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# Causes and Consequences of Breeding Synchrony in the Snow Bunting (*Plectrophenax nivalis*)

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## **Abstract**

Climate warming is happening rapidly in the Arctic and migratory birds are among the species expected to be affected by the predicted shifts in spring phenology. Using time-series data (1998 - 2014) from a population of snow bunting (*Plectrophenax nivalis*) nesting in High Arctic Svalbard, I investigated climatic effects on interannual variation in breeding synchrony and its fitness consequences. Breeding synchrony was here defined as the temporal synchrony in egg-laying on the population-level, which was estimated using a Synchrony Index (SI). Multi-model comparisons of linear regression models were used in three sections of analyses; i) onset of breeding in relation to climate, ii) breeding synchrony in relation to onset of breeding and climate, and iii) reproductive success in relation to breeding synchrony and climate. Timing of onset of breeding was negatively related to spring temperature. Furthermore, SI was positively related to spring precipitation and onset of breeding. Reproductive success, measured as mean number of fledglings, was positively related to breeding synchrony and mean summer temperature. This long-term study gives insight to how the breeding phenology of a passerine migrant is affected by local climatic conditions in the High Arctic. The present study indicates that the dynamics of the study population may be altered with expected climatic warming.

## Abstract in Norwegian

Klimaendringer skjer raskt i Arktis og migrerende fuglearter antas å bli sterkt påvirket av de påfølgende miljøendringene som følger av høyere temperaturer og tidligere vår. Ved bruk av langtidsserier (1998 - 2014) fra en populasjon snøspurv (*Plectrophenax nivalis*) som hekker i høy-arktisk, undersøkte jeg klimaeffekter på mellomårsvariasjon i hekkesynkronitet, og hvordan dette påvirket reprodutiv suksess på populasjonsnivå. Hekkesynkronitet ble i dette studiet definert som temporal synkronitet i egglegging, og ble estimert ved å bruke en indeks, Synkrony Index (SI). Rangering av lineære modeller ble brukt i analysene, som ble utført i tre seksjoner; i) hekkestart påvirket av klimavariabler, ii) hekkesynkronitet påvirket av hekkestart og klimavariabler og iii) reprodutiv suksess påvirket av hekkesynkronitet og klimavariabler. Hekkestart var negativt påvirket av vårtemperatur. Videre var hekkesynkronitet positivt påvirket av vårnedbør og tidspunkt for hekkestart. Reprodutiv suksess, målt som årlig gjennomsnittlig antall utfløyne unger, var positivt påvirket av hekkesynkronitet og sommertemperatur. Med dette gir studiet innsikt i hvordan hekkefenologien til en migrerende spurvefugl ble påvirket av lokale klimaforhold i høy-arktisk. Studiet indikerer at populasjonens dynamikk kan endres med forventet stigning i vår og sommertemperaturer.

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## Introduction

Recent climate change has had impacts on a wide range of ecosystems across the globe (Parmesan, 2006), and clear evidence of biological responses related to the rapidly warming climate exists for a range of species (Walther et al., 2002, Parmesan and Yohe, 2003, Parmesan, 2006). These responses include changes in phenology, such as advancement of vegetation growth in spring (Linderholm, 2006, Delbart et al., 2008). Phenology can broadly be defined as seasonal activities in plants and animals (Walther et al., 2002). In several bird populations, warming-induced phenological shifts towards earlier breeding have been reported in temperate, boreal and subarctic areas (Crick and Sparks, 1999, Walther et al., 2002, Both et al., 2004, Liebezeit et al., 2014). Well-known examples are populations of great tits (*Parus major*) (Charmantier et al., 2008) and pied flycatchers (*Ficedula hypoleuca*) in the Netherlands and in the United Kingdom where onset of breeding has advanced linearly with an increase in spring temperatures (Visser et al., 1998, Visser and Both, 2005, Both et al., 2010). In the Netherlands, mistimed reproduction relative to the peak in food resources has been observed in great tits, pied flycatchers and blue tits (*Cyanistes caeruleus*) (Visser et al., 1998, Both et al., 2009).

