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Breeding success in Arctic snow buntings (*Plectrophenax nivalis*) in relation to climatic variations

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Abstract

The ongoing global warming is especially pronounced in the arctic, and it is therefore important to investigate the effects of these changes on arctic ecosystems. In this study the snow bunting (*Plectrophenax nivalis*) breeding in Spitsbergen, Svalbard was used as a model species to investigate how climatic variations affect avian reproduction. Both large-scale climatic parameters and local weather variables were included in an analysis of how these factors affect snow bunting breeding success. It turned out that both big scale and local variables were important. Locale temperature and wind were important for time of breeding. Temperature, precipitation, winter index of North Atlantic Oscillation (NAOw) and winter index of Arctic Oscillation (AOw) were important for number of fledged chicks. Furthermore wind and air pressure were important for nestling growth rate.

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1 Introduction

Global warming is supposed to have large ecological consequences, especially in arctic areas, resulting in higher temperatures and increased level of precipitation. Investigating the ecological changes in arctic regions is therefore important because the results can help us to predict which changes that can be expected in other regions of the world. It can also help us predict further changes in the arctic.

High arctic ecosystems are characterised by low species diversity as compared with temperate regions. The local species have evolved special adaptations to the harsh arctic surroundings and it is reasonable to assume that they are vulnerable to environmental disturbances. This is especially important in the breeding season, which is a critical period, and which is often subject to stochastic variation in abiotic factors like the climatic ones.

The snow bunting (*Plectrophenax nivalis*) is the only passerine species that has adapted to regular breeding in the high arctic region of Svalbard, and it may be vulnerable to changes in abiotic factors. Because of this, the snow bunting is well suited as an indicator species for terrestrial arctic ecosystems (Jarvinen and Rajasarkka, 1992).

1.1 NAO and AO changes and the consequences in high arctic areas

The North Atlantic oscillation (NAO) is used as an index for variation in big scale climatic ”conditions” (Hurrell, 1995). Arctic oscillation (AO) is another climatic index highly correlated with the NAO (Thompson and Wallace, 1998, Dyrset, 2006).

NAO is a climatic phenomenon in the North Atlantic Ocean. It describes co-variability in sea-level pressure between the Iceland low and the Azores high (NSIDC, 2012). NAO is in a positive phase when it is low-pressure conditions at Iceland compared to the pressure at the Azores. NAO is negative when the pressure is high at Iceland compared to the pressure at the Azores. Negative NAO leads to eastern wind and colder temperatures. Through east-west oscillation motions of the Icelandic low pressure and the Azores high pressure, it controls the strength and direction of westerly winds and storm tracks across the North Atlantic. This phenomenon can lead to consequences for the marine and terrestrial ecosystems. During a positive phase, warm lower-latitude air will advect over northern Europe and Scandinavia (Meltofte et al., 2008) and the climate will be relatively warm and humid compared to the mean (Visbeck et al., 2001, Dyrset, 2006). NAO has shown an upward trend during the past several decades (Greatbatch, 2000).

AO is defined as the leading mode of variability from a linear principal component analysis of northern hemisphere sea-level pressure. It emerges as a robust pattern dominating both the intra-seasonal and inter-annual variability in sea-level pressure (NSIDC, 2012). AO is an index of the dominant pattern of non-seasonal sea-level pressure variations north of 20°N latitude, and it is characterized by pressure anomalies of one sign in the arctic with the opposite anomalies centred about 37-45°N. When the AO index is in its high positive phase, the atmospheric pressure over arctic is lower than normal, leading to higher winter temperatures and more precipitation (Thompson et al., 2000, Dyrset, 2006). In the summer this will lead to low atmospheric pressure with more cloudy and humid climate combined with lower temperature (NOAA, 2012). Over most of the past century, the AO index alternated between its positive and negative phases. But for the last 40 years the oscillation has tended to stay in a positive phase, causing a lower than normal arctic air pressure and consequently higher temperatures in much of the United States and northern Eurasia, including the arctic.

In addition to the regional indexes, local climate regimes, which do not have direct coherence with atmospheric circulations, can also influence local temperature. Ocean surface temperature, the cover of sea ice, clouds and wind directions in coherence with topography and other possible predictors may have great climatic impacts. Such factors have also been significant in explaining the variation in temperatures measured on Svalbard since 1912 (Hanssen-Bauer and Forland, 1998).

1.2 Climate change and avian reproduction

Climate change can affect avian reproduction in many ways, especially by influencing the timing of migration and reproduction.

Migratory birds have an annual cycle migrating between summer and winter areas. Some species coordinate their annual cycle and breeding with ecological factors like temperature, rainfall and food supply, while others coordinate their annual cycle by a rigid *Zeitgeber*, like photoperiod. For both these groups earlier spring can be a challenge. Reproduction may be initiated much earlier or later than the time of maximum food requirement of the offspring, and if environmental changes in the winter area do not correspond with those in the breeding area, it is likely that for those species coordinating their cycle with ecological factors there will be a mismatch between food availability and hatching (Both and Visser, 2001). Birds coordinating their annual cycle by photoperiod will also have significant challenges adjusting their cycle so that sufficient food supplies are available for breeding and other energy-requiring activities (Carey, 2009).

