37	46
2006	29	50
2007	35	45
2008	30	30
2009	34	19
2010	35	47
2011	35	40
2012	35	54
2013	41	52
2014	24	56
2015	46	43
2016	50	46
2017	32	24
2018	25	60

Table A3: Correlation between standardized explanatory variables. April temp = April mean temperature, May temp = May mean temperature, June temp = June mean temperature, July temp = mean temperature from first 15 days of July, April prec = April precipitation, May prec = May precipitation, AOw = mean Arctic Oscillation from November to March, Winter end = day of winter end, Winter snow = total winter snowfall, May snow = total May snowfall, May rain = May rainfall. Winter end, winter snowfall, May snowfall and May rainfall are explained in methods.

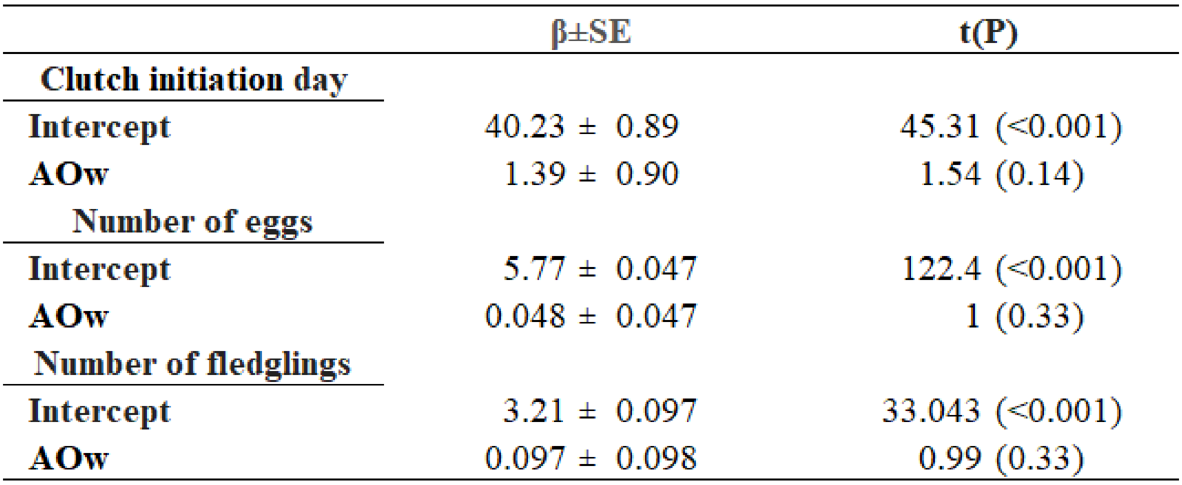
	April temp	**May temp**	**June temp**	**July temp**	**April prec**	**June prec**	**July prec**	**AOw**	**Winter end**	**Winter snow**	**Fox**	**May snow**	**May rain**
April temp	1	0.42	0.66	0.16	0.09	0.08	0.15	-0.1	-0.72	0.01	-0.05	-0.18	0.18
May temp	0.42	1	0.52	0.32	-0.01	0.15	0.48	-0.28	-0.83	-0.24	-0.09	-0.34	0.2
June temp	0.66	0.52	1	0.48	-0.11	-0.02	0.37	0.07	-0.61	0.01	-0.15	0.16	0.18
July temp	0.16	0.32	0.48	1	-0.27	-0.11	0.14	0.02	-0.46	0.06	0.11	-0.02	-0.04
April prec	0.09	-0.01	-0.11	-0.27	1	-0.05	-0.06	0.01	0.16	0.52	-0.32	-0.05	-0.09
June prec	0.08	0.15	-0.02	-0.11	-0.05	1	0.21	-0.14	-0.04	-0.11	0.06	0.11	0.11
July prec	0.15	0.48	0.37	0.14	-0.06	0.21	1	-0.22	-0.33	0.01	-0.13	0.07	0.23
AOw	-0.1	-0.28	0.07	0.02	0.01	-0.14	-0.22	1	0.17	0.05	0.36	0.08	-0.27
Winter end	-0.72	-0.83	-0.61	-0.46	0.16	-0.04	-0.33	0.17	1	0.19	0.04	0.36	-0.12
Winter snow	0.01	-0.24	0.01	0.06	0.52	-0.11	0.01	0.05	0.19	1	-0.48	0.3	0.06
Fox	-0.05	-0.09	-0.15	0.11	-0.32	0.06	-0.13	0.36	0.04	-0.48	1	-0.2	0.13
May snow	-0.18	-0.34	0.16	-0.02	-0.05	0.11	0.07	0.08	0.36	0.3	-0.2	1	0.39
May rain	0.18	0.2	0.18	-0.04	-0.09	0.11	0.23	-0.27	-0.12	0.06	0.13	0.39	1

Table A4: Temporal trends in environmental covariates and snow bunting reproduction data on Svalbard in 1998-2018 in the study system, shown as a) coefficient estimates (β), standard error (SE) and test statistics (t- and P-values) for linear models with year as predictor and as b) coefficient estimates (β), standard error (SE) and test statistics (z- and P-values) for generalized linear models. * denotes significant p-values at 0-05-level.