In the Arctic, the phenological changes associated with climate warming are expected to exceed those in temperate areas, because both timing of snowmelt and temperature increase are critical factors regulating vegetation growth and arthropod emergence (Høye et al., 2007). Additionally, due to the *Arctic amplification* (Overpeck et al., 1997), climate warming in the Arctic is happening more than twice as rapidly relative to temperate areas (Overpeck et al., 1997, IPCC, 2014). Moreover, the already harsh and unpredictable Arctic weather conditions (Walsh et al., 2005, Weatherhead et al., 2010) are likely to be more variable with future changes (Høye et al., 2007, Walsh et al., 2011, Post et al., 2001). Therefore, birds migrating to Arctic breeding grounds have to be highly flexible when timing their reproduction (Wingfield and Hunt, 2002, Martin and Wiebe, 2004, Walker et al., 2015). They must be able to adjust breeding in case of harsh weather and rely on available food and nest resources for reproductive success (Martin and Wiebe, 2004) Long distance migrants are in general expected to be more at risk in face of earlier springs, because they must rely on endogenous cues to initiate migration to the breeding ground (Both and Visser, 2001).

Timing of reproduction is an important life history trait in the avian life cycle (Perrins, 1970). According to life history theory, each individual will time reproduction to the optimal conditions for nestling growth and survival (Lack, 1968). The optimal timing of breeding in seasonal environments is when the nestling feeding period match peaks in resource availability and favourable weather conditions (Perrins, 1996, Dunn, 2004). How individuals in a population time their reproduction relative to each other can give information of the population level response to ecological factors (Findlay and Cooke, 1982, Post and Forchhammer, 2004). If many females respond similarly to the same conditions, and thus time reproduction in temporal proximity with each other, the breeding season will be temporally synchronous (Westneat, 1992).

The synchronized timing of breeding by females in a population is here called *breeding synchrony* (Kempnaers, 1993). Others have called it *nesting synchrony* (Westneat, 1992) or *nesting density* (Dickey et al., 2008). Among other researchers, Lack (1968) proposed a selective advantage to individuals that were timing their reproduction in synchrony with individuals of the same population, due to an increased ability to provide resources to clutches or nestlings (Lack, 1968, Perrins, 1970). In addition to the timing to favourable environmental conditions at the nesting ground (Ringsby et al., 2002, Smith et al., 2010), other advantages of breeding synchrony can be reduced predation pressure (Darling, 1938, Ims, 1990, Weatherhead and Sommerer, 2001) and increased efficiency in foraging (Emlen and Demong, 1975). Breeding synchrony may also be related to the rate of extra-pair paternity, as high synchrony among breeding females could lead to lower extra-pair paternity in the population (Stutchbury and Morton, 1995).

Understanding the abiotic factors acting on important life history events, such as reproduction, is important and necessary to be able to predict how populations may respond to future changes in the environment (Post et al., 2009). Relative to temperate regions, there is a shortage of long-term studies examining breeding phenology of birds in the High Arctic in relation to climate (but see Hoset et al., 2004, Dickey et al., 2008, Fossøy et al., 2014, Liebezeit et al., 2014, Jensen et al., 2014). Moreover, few studies have investigated whether and how population level breeding synchrony is affected by local and regional climate, and its potential impacts on the reproductive output.

In this study, I examined climatic effects and consequences of interannual variation in timing



of breeding and breeding synchrony, using time-series data from a population of snow bunting (*Plectrophenax nivalis*) nesting in the High Arctic. These data showed a large variation in egg-laying dates and breeding synchrony, which accordingly offered a unique possibility to study the interactions between breeding phenology and reproductive success in relation to climatic conditions. Being a small passerine species migrating to the High Arctic, the snow bunting have to cope with unpredictable weather conditions before and during the breeding season, which can affect the reproductive success negatively (Walker et al., 2015). For instance, low temperatures may affect breeding phenology directly through increased thermoregulatory costs (Visser et al., 2009), and indirectly through reduced resource availability, as insect activity often is temperature dependent (Taylor, 1963). In the study population, Hoset et al. (2004) found that snow bunting parental feeding rate and, in turn, reproductive success was affected by local temperature fluctuations during the breeding season. Local temperature was also found to correlate with the proportion of extra-pair offspring (Hoset et al., 2014). Additionally, Fossøy et al. (2014) found that reproductive success was reduced in years with early egg-laying, and positively correlated with the Arctic Oscillation (AO) winter index, which is associated with colder and more cloudy summer conditions (Thompson and Wallace, 2000).