In studies done by Visser et al., (2004) and Moller et al., (2010) it was found that there is a difference between long-distance migrants and short distance migrants in how they respond to climatic changes. Long distance migrants, mostly use internal clocks or cues such as photoperiod to time the start of spring migration (Gwinner, 1996, Visser et al., 2004). They will have an extra handicap in adjusting to an optimal breeding date in a changing climate. This is because on the wintering grounds it is often impossible to predict changes in the onset of optimal reproductive conditions on the breeding grounds, and this constrains their adjustment to climate change (Both and Visser, 2001, Coppack and Pulido, 2004, Visser et al., 2004).

It has been found that long-distance migrants coordinating their annual cycle by photoperiod have advanced their migration phenology only a little during the second half of the twentieth century (mean rate of advancement of arrival date by the long-distance migrant is 0.15 days per year). By contrast, short-distance migrants have advanced their spring migration considerably (mean rate of advancement 0.37 days per year) (Saino et al., 2009, Moller et al., 2010). The Svalbard snow bunting is a short-distance migrant (Cramp and Perrins, 1994).

Because it is a common pattern that earlier breeders have larger clutches, (Pietiainen and Kolunen, 1993, Weidinger, 1996, Hipfner et al., 1999, Nooker et al., 2005) one may reckon that earlier breeding could lead to larger clutch sizes. However in a study done by (Stenseth and Mysterud, 2002) it was found that there was no trend towards larger clutches with earlier spring conditions and increasing temperatures. This result may suggest that birds shift their clutch sizes in response to higher temperatures only to some critical level, beyond which no major changes occur. Winkler et al., (2002) also found the lowest variances in laying dates during the most recent and warmest years, suggesting some genetic constraint preventing birds from laying eggs earlier (Stenseth and Mysterud, 2002).

No plants or animals live in isolation from other species. Interactions between species are therefore important. An example with the autumnal moth (*Epirrita autumnata*) shows that the warmer climate is positive for population growth, but that it also leads to an increase in parasitoid abundances, which is likely to play an important role in the regulation of moth populations. This example highlights that climate does not only affect a population in one single way, and that both direct and indirect effects of climate are important for population growth (Stenseth and Mysterud, 2002).

Given the diversity of invertebrate responses to climate change, (Winkler et al., 2002) the avian insectivores least affected by climate change will be those with the greatest diversity of suitable prey during the egg-laying and chick-rearing periods. These will be the species whose requirements will best match the new conditions (Stenseth and Mysterud, 2002).

A problem can arise for those birds with endogenously strongly controlled life cycles because they probably respond too slowly to changes, particularly in species that have long generation times (Møller et al., 2010).

1.3 The snow bunting as a model species

The snow bunting has a circumpolar distribution on the northern hemisphere "above" 60 degrees and is found in the high mountain areas of Norway, and also along the coast of northern Norway and in Svalbard. It is the only passerine species breeding regularly as far north as in the high arctic environment of Svalbard and is well adapted to this harsh environment (Hoset et al., 2009). In the present study I will therefore use the snow bunting as a model species when investigating the relations between climatic factors and breeding success. The snow bunting is also a suitable species to use because it feeds its nestlings with insects. Insect abundance is probably highly sensitive to changes in climate parameters.

2 Aim of the study

In this study, the already collected data on reproduction in snow buntings in Adventdalen each year in the period 1998 – 2010 was analysed together with additional data collected in 2011. The purpose of the study is to analyse variation in snow bunting breeding success in relation to annual climatic parameters. It is thus a follow-up study of (Dyrset, 2006) who studied the topic for the period 1998 – 2005. Here I analysed how regional and local climatic factors affected reproductive success in snow buntings across the 13 years.

As earlier mentioned the atmospheric circulation can partly explain the observed climatic variation in arctic regions, but local conditions like temperature, precipitation, cloud cover and air pressure will also be taken into account. I will also focus on the question if it is the big scale climatic indices or the local conditions that has the strongest influence on the reproductive success of the snow bunting.

The following hypothesis were tested:

Reproductive success among snow buntings in Svalbard is affected by climatic factors.

I will test this hypothesis by relating several local and regional factors such as local temperature, precipitation, wind, air pressure, cloud cover, NAO and AO to several factors of reproductive success such as date of egg-laying, clutch size, chick weight and fledging success. In particular, I will look at the relative relationship of local versus regional climate and reproductive success.