a)		**β±SE**	**t(P)**
April temperature			
	Intercept	-265.21 ± 245.78	-1.08 (0.29)
	Year	0.13 ± 0.12	1.04 (0.31)
May temperature			
	Intercept	-315.26 ± 116.26	-2.71 (0.014*)
	Year	0.16 ± 0.058	2.70 (0.014*)
June temperature			
	Intercept	-179.47 ± 49.80	-3.60 (0.0019*)
	Year	0.091 ± 0.025	3.68 (0.0016*)
July temperature			
	Intercept	-58.55 ± 51.09	-1.15 (0.27)
	Year	0.033 ± 0.025	1.29 (0.21)
April precipitation			
	Intercept	215.88 ± 384.57	0.56 (0.58)
	Year	-0.10 ± 0.19	-0.54 (0.60)
May precipitation			
	Intercept	-803.20 ± 378.67	-2.12 (0.047*)
	Year	0.40 ± 0.19	2.14 (0.046*)
June precipitation			
	Intercept	162.32 ± 414.68	0.39 (0.70)
	Year	-0.0770 ± 0.21	-0.37 (0.71)
July precipitation			
	Intercept	-994.08 ± 599.81	-1.66 (0.11)
	Year	0.50 ± 0.30	1.67 0.111
Winter end day			
	Intercept	1976.16 ± 815.31	2.42 (0.026*)
	Year	-0.97 ± 0.41	-2.39 (0.027*)
Winter snowfall			
	Intercept	83.23 ± 1308.00	0.064 (0.95)
	Year	0.0047 ± 0.65	-0.0070 (0.99)
Fox litter percentage			
	Intercept	-4.05 ± 7.70	-0.53 (0.61)
	Year	0.0022 ± 0.0038	0.56 (0.58)
Clutch initiation			
	Intercept	215.72 ± 305.47	0.71 (0.49)
	Year	-0.087 ± 0.15	-0.58 (0.57)
Clutch size			
	Intercept	23.84 ± 15.21	1.57 (0.13)
	Year	-0.0090 ± 0.0076	-1.19 (0.25)
Chicks fledged			
	Intercept	-32.12 ± 31.51	-1.02 (0.32)
	Year	0.018 ± 0.0150	1.12 (0.28)
b)		**β±SE**	**z(p)**
Hatching probability			
	Intercept	45.27 ± 16.22	2.79 (0.0053*)
	Year	-0.0212 ± 0.0081	-2.63 (0.0085*)
P(at least one fledgling)			
	Intercept	-18.85 ± 21.51	-0.88 (0.38)
	Year	0.0099 ± 0.011	0.93 (0.36)
Fledging probability			
	Intercept	-4.16 ± 9.56	-0.44 (0.66)
	Year	0.0025 ± 0.0048	0.52 (0.60)

Table A5: Coefficient estimates (β), standard error (SE) and test statistics (t- and P-values) for linear mixed effects models fitted using Arctic Oscillation winter index (AOw) as the explanatory variable, controlling for year as random effect. Response variables are snow bunting measures from Svalbard,



	β±SE	t(P)
Clutch initiation day		
Intercept	40.23 ± 0.89	45.31 (<0.001)
AOw	1.39 ± 0.90	1.54 (0.14)
Number of eggs		
Intercept	5.77 ± 0.047	122.4 (<0.001)
AOw	0.048 ± 0.047	1 (0.33)
Number of fledglings		
Intercept	3.21 ± 0.097	33.043 (<0.001)
AOw	0.097 ± 0.098	0.99 (0.33)

Table A6: All models with $\Delta AIC_c < 2$ from model selection with timing of clutch initiation as response variable. All covariates not represented in these models were excluded. Table shows parameter estimates (β) for intercept and explanatory variables. AIC_c , ΔAIC_c and AIC_c weight (w_i) are shown for all candidate models. "NP=Nat" = Nesting placement natural nest in contrast to nest boxes, All Temp = mean daily temperature for all days between April 1st and July 15th, A/M Temp = Average daily temperature in April and May, April prec = total April precipitation, June prec = total June precipitation, May rain = total May rainfall, May snow = total May snowfall, Winter snow = total winter snowfall. "NP:" denotes interaction effect between nest placement and other explanatory variables. Wi = model weight.