Focusing on the climatic causes and fitness consequences of breeding synchrony, I addressed three interconnected research questions; First, I investigated how a series of climatic factors affected timing of onset of breeding. Based on Fossøy et al. (2014) and literature outlined above, I predicted that elevated spring temperatures gave earlier onset of breeding. Second, I investigated whether the variation in breeding synchrony was linked to timing of onset of breeding and climatic conditions. If the observed variation in breeding synchrony in the study population is the result of females optimizing their timing of breeding to fluctuating environmental conditions, it may be that unfavourable climatic conditions in spring will delay the breeding phenology, leading to a narrower, more synchronized breeding season in the population. For instance, delayed snowmelt was found to postpone egg-laying in the High Arctic pink footed geese (*Anser brachyrhynchus*) (Madsen et al., 2007, Jensen et al., 2014) and white crowned sparrow (*Zonotrichia leucophrys*), in Morton (1978) as described in a review by Carey (2009). Based on this, I expected that delayed timing of breeding had a synchronizing effect on the breeding season. Third, I investigated the consequences of breeding synchrony and climatic variables for reproductive success. Dickey et al. (2008) found a positive relationship between high spring temperatures and high spring precipitation

and reproductive success in a long-term study of the greater snow geese (*Chen caerulescens atlantica*) in the Arctic Canada. High mean temperatures and low snowcover in spring were associated with increased breeding synchrony. Based on this study and life history theory outlined above, I predicted that years with synchronous breeding had higher reproductive success. Based on Hoset et al. (2004) and Fossøy et al. (2014), I also predicted that the reproductive success was affected by local and regional climatic conditions

## Methods

### *Study system*

The fieldwork was conducted in the Adventdalen valley in Spitsbergen, Svalbard (78° 13'N, 15° 38'E, Fig. 1). This area is nesting ground for a population of snow buntings (*Plectrophenax nivalis*), which has been monitored annually since 1998. Adventdalen is located in the central part of the High Arctic island of Spitsbergen, south of Isfjorden in the ice-free area of Nordenskiöld Land peninsula, and is close to the permanent settlement of Longyearbyen. The climate is cold with harsh weather conditions despite low annual precipitation. In the period of 1998 - 2014, the mean annual air temperature was -3.6 °C and the annual precipitation 200 mm, recorded at the Norwegian Meteorological Institute's station at Svalbard Airport ([www.eKlima.met.no](http://www.eKlima.met.no)) close to the study site. The valley is characterized by High Arctic tundra vegetation with different plant communities of moss tundra, snow beds, ice wedges and landslides, dominated by bryophytes, lichens, grasses and other pioneer vegetation like *Bistorta vivipara* and *Saxifraga oppositifolia* (Elvebakk, 1994, Elvebakk, 2005), making suitable microclimate for arthropods, of which over 500 species are described in Svalbard (Ávila-Jiménez et al., 2010).

Except from the Svalbard rock ptarmigan (*Lagopus muta hyperborea*), the snow bunting is the only exclusively terrestrial bird species breeding regularly on Svalbard, and the only passerine nesting in these latitudes. The wintering ground and the migration route for the focal population is not known. Males arrive to Adventdalen from the end of March to the middle of April, often preceding the females (Cramp et al., 1994). The snow bunting is territorial and nest in natural cavities, crevices, and piles of boulders, but also in suitable sites associated with human settlement. The population in Adventdalen has for instance taken advantage of several nest boxes in trestles from an old cableway (Hoset et al., 2009). The modal clutch size is 6 eggs, with approximately 13 days of incubation and a 13 days nestling period (Cramp et al., 1994). The snow bunting is altricial, i.e. has naked nestlings, which are fed with insects and arachnids, while the adult diet mostly consist of seeds (A. Moksnes and Y. Espmark, unpublished data). The main predator is the Arctic fox, (*Alopex lagopus*), which predate on average approximately 12 % of the monitored nests annually (A. Moksnes, unpublished data). There are few avian predators on Svalbard; the Arctic skua, (*Stercorarius parasiticus*), and the glaucous gull, (*Larus hyperboreus*), which have rarely been observed predate snow bunting nests (A.Moksnes, pers.comm., July 2014). Parasitic mites (e.g.

*Isospora plectrophenaxia*) are found in nests in Adventdalen during the breeding season, but impact on snow bunting nestling growth is not documented (Dolnik and Loonen, 2007, Gwiazdowicz et al., 2012).

### *Data collection*

Reproductive and biometric data were sampled annually from the middle of May to late July from 1998 - 2014, with a