3 Methods

3.1 Study area

The fieldwork was conducted in Adventdalen, outside Longyearbyen in Svalbard (78 degree 13 ` N, 15 degree 38 ` E) during the breeding season from 6 June to 6 July 2011. The study area comprised the near surroundings of the cableway earlier used for coal transportation from the coalmines in Adventdalen to Longyearbyen, a distance of about 8 km. In this area many of the snow buntings are breeding in nest boxes, which are placed on the trestles supporting the cableway (Bangjord et al., 1999, Hoset et al., 2009). In addition to nest boxes the snow bunting also breeds in natural nest sites like crevices, cavities in screes and under boulders and also in suitable sites in different man-made constructions like buildings etc.

3.2 Study species

The snow bunting is well adapted to the harsh environment on Svalbard (Hoset et al., 2009). Most of the males arrive during April, and the females arrive 2-4 weeks later (Norderhaug, 1989, Dyrset, 2006). Start of breeding and also the length of the breeding season varies but yearly studies on Svalbard since 1997 show that most of the breeding population start egg-laying before the middle of June. The most common clutch size is 6 eggs, the incubation period is around 13 days and the nestling period lasts for another 13 days (Norderhaug, 1989, Dyrset, 2006). Both parents are feeding the offspring in this period with a diet mostly consisting of insects and spiders. When the weather conditions are favourable, a snow bunting pair can have two clutches in one breeding season (Espmark & Moksnes, upubl., Dyrset, 2006). The breeding season last for 3 to 7 weeks on Svalbard, depending on the weather conditions. The start of the breeding season is initiated by increasing temperature, which seems to have a significant influence on the reproductive cycle (Hoset et al., 2004). The temperature influences on the parents feeding rate. When it is cold, the young use more energy for thermoregulation, so it will be less energy available for growth. The parents compensates for this by increasing the feeding rate in cold weather. (Hoset et al., 2004) found a positive correlation between temperature in the breeding season and reproductive success. A probable reason for this is that temperature affects the food abundance consisting of insects and spiders (Hoset et al., 2004).

Due to the low species diversity so far north, there is not much predation on the snow bunting, except from some nest-predation by the arctic fox (*Alopex lagopus*). The nest predation rate is around 12 % as a yearly mean. Nest predation is not expected to have a significant effect in the nest boxes since they are placed out of reach for arctic foxes.

3.3 Data on breeding success

In total I have data from 13 years, and there were between 31 and 84 nest each year, which I could use in the analysis.

The time of nest building and date for first egg laid and also the length of the breeding season were recorded by direct field observations. Date for first egg laid is calculated from 1 May. If nests were found during the incubation stage, the eggs were floated to determine incubation start and thereby the start of egg laying (Hays and Lecroy, 1971). For most nests this was also controlled by backdating from the observed hatching date. Furthermore, the clutch size, hatching date, number of eggs hatched and number of nestlings fledged was registered. Breeding success was defined as the number of successful fledglings which is the number of healthy chicks heavier than 15 g on day 9 counted from, and including, the hatching day, since smaller chicks were likely to die before they fledge (A. Moksnes & Y. Espmark, unpubl. data). The chicks were weighed and ringed on day 9, and further inspections of the nest were avoided, because of the risk of provoking the young to leave the nest prematurely (Hussell, 1985, Hoset et al., 2009). The growth rate were calculated by taking all the chicks heavier than 15 g or more on day 9 and then take the total weight and divide on number of chicks and on number of days.

As already mentioned the data on snow bunting breeding success in the study area have been collected each year in the period 1998-2010 except for 2004. Together with data from 2011 this constitute the material used for analysing the breeding success of the snow bunting in relation to both local and big scale climatic parameters between years.

In the dataset all the known second breeding events of one female in the same year were removed. Some of the females were marked, so in these cases this was not a problem. Clear outliers in the distribution of date for first egg laid were also expected to be second breeders and were removed from the dataset. For individually marked females documented to breed in more than one year only the first breeding was included in the dataset to avoid pseudo replications.

In the analysis with date of first egg laid and number of eggs as response variables, the whole dataset were used, but for the analysis with number of fledged chicks and growth rate all the interrupt nesting including predation by arctic fox or birds, natural disaster (like flooding, snow etc.), accidents, chats and unfertilized eggs were removed. The exceptions were those with unknown reason. These I included in the dataset.

3.4 Data on climate

Data on locale temperature, precipitation, wind, air pressure and cloud cover was obtained from the meteorological station at Longyearbyen airport (Lippestad, 2012). Hoset et al. (2004) have shown that data from this station are representative also for our study area in Adventdalen. All these data are available on Internet, which was also the case for the big scale climate indices, NAO and AO, which I got from "Climate Prediction Center of the National weather service" (Team, 2012). Winter NAO (NAOw) and AO (AOw) were calculated as the monthly mean for December, January, February and March. Summer NAO (NAOs) and AO (AOs) were calculated as the monthly mean for April, May, June and July. Consequently NAOw and AOw refer to the time when the snow bunting is in its winter area before migration and NAOs and AOs refer to the migration to the breeding area and the breeding period. Spring values for local weather for the date of first egg laid and number off eggs were calculated as the monthly mean of April and Mai. This time period is the time when the snow buntings arrive at the breeding site and the egg laying and incubation starts. Summer values for locale weather for number of chicks fledged and growth rate were calculated as the monthly mean of June and July. This time period includes incubation, hatching and chick rearing.