		Explanatory variables												Model selection criteria		
Model rank	Intercept	NP=Nat	All Temp	A/M Temp	April Prec	June Prec	May Rain	May Snow	Winter snow	NP:A/M Temp	NP:June Prec	NP:May Snow	NP:Winter Snow	AICc	ΔAICc	wi
1	38.69	2.52		-3.03					-0.92					10529.56	0.00	0.0535
2	38.69	2.53		-2.95										10529.59	0.03	0.0528
3	38.69	2.52	-2.91											10530.03	0.48	0.0422
4	38.66	2.53	-2.68			-1.36		1.39	-1.22		-0.70	0.64		10530.21	0.65	0.0386
5	38.70	2.51	-2.96						-0.84					10530.38	0.82	0.0355
6	38.69	2.53		-2.79			-0.70							10530.49	0.93	0.0337
7	38.69	2.51		-2.85				0.66	-1.10					10530.60	1.04	0.0318
8	38.69	2.51		-2.89			-0.63		-0.87					10530.60	1.04	0.0318
9	38.65	2.54		-2.73		-1.20		1.22	-1.21		-0.70	0.65		10530.62	1.06	0.0315
10	38.69	2.52		-2.97		-0.58			-0.98					10530.71	1.15	0.03
11	38.69	2.50	-2.69			-0.89		1.00	-1.23					10530.74	1.18	0.0296
12	38.68	2.53		-2.86				0.96	-1.10			0.51		10530.77	1.21	0.0292
13	38.69	2.50	-2.78					0.83	-1.08					10530.86	1.30	0.0279
14	38.68	2.52	-2.69			-0.91		1.29	-1.22			0.51		10530.91	1.35	0.0272
15	38.68	2.51	-2.68			-1.25		1.02	-1.22		-0.55			10530.98	1.42	0.0263
16	38.68	2.52		-2.96		-0.93			-0.97		-0.54			10531.01	1.46	0.0258
17	38.69	2.52	-2.91		-0.66									10531.04	1.48	0.0255
18	38.69	2.53		-2.92	-0.49									10531.04	1.48	0.0255
19	38.69	2.52	-2.75				-0.67							10531.05	1.50	0.0253
20	38.68	2.53		-2.89		-0.49								10531.06	1.50	0.0252
21	38.69	2.51	-2.92			-0.73			-0.92					10531.06	1.50	0.0252
22	38.68	2.52	-2.78					1.12	-1.08			0.50		10531.09	1.53	0.0248
23	38.69	2.52	-2.86			-0.64								10531.12	1.57	0.0245
24	38.69	2.52		-2.73		-0.73		0.82	-1.22					10531.22	1.67	0.0233
25	38.67	2.54		-2.89		-0.84					-0.55			10531.30	1.74	0.0224
26	38.67	2.53		-2.74		-0.74		1.12	-1.22			0.52		10531.34	1.78	0.0219
27	38.68	2.53		-2.85				0.33						10531.37	1.81	0.0216
28	38.70	2.50		-3.14					-0.92	-0.19				10531.38	1.82	0.0216
29	38.68	2.51	-2.91			-1.08			-0.91		-0.54			10531.38	1.82	0.0215
30	38.67	2.53	-2.86			-0.99					-0.55			10531.38	1.83	0.0215
31	38.69	2.51		-3.05						-0.18				10531.41	1.85	0.0212
32	38.67	2.52		-2.72		-1.09		0.84	-1.21		-0.55			10531.46	1.90	0.0207
33	38.69	2.52		-3.03					-0.85				0.11	10531.49	1.93	0.0204
34	38.69	2.52	-2.79					0.50						10531.50	1.94	0.0203
35	38.70	2.50	-2.82				-0.61		-0.80					10531.52	1.96	0.02
36	38.67	2.54		-2.85				0.62				0.51		10531.53	1.97	0.02

Table A7: All models with $\Delta AIC_c < 2$ from model selection with number of eggs as response variable. All covariates not represented in these models were excluded. Table shows parameter estimates (β) for intercept and explanatory variables. AIC_c , ΔAIC_c and AIC_c weight (w_i) are shown for all candidate models. NP = Nesting placement natural nest in contrast to nest boxes, AprilPrec = total April precipitation, COV = coefficient of variance for clutch initiation, JunePrec = total June precipitation, MayRain = total May rainfall, MayTemp = May temperature, MedianCI = Median clutch initiation date, MJtemp = average daily temperature in May and June, Snowfall = total winter snowfall. "NP:" denotes interaction effect between nest placement and other explanatory variables. Wi = model weight.

		Explanatory variables											Model selection criteria		
Model rank	Intercept	NP=Nat	AprilPrec	COV	JunePrec	MayRain	MayTemp	MedianCI	MJtemp	SnowFall	NP:MayRain	NP:MayTemp	AICc	ΔAICc	wi
1	5.85	-0.16				0.04	-0.11	-0.13			-0.12		3569.49	0.00	0.1150
2	5.85	-0.16				0.04	-0.09	-0.12		0.05	-0.12		3570.04	0.55	0.0874
3	5.85	-0.17	0.04			0.05	-0.10	-0.12			-0.12		3570.34	0.85	0.0752
4	5.85	-0.16		-0.05		0.03	-0.08	-0.15			-0.12		3570.36	0.87	0.0745
5	5.85	-0.16				0.04	-0.08	-0.13			-0.11	-0.05	3570.44	0.95	0.0714
6	5.85	-0.16				0.03	-0.06	-0.12		0.05	-0.11	-0.05	3571.01	1.52	0.0538
7	5.85	-0.16	0.04			0.04	-0.07	-0.12			-0.11	-0.05	3571.26	1.77	0.0475
8	5.85	-0.16		-0.05		0.03	-0.05	-0.15			-0.11	-0.05	3571.36	1.87	0.0451
9	5.85	-0.16		-0.09		0.02		-0.14			-0.12		3571.41	1.92	0.0440
10	5.85	-0.16			-0.01	0.04	-0.11	-0.13			-0.12		3571.42	1.93	0.0439
11	5.85	-0.16	0.03	-0.04		0.04	-0.08	-0.14			-0.12		3571.44	1.95	0.0433
12	5.86	-0.16		-0.07		0.03		-0.15	-0.06		-0.12		3571.47	1.98	0.0427