3.5 Statistical analysis

All statistical analysis was carried out in R version 2.14.1. Because so many explanatory variables were looked at in this thesis, I first used univariate tests (Appendix A) to get an overview over the variables and to only choose those variables having a clear association with the response variables for further analysis. All the predictor variables were tested against all the response variables. Based on the significance of the explanatory variable they were chosen for further analysis in a multivariate generalized estimating equations model (GEEs). All the explanatory variables having a p-value smaller than 0.1 were included in a multivariate analysis for each of the response variables. Nest height and date of first egg laid was included to account for the ecological effect of these variables.

GEEs were used to control for non-independence of data collected within each year. GEEs were used rather than standard mixed-model approaches because GEEs estimate an overall slope across groups. In this study, I wanted to test for a relationship across years and not within. GEE-models were used even though the distribution of the data was not perfect for the number of fledged chicks. The reason for this was to get the results with the different response variables to be comparable to each other. To check if it would have been any different results using a different model, a mixed model with c-bind function was also used. The results were identical. For all analysis the significance level was set to $p<0.05$.

Because of the strong correlation between NAO and AO (Appendix B, figure I and II), two models for each response variable were made. One including NAO and one including AO.

4 Results

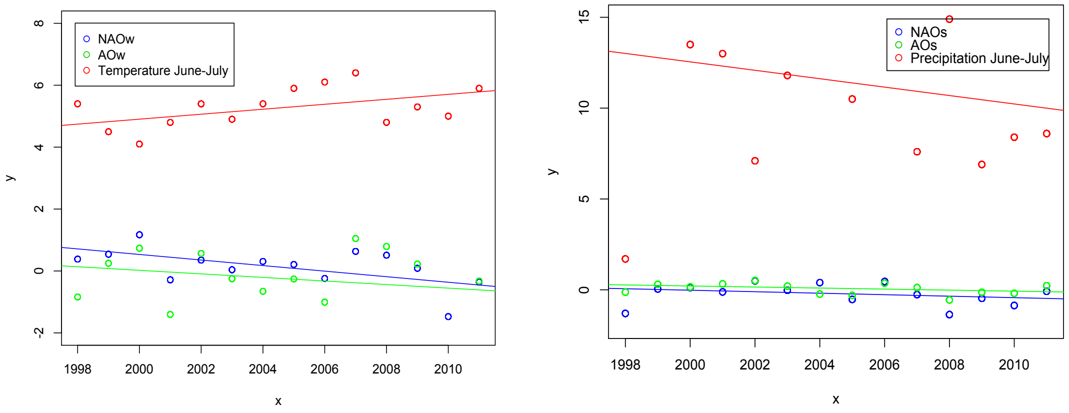
4.1 Main variables

4.1.1 NAOw, AOw and temperature in June and July during the study period.

NAOw (Estimate = -0.089768, SE = 0.004438, t-value = -20.23, $p < 0.001$), and AOw (Estimate = -0.057517, SE = 0.008383, t-value = -6.861, $p < 0.001$), showed a significant decline during the study period, while temperature showed a significant increase during the study period (Estimate = 8.01e-02, SE = 4.83e-03, t-value = 16.6, $P < 0.001$) (Figure 1A).

4.1.2 NAOs, AOs and summer precipitation during the study period.

NAOs (Estimate = -0.041011, SE = 0.004434, t-value = -9.249, $p < 0.001$), AOs (Estimate = -0.028602, SE = 0.002316, t-value = -12.35, $p < 0.001$) and precipitation in June - July (Estimate = -0.232, SE = 0.043, t-value = -5.39 $p = 0.001$) showed a significant decrease during the study period (Figure 1B).



A **B**

Figure 1. A: Variation of NAOw, AOw and summer temperature, B: Variation in NAOs, AOs and summer precipitation during the study period.

4.2 Date of first egg laid

The temperature in April-May correlated significantly negatively to date of first egg laid. Wind correlated significantly positively to the date of first egg laid and nest height showed a significant negative correlation with date of first egg laid. NAOw and AOw were significantly positively correlated with date of first egg laid in the univariate tests (Appendix A). The results were not significant in the multivariate tests, but there were still a positive association (Table 1 and 2).

Table 1. Multivariate analysis with date of first egg laid as response variable. NAOw, temperature, wind in April – May and nest height are the explanatory variables. SE = standard error, W = Wald statistics. N = 830

Response and predictor variables	Estimate	SE	W	P-value
Date of first egg laid				
NAOw	1.653	0.994	2.76	0.096
Temperature April -May	-2.030	0.375	29.31	<0.001
Wind April – May	4.432	1.312	11.42	<0.001
Nest height	-0.946	0.125	57.20	<0.001

Table 2. Multivariate analysis with first egg laid as response variable. AOw, temperature, wind in April – May and nest height are the explanatory variables. N = 830.

Response and predictor variables	Estimate	SE	W	P-value
Date of first egg laid				
AOw	1.090	0.644	2.87	0.091
Temperature April -May	-2.121	0.410	26.72	<0.001
Wind April – May	4.581	1.656	7.65	0.006
Nest height	-0.938	0.107	76.82	<0.001

4.3 Number of eggs

Date of first egg laid correlated significantly negatively with the number of eggs. Precipitation and nest height did not correlate significantly with number of eggs (Table 3).

Table 3. Multivariate analysis with number of eggs as response variable. Precipitation in April - May, nest height and date of first egg laid were the explanatory variables. N= 756.

Response and predictor variables	Estimate	SE	W	P-value
Number of eggs				
Precipitation April - May	0.02602	0.01974	1.74	0. 19
Nest height	0.01194	0.02034	0.34	0.56
Date of first egg laid	-0.03065	0.00533	33.06	8.9e-09 ***

4.4 Number of chicks fledged

NAOw, AOw, temperature in June – July and date of first egg laid correlated significantly positively to number of chicks fledged. Precipitation showed a negative correlation to number of chicks fledged, which were significant in the model with NAOw (Table 4), and nearly significant in the model with AOw (Table 5). Nest height was associated with number of fledged chicks, but it was not significant.

Table 4. Multivariate analysis with number of chicks fledged as response variable. NAOw, precipitation, temperature and air pressure in June - July were the explanatory variables. N = 623.

Response and predictor variables	Estimate	SE	W	P-value
Number of chicks fledged				
NAOw	0.43540	0.06954	39.20	<0.001
Precipitation June – July	-0.03526	0.01502	5.51	0.019
Temperature June - July	0.26842	0.05885	20.80	<0.001
Air pressure – June – July	-0.00688	0.02609	0.07	0.79
Nest height	-0.06951	0.03675	3.58	0.059
Date of first egg laid	0.01760	0.00802	4.82	0.028

Table 5. Multivariate analysis with number of chicks fledged as response variable. AOw, precipitation, temperature and air pressure in June – July were the explanatory variables. N= 623.

Response and predictor variables	Estimate	SE	W	P-value
Number of chicks fledged				
AOw	0.26282	0.04697	31.31	<0.001
Precipitation June – July	-0.03217	0.01945	2.74	0.098
Temperature June - July	0.20246	0.09212	4.83	0.028
Air pressure – June – July	-0.00728	0.03376	0.05	0.83
Nest height	-0.06933	0.03606	3.70	0.055
Date of first egg laid	0.02089	0.00779	7.19	0.007

4.5 Growth rate

Nest height correlated significantly negatively and date of first egg laid correlated significantly positively with growth rate. In the model with NAOs wind and air pressure correlated significantly positively to growth rate, but did not show any significant result in the model with AOs. NAOs, AOs and cloud cover did not show any significant relation to growth rate (Table 6 and 7).

Table 6. Multivariate analysis with growth rate as response variable. NAOs, precipitation and air pressure in June - July were the explanatory variables. N = 460.

Response and predictor variables	Estimate	SE	W	P-value
Growth rate				
NAOs	0.01180	0.07607	0.02	0.88
Wind June – July	0.09335	0.03630	6.61	0.010
Air pressure – June – July	0.01796	0.00885	4.12	0.042
Cloud cover – June – July	0.03768	0.07115	0.28	0.59
Nest height	-0.02416	0.00525	21.15	<0.001
Date of first egg laid	0.01010	0.00362	7.80	0.005

Table 7. Multivariate analysis with growth rate as response variable. AOs, precipitation, air pressure in June – July, and nest height were the explanatory variables. N = 460. For symbols, see Table 1.

Response and predictor variables	Estimate	SE	W	P-value
Growth rate				
AOs	-0.06935	0.19399	0.13	0.72
Wind June – July	0.05624	0.08552	0.43	0.51
Air pressure – June – July	0.01188	0.01133	1.10	0.29
Cloud cover – June – July	0.02217	0.07193	0.09	0.76
Nest height	-0.02395	0.00529	20.50	<0.001
Date of first egg laid	0.01028	0.00364	7.96	0.005

5 Discussion

The temperature showed an upward trend while precipitation, NAO and AO showed a decrease during my study period.

According to theory on how NAO and AO influence the weather in the arctic region around Svalbard a decrease in temperature and precipitation should be expected when there is a decrease in NAO and AO (Visbeck et al., 2001, Dyrset, 2006). During my study period there was however an increase in temperature in the summer although there was a decrease in NAOs and AOs. A possible reason for this could be that a decline in NAOw and AOw lead to less snow due to drier weather in the winters, and that less snow leads to warmer spring and summer (Meltofte et al., 2008). Summer precipitation had a decrease during my study period, which was expected according to the decline in NAO and AO.