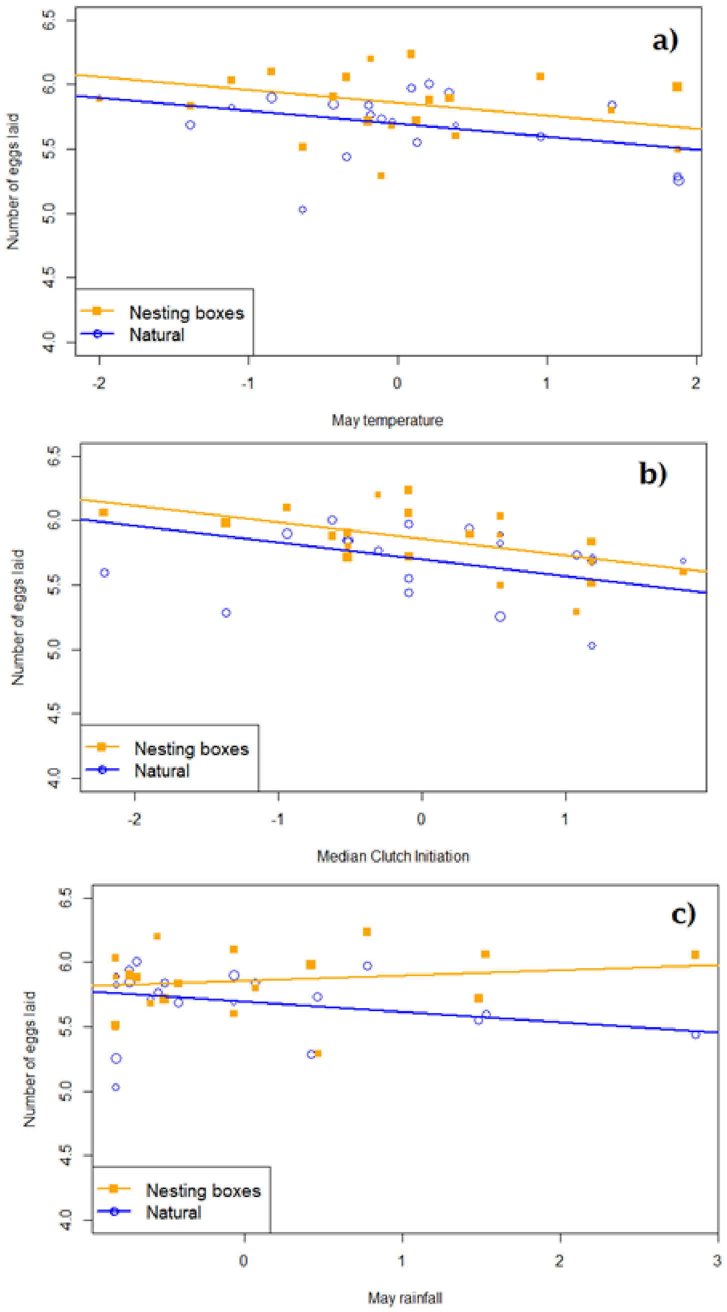


Figure A2: Effect plots of estimates from top ranked model in Appendix A1 Table A7 showing effect on number of eggs per snow bunting brood on Svalbard from 1998 to 2018 of a) May mean temperature, b) Median clutch initiation, c) May rainfall. X-axes are standardized. Sizes of data points are scaled to number of observations.

Table A8: All models with $\Delta AIC_c < 2$ from model selection with hatching probability as response variable. All covariates not represented in these models were excluded. Table shows parameter estimates (β) for intercept and explanatory variables. AIC_c , ΔAIC_c and AIC_c weight (w_i) are shown for all candidate models. NP = Nesting placement natural nest in contrast to nest boxes, AprilTemp = April mean temperature, COV = coefficient of variance for clutch initiation, JunePrec = total June precipitation, MaySnow = total May snowfall, MedianCI = Median clutch initiation date, Snowfall = total winter snowfall. "NP:" denotes interaction effect between nest placement and other explanatory variables. Wi = model weight.

	Explanatory variables												Model selection criteria		
Model rank	Intercept	NP=Nat	AprilTemp	COV	JunePrec	MaySnow	MedianCI	SnowFall	NP:AprilTemp	NP:JunePrec	NP:MaySnow	NP:SnowFall	AICc	ΔAICc	wi
1	2.80	-0.26	0.21		-0.31	0.24		-0.21		0.23		0.19	2035.03	0.00	0.1188
2	2.79	-0.25	0.28		-0.30	0.22	0.11	-0.18		0.23		0.20	2035.59	0.55	0.0901
3	2.78	-0.25	0.20		-0.28	0.20				0.20			2035.66	0.62	0.087
4	2.77	-0.24	0.28		-0.27	0.18	0.12			0.20			2035.91	0.87	0.0768
5	2.78	-0.25	0.20		-0.29	0.23		-0.09		0.20			2036.41	1.37	0.0598
6	2.80	-0.26	0.21	-0.07	-0.27	0.20		-0.22		0.23		0.19	2036.82	1.79	0.0486
7	2.80	-0.26	0.23		-0.31	0.24		-0.21	-0.05	0.23		0.19	2036.92	1.89	0.0462
8	2.80	-0.27	0.21		-0.32	0.26		-0.22		0.24	-0.04	0.20	2036.94	1.90	0.0459