5.1 Date of first egg laid

NAOw and AOw showed a positive association with date of first egg laid, but these results were not significant in the multivariate model although they were so in the univariate tests. High NAOw at the northern European latitudes is normally associated with increased level of precipitation, higher temperature and thereby advanced spring events (Møller et al., 2010) and then also date of first egg laid. The reason why NAOw and AOw did not have any significant correlation with date of first egg laid in the multivariate model could be explained by the strong negative correlation between NAOw/AOw and spring temperature (Appendix C, figure III and IV).

There was a significant negative correlation between temperature and date of first egg laid, i.e. the egg laying started earlier in warm springs. On the other hand, wind was significantly positively correlated with date of first egg laid. Temperature is an important factor for food availability, and food availability is often the important determinant for laying date (McCleery and Perrins, 1998, Crick et al., 1997). A number of experimental food supplementation studies have also confirmed that improved parental condition advances laying (Martin, 1987, Meijer et al., 1990, Laaksonen et al., 2006). During the study period NAOw decreased, temperature and wind increased, and date of first egg laid advanced.

Nest height has a negative correlation with date of first egg laid, meaning that nests are situated higher above the ground early in the breeding season. This is probably because snow buntings prefer the nest boxes, which are often a meter or two above the ground and occupy them in the start of the breeding season. This reference could be due to unsuitable conditions with much snow and ice on the ground. Another explanation could be that early males with high social rank prefer the boxes because their nest is then protected against predation from the arctic fox. The trestles are also good song posts for the territorial males.

5.2 Number of eggs

Date of laying was the only factor significantly associated with number of eggs in the multivariate test, with more eggs in the earlier clutches. This is a pattern common in most bird species (Hoset et al., 2009). One explanation for the larger clutches in the start of the breeding season is that the birds in best condition and highest social rank arrive first to the breeding ground and lay large and early clutches (Pietiainen and Kolunen, 1993, Weidinger, 1996, Hipfner et al., 1999, Nooker et al., 2005). The young from these clutches would probably be large and well suited for surviving the migration (Hoset et al., 2009) and can then also contribute more to the future breeding population than the chicks hatched later (Verboven and Visser, 1998). The early breeders would also have the possibility to raise a second clutch in the same breeding season.

5.3 Number of fledged chicks

For number of chicks fledged, which are the main measure on reproductive success in this study, NAOw, AOw and temperature showed a positive correlation, while precipitation was negatively correlated with number of fledged chicks. In my study this is the most interesting result, showing that the snow bunting reproductive success is influenced not only be local weather conditions, but also by global climatic changes.

The positive correlation between number of fledged chicks and date of first egg is in accordance with previous results in the population (Hoset et al., 2009). This is not however the most common pattern among birds (Nooker et al., 2005). The reason for this result is probably that the conditions for rising chicks are better later in the season because of increasing temperature leading to an increase in insect activity at Svalbard (Hoset et al., 2009).

The almost significant negative correlation between number of chicks fledged and nest height could be explained by better microclimate conditions near the ground with higher temperature and less wind (Deeming, 2002) because of a better shelter against harsh weather than nests higher above the ground. The better conditions near the ground leads to less energy required for thermoregulation and allowing more energy to be used for growth and survival.

The positive correlation between temperature and number of chicks fledged has also been shown in earlier studies (Hoset et al., 2004). This positive correlation can have many reasons. High temperatures in the incubation period can limit energy costs that are linked to thermoregulation by the parents. There is also often more food available when temperature is high. When the food availability is good, the parents can also use more time on incubation (Deeming, 2002). It is shown that when the female use less time in the nest, there is a lower breeding success (Lyon and Montgomerie, 1985, Dyrset, 2006).

Not unexpected precipitation showed a significant negative correlation with number of chicks fledged. The main reason for this is probably that precipitation can lead to lower temperatures and also make it more difficult for the parents to find insects that are less active during rain (Avery and Krebs, 1984, Hoset et al., 2009).

The positive correlation between NAOw and AOw and number of chicks fledged is somehow harder to explain. Since NAOw and AOw is calculated as the mean monthly index value from December to March and the chicks hatch in early summer the correlation between number of fledged chicks and NAOw and AOw must be caused by an indirect effect. Often there can be a delay in ecological responses to climate. This might be the explanation here. As already mentioned an increase in NAO leads to advanced spring events (Møller et al., 2010). This might lead to more insects earlier in the spring, and since food often is the limiting factor for growth of the chicks early in the breeding season (Hoset et al., 2009), this could be the reason why NAO is positively correlated with number of chicks fledged.

Alternatively, adult condition could be directly affected by NAOw in their wintering areas, which could also affect their breeding success the following summer. NAO and AO have the unique feature of embracing spatial variation of climate on a much larger scale than locale weather measurements (Stenseth et al., 2003, Forchhammer and Post, 2004, Stenseth and Mysterud, 2005, Meltofte et al., 2008), and since migratory birds are moving over larger areas NAO and AO could also influence the birds in other parts of their migratory cycle.

Since NAO and AO are large-scale climatic indices they can also explain the effect of co-occurrence of several dependent weather variables (Stenseth et al., 2003, Descamps et al., 2010). Most measures of locale weather factors fail to capture this complexity. Because of this NAO and AO will be a far better measure of how organisms integrate weather changes in their responses than local weather variables.

5.4 Growth rate

The negative correlation between nest height and growth rate can be explained by the same reason as earlier mentioned for number of fledged chicks with less energy required near the ground.

Date of first egg laid had a significant positive effect on chick growth meaning that the chicks are bigger in the later clutches. As discussed above under number of chicks fledged, warmer weather and more food available later in the breeding season is most likely the explanation for this correlation.

5.5 General discussion

The winter index of NAO have mainly been associated with global climate change (Hurrell, 1995) and it is therefore interesting that NAOw was correlated with number of fledged chicks. From this study it might seems like global climate change is positive for the birds when higher NAO values and temperatures which is associated with global warming leads to more fledged chicks. Higher NAO values and then warmer and more humid climate can though also be negative to the birds while this may facilitate for instance survival, fecundity, and development of parasites (Møller et al., 2010) which can be harmful to the birds.

6 Conclusion

Temperature had a significant positive effect on reproductive success in the way that higher temperature led to advanced date of first egg laid and a higher number of chicks fledged. Precipitation had a significant negative effect on reproductive success by influencing the number of young fledged. The regional climate index, AO and NAO, showed strong positive effects in addition to locale climatic variables on number of chicks fledged, suggesting that there are independent effects of local and regional factors. The results also show that it is laid more eggs in early clutches, but that there are more fledged chicks and larger chicks in later clutches. Further studies are necessary to get a better understanding of the evolutionary trade-off between early and late breeding in arctic snow buntings.

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Appendix A

Univariate tests:

First egg laid:

Table I. Univariate analysis with date of first egg laid as response variable. SE = Standard Error, W = Wald statistic, N = 766.

Response and predictor variables	Estimate	SE	W	P-value
Date of first egg laid				
NAOw	3.81	1.02	14.1	<0.001
NAOs	-2.338	2.029	1.328	0.33
AOw	1.89	1.07	3.09	0.099
AOs	-3.61	3.43	1.11	0.19
Temperature April –May	-1.285	0.353	13.3	<0.001
Precipitation April – May	-0.400	0.534	0.56	0.21
Wind April – May	-3.137	0.984	10.2	0.003
Air pressure – April – May	0.0279	0.4629	0	0.93
Cloud cover – April – May	-4.07	2.25	3.26	0.18
Nest height	-0.839	0.142	35.2	<0.001

Number of eggs laid:

Table II. Univariate analysis with number of eggs as response variable. See table I for symbols. N= 756

Response and predictor variables	Estimate	SE	W	P-value
Number of eggs				
NAOw	0.0347	0.0580	0.36	0.55
NAOs	0.0558	0.0648	0.74	0.39
AOw	0.0477	0.0542	0.77	0.38
AOs	0.0804	0.1758	0.21	0.65
Temperature April – May	0.0341	0.0232	2.16	0.14
Precipitation April – May	0.0400	0.0237	2.86	0.091
Wind April – May	0.0227	0.0475	0.23	0.63
Air pressure – April – May	-0.0118	0.0127	0.86	0.36
Cloud cover– April – May	0.111	0.100	1.22	0.27
Nest height	0.0429	0.0191	5.06	0.025
Egg1	-0.03252	0.00621	27.4	<0.001

Number of chicks fledged:

Table III. Univariate analysis with number of chicks fledged as response variable. See table I for symbols. N = 623

Response and predictor variables	Estimate	SE	W	P-value
Number of chicks fledged				
NAOw	0.42211	0.09318	20.52	<0.001
NAOs	0.214	0.187	1.31	0.25
AOw	0.2867	0.0552	27	<0.001
AOs	0.220	0.357	0.38	0.54
Temperature June – July	0.256	0.184	1.94	0.16
Precipitation June – July	-0.0394	0.0197	4.02	0.045
Wind June – July	0.201	0.127	2.53	0.11
Air pressure – June – July	0.0560	0.0265	4.46	0.035
Cloud cover – June – July	-0.314	0.339	0.86	0.35
Nest height	-0.0698	0.0392	3.17	0.075
Egg1	0.0282	0.0134	4.45	0.035

Chicks weights:

Table IV. Univariate analysis with growth rate as response variable. See table I for symbols. N = 460