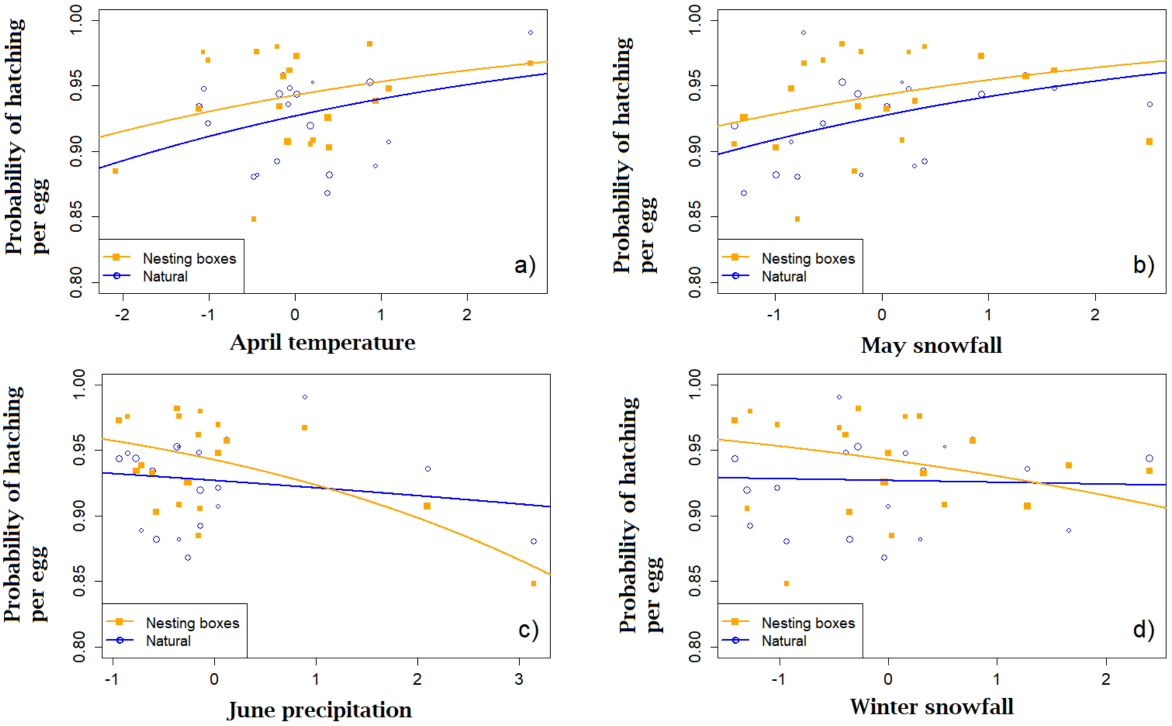


Figure A3: Effect plots of estimates from top model in Appendix A1 Table A8 showing effect on the probability for each snow bunting egg of hatching on Svalbard from 1998 to 2018 of a) April mean temperature, b) May snowfall, c) June precipitation, d) Winter snowfall. X-axes are standardized. Sizes of data points are scaled to number of observations.

Table A9: All models with $\Delta AIC_c < 2$ from model selection with probability of having at least one fledgling as response variable, using both extrinsic and intrinsic covariates. All covariates not represented in these models were excluded. All covariates not represented within models with ΔAIC_c of 2 have been excluded. Table shows parameter estimates (β) for intercept and explanatory variables. AIC_c , ΔAIC_c and AIC_c weight (w_i) are shown for all candidate models. NP = Nesting placement natural nest in contrast to nest boxes, COV = coefficient of variance for clutch initiation, HatchedEggs = yearly average proportion of eggs to hatch per brood, July15prec = total precipitation of the first fifteen days of July, July15temp = average temperature of the first fifteen days of July, JunePrec = total June precipitation, MayRain = total May rainfall, MedianCI = Median clutch initiation date, WinterEnd = timing of end of winter. "NP:" denotes interaction effect between nest placement and other explanatory variables. Wi = model weight.

	Explanatory variables												Model selection criteria		
Model rank	**Intercept**	**NP=Nat**	**COV**	**HatchedEggs**	**July15Prec**	**July15Temp**	**JunePrec**	**MayRain**	**MedianCI**	**WinterEnd**	**NP:JulyPrec**	**NP:JulyTemp**	**AICc**	**ΔAICc**	**wi**
1	3.42	0.71					0.45			0.52			415.07	0.00	0.071
2	3.47	0.75				0.21	0.49			0.63			415.35	0.27	0.062
3	3.44	0.74					0.52		-0.19	0.60			415.67	0.60	0.0527
4	3.52	0.74	0.78	0.61	0.85	0.03				1.39	0.89	-0.70	415.83	0.76	0.0486
5	3.47	0.72					0.60	-0.21	-0.30	0.66			416.20	1.13	0.0404
6	3.41	0.70	0.65	0.48		0.52				1.15			416.21	1.14	0.0402
7	3.48	0.77				0.19	0.55		-0.15	0.68			416.38	1.31	0.0369
8	3.45	0.74		0.14		0.23	0.43			0.63			416.42	1.35	0.0362
9	3.40	0.70		0.11			0.41			0.51			416.52	1.45	0.0344
10	3.46	0.71	0.48	0.36		0.44	0.32			1.05			416.55	1.48	0.0339
11	3.52	0.76	0.72	0.64	0.95	-0.03			-0.19	1.41	0.92	-0.70	416.60	1.53	0.0331
12	3.42	0.73		0.15			0.46		-0.21	0.59			416.70	1.63	0.0315
13	3.44	0.71			0.08		0.44			0.56			416.87	1.79	0.029
14	3.43	0.70					0.46	-0.07		0.52			416.88	1.81	0.0288
15	3.42	0.69	0.73	0.55	0.23	0.46				1.28			416.93	1.85	0.0281
16	3.43	0.72	-0.08				0.46			0.47			416.95	1.88	0.0277
17	3.49	0.78				0.08	0.49			0.63		-0.19	416.96	1.89	0.0277
18	3.43	0.66	0.77	0.57	0.56	0.50				1.34	0.47		416.97	1.89	0.0275
19	3.46	0.77		0.19		0.21	0.48		-0.18	0.69			416.97	1.90	0.0275
20	3.57	0.76	0.63	0.50	0.79	-0.02	0.25			1.28	0.90	-0.71	417.04	1.97	0.0266
21	3.46	0.72		0.25	0.60		0.44		-0.30	0.77	0.48		417.07	2.00	0.0262

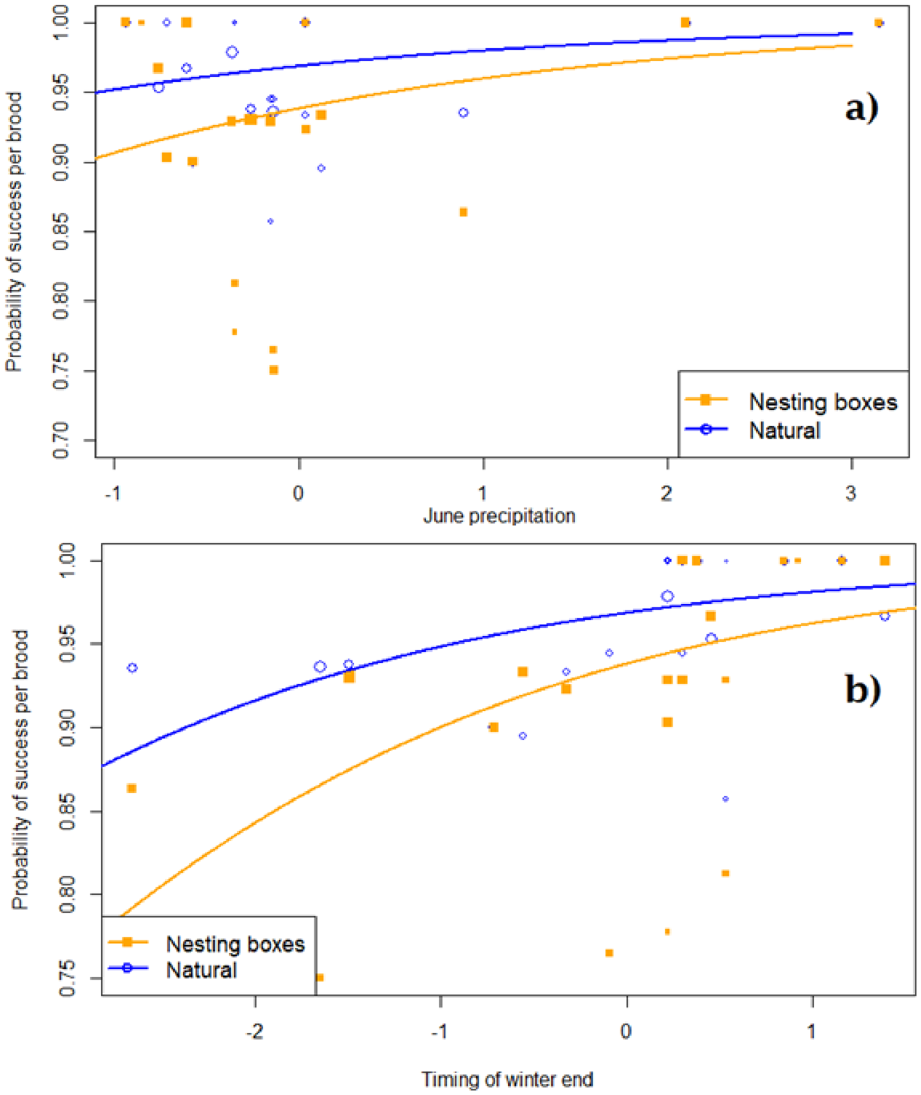


Figure A4: Effect plots of estimates from top ranked model in Appendix A1 Table A9 showing effect on probability of having at least one fledgling per snow bunting brood on Svalbard from 1998 to 2018 of a) June precipitation, b) Winter end day. X-axes are standardized. Sizes of data points are scaled to number of observations.

Table A10: All models with $\Delta AIC_c < 2$ from model selection with probability of having at least one fledgling as response variable, using only extrinsic covariates and including fox. All covariates not represented in these models were excluded. All covariates not represented within models with ΔAIC_c of 2 have been excluded. Table shows parameter estimates (β) for intercept and explanatory variables. AIC_c , ΔAIC_c and AIC_c weight (w_i) are shown for all candidate models. NP = Nesting placement natural nest in contrast to nest boxes, FoxPerc= fox litter percentage, July15prec = total precipitation of the first fifteen days of July, July15temp = average temperature of the first fifteen days of July, JunePrec = total June precipitation, SnowFall = total winter snowfall. "NP:" denotes interaction effect between nest placement and other explanatory variables. Wi = model weight.