Response and predictor variables	Estimate	SE	W	P-value
Growth rate				
NAOw	-0.00784	0.06905	0.01	0.91
NAOs	-0.0998	0.0593	2.83	0.094
AOw	-0.0417	0.0353	1.4	0.24
AOs	-0.2226	0.1000	4.95	0.026
Temperature June – July	-0.0128	0.0364	0.12	0.73
Precipitation June – July	-0.00105	0.00871	0.01	0.9
Wind June – July	0.1427	0.0299	22.8	<0.001
Air pressure – June – July	0.02253	0.00779	8.37	0.004
Cloud cover– June – July	-0.1478	0.0724	4.16	0.041
Nest height	-0.03197	0.00489	42.7	<0.001
First egg laid	0.01312	0.00293	20	<0.001

Appendix B

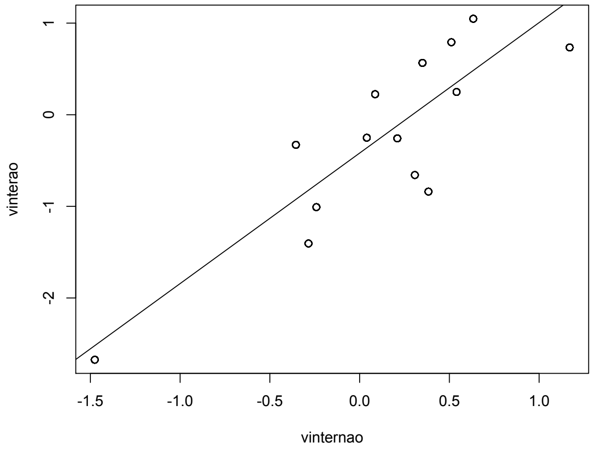

Figure III. Correlation between NAOw and AOw. Estimate = 1.42452, SE = 0.02455, t-value = 58.03, p < 2e-16

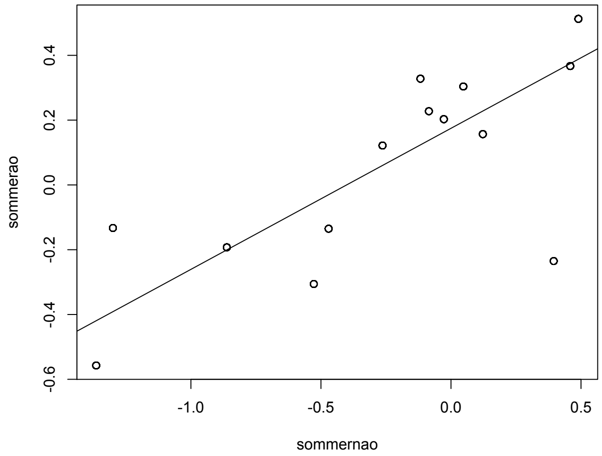

Figure IV. Correlation between NAOs and AOs. Estimate = 0.435361, SE = 0.010129, t-value = 42.98, p < 2e-16

Appendix C

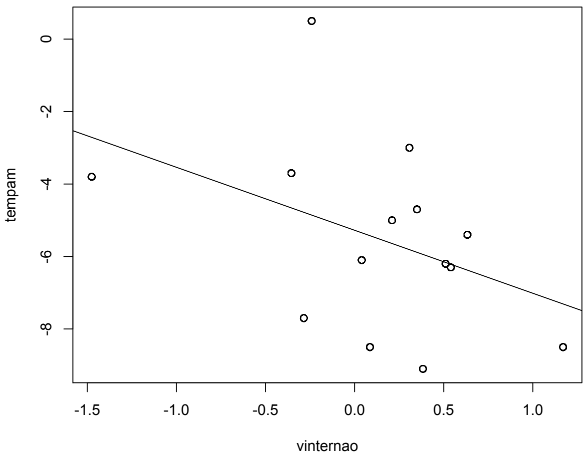

Figure III. NAOw show a strong negative correlation with spring temperature during the study period, with Estimate = -1.7379 SE = 0.1128 t-value = -15.4 P-value < 2e-16.

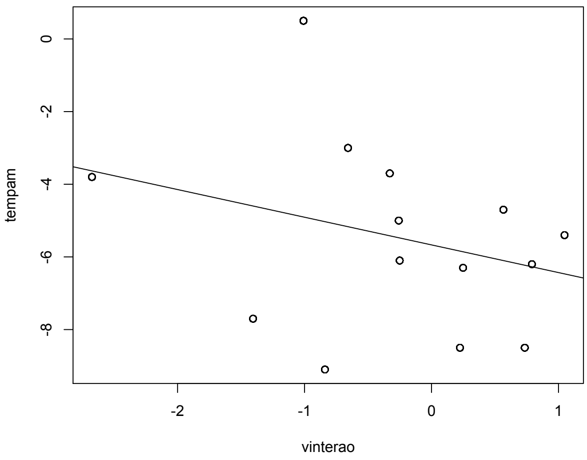

Figure IV. AOw show a strong negative correlation with spring temperature during the study period, with Estimate = -1.7618 SE = 0.0742 t-value = -10.3 P-value < 2e-16 respectively.