	Explanatory variables										Model selection criteria		
Model rank	**Intercept**	**NP**	**FoxPerc**	**July15Prec**	**July15Temp**	**JunePrec**	**SnowFall**	**NP:FoxPerc**	**NP:July15Prec**	**NP:SnowFall**	**AICc**	**ΔAICc**	**wi**
1	1.42	-0.56	0.09	-0.32	0.24		0.36	-0.39	0.23	-0.51	1357.84	0.00	0.1178
2	1.40	-0.54	0.11	-0.18	0.25		0.35	-0.43		-0.51	1358.56	0.71	0.0824
3	1.42	-0.56	0.10	-0.31	0.23	-0.05	0.36	-0.39	0.23	-0.52	1359.42	1.58	0.0535

Table A11: All models with $\Delta AIC_c < 2$ from model selection with probability fledging for chicks that hatch in broods with at least one fledgling. All covariates not represented in these models were excluded. Table shows parameter estimates (β) for intercept and explanatory variables. AIC_c , ΔAIC_c and AIC_c weight (w_i) are shown for all candidate models. NP = Nesting placement natural nest in contrast to nest boxes, COV = coefficient of variance for clutch initiation dates, JJtemp = mean daily temperature for June and the first fifteen days of July, July15prec = total precipitation of the first fifteen days of July, July15temp = average temperature of the first fifteen days of July, JunePrec = total June precipitation, MaySnow = total May snowfall, MedianCI = median clutch initiation day, SnowFall = total winter snowfall. "NP:" denotes interaction effect between nest placement and other explanatory variables. Wi = model weight.

	Explanatory covariates												Model selection criteria		
Model rank	**Intercept**	**NP=Nat**	**COV**	**JJtemp**	**July15Prec**	**July15Temp**	**JunePrec**	**MaySnow**	**MedianCI**	**SnowFall**	**NP:JulyTemp**	**NP:MaySnow**	**AICc**	**ΔAICc**	**wi**
1	1.21					0.18		0.15	0.22				2250.32	0.00	0.066
2	1.21			0.18				0.11	0.26				2250.41	0.09	0.063
3	1.21			0.19				0.09	0.28	0.05			2251.39	1.08	0.0386
4	1.21	0.00				0.18		0.20	0.22			-0.12	2251.54	1.22	0.0358
5	1.21				0.04	0.16		0.15	0.21				2251.66	1.34	0.0338
6	1.21	0.00				0.14		0.20	0.22		0.10	-0.11	2251.71	1.40	0.0329
7	1.20	0.00		0.19				0.16	0.26			-0.12	2251.76	1.44	0.0321
8	1.21			0.19			0.04	0.10	0.26				2251.86	1.55	0.0305
9	1.21		-0.13	0.20			0.12		0.24				2251.99	1.67	0.0286
10	1.21					0.18	0.02	0.14	0.22				2252.09	1.77	0.0273
11	1.21	0.01				0.13		0.14	0.22		0.11		2252.09	1.78	0.0272
12	1.21					0.18		0.14	0.23	0.02			2252.16	1.84	0.0263
13	1.21			0.17	0.03			0.11	0.25				2252.19	1.87	0.0259
14	1.21			0.22					0.32	0.08			2252.21	1.89	0.0257
15	1.21		0.02			0.18		0.16	0.23				2252.25	1.93	0.0251

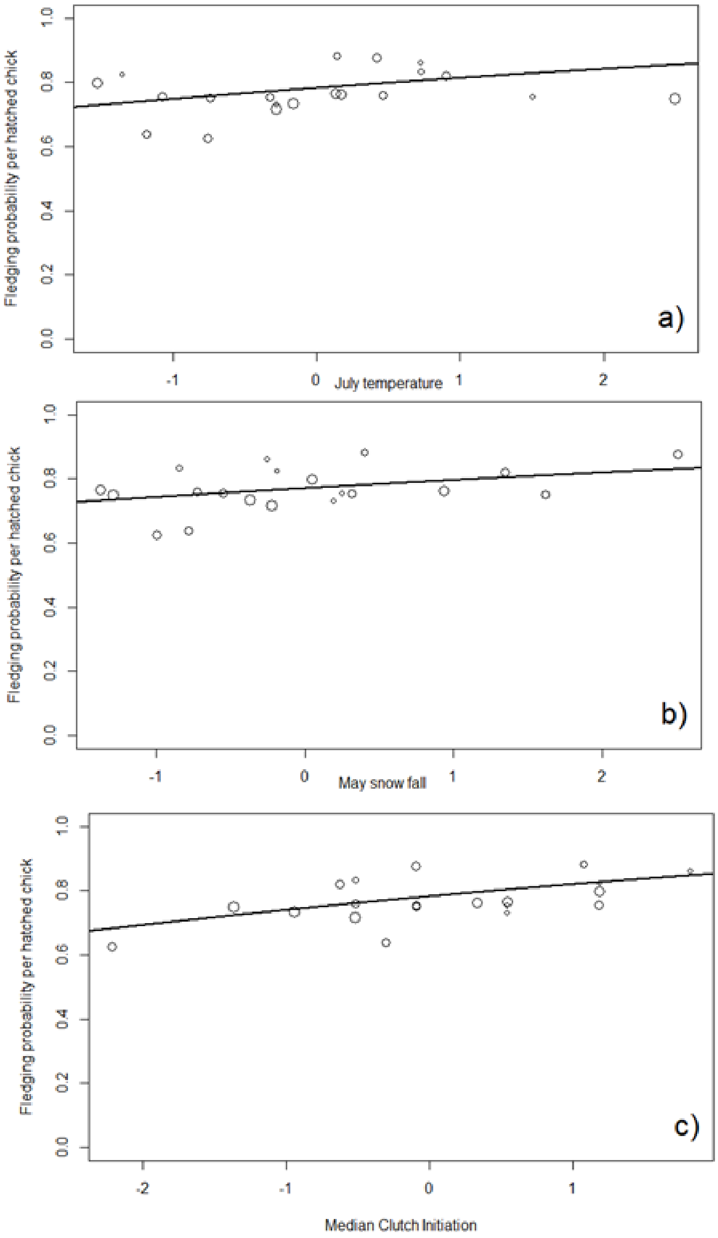


Figure A5: Effect plots of estimates from top ranked model in Appendix A1 Table A12 showing effect on number of snow bunting fledglings from broods with at least one fledgling from time-series data from 1998 to 2018 on Svalbard of a) July mean temperature, b) May snowfall, c) Median clutch initiation day. Sizes of data points are scaled to the number of observations.

Table A12: All models with $\Delta AIC_c < 2$ from model selection with probability of fledging for chicks that hatch in broods with at least one fledgling. Table shows parameter estimates (β) for intercept and explanatory variables. AIC_c , ΔAIC_c and AIC_c weight (w_i) are shown for all candidate models. NP = Nesting placement natural nest in contrast to nest boxes, FoxPerc= fox litter percentage, JJtemp = mean daily temperature for June and the first fifteen days of July, July15temp = average temperature of the first 15 days of July, JunePrec = total June precipitation, JuneTemp = mean June daily temperature, MaySnow = total May snowfall, SnowFall = total winter snowfall, WinterEnd = timing of end of winter. "NP:" denotes interaction effect between nest placement and other explanatory variables. Wi = model weight.

	Explanatory variables												**Model selection criteria**		
Model rank	**Intercept**	**NP**	**FoxPerc**	**JJtemp**	**July15Temp**	**JunePrec**	**JuneTemp**	**MaySnow**	**SnowFall**	**WinterEnd**	**NP:FoxPerc**	**NP:JulyTemp**	**AICc**	**ΔAICc**	**wi**
1	4.07	-0.21			0.12			0.29					2749.76	0.00	0.0562
2	4.08	-0.21	0.08		0.11			0.31					2750.24	0.48	0.0443
3	4.07	-0.21		0.11				0.27					2750.46	0.70	0.0396
4	4.07	-0.21	0.09	0.11				0.29					2750.57	0.81	0.0375
5	4.07	-0.21			0.16			0.29				0.08	2750.63	0.87	0.0363
6	4.07	-0.21	0.10					0.35		-0.11			2750.85	1.09	0.0326
7	4.07	-0.21	0.10				0.10	0.29					2750.86	1.10	0.0325
8	4.07	-0.21			0.12	-0.06		0.30					2750.93	1.17	0.0313
9	4.07	-0.21	0.11			-0.09		0.36		-0.12			2750.97	1.21	0.0307
10	4.07	-0.22						0.29					2750.99	1.23	0.0304
11	4.08	-0.20	0.12		0.11			0.31			0.08		2751.07	1.31	0.0292
12	4.08	-0.21	0.09		0.11	-0.07		0.32					2751.12	1.36	0.0285
13	4.08	-0.21	0.08		0.16			0.31				0.08	2751.14	1.38	0.0282
14	4.07	-0.21					0.09	0.27					2751.19	1.43	0.0276
15	4.07	-0.22						0.32		-0.10			2751.20	1.44	0.0273
16	4.07	-0.21	0.09					0.31					2751.28	1.53	0.0262
17	4.07	-0.20	0.13	0.10				0.29			0.08		2751.45	1.69	0.0241
18	4.07	-0.21	0.09	0.10		-0.06		0.30					2751.55	1.79	0.0229
19	4.07	-0.21	0.11			-0.07	0.10	0.30					2751.58	1.82	0.0226
20	4.07	-0.21		0.10		-0.06		0.28					2751.73	1.97	0.021
21	4.07	-0.21			0.12			0.30	-0.01				2751.75	1.99	0.0208
22	4.08	-0.20	0.14				0.10	0.29			0.08		2751.75	1.99	0.0208

Appendix A2

Methodology for sensitivity analysis

The following formulas were used, and the sensitivity estimates compared to see which would change the final value the most. The values for brood success and fledging success were added to one another before plotting, as they are both values relating to the probability of fledging.

$$E_{Fledgling} = M_{Egg} \cdot M_{Hatch} \cdot M_{BS} \cdot M_{FS}$$

$$S_{Egg} = (M_{Egg} + SD_{Egg})M_{Hatch} \cdot M_{BS} \cdot M_{FS} - E_{Fledgling}$$

$$S_{Hatch} = M_{Egg}(M_{Hatch} + SD_{Hatch})M_{BS} \cdot M_{FS} - E_{Fledgling}$$

$$S_{BS} = M_{Egg} \cdot M_{Hatch}(M_{BS} + SD_{BS})M_{FS} - E_{Fledgling}$$

$$S_{FS} = M_{Egg} \cdot M_{Hatch} \cdot M_{BS}(M_{FS} + SD_{FS}) - E_{Fledgling}$$

Formula A1: Formula for calculating sensitivity to changes in fecundity measures.
E = Expected value, S = Sensitivity estimate, M = Mean, SD = Standard deviation,
egg = number of eggs, Hatch = hatching probability, BS =brood success (probability of having at least one fledgling), FS = fledging success (probability that a chick fledges given that it hatched).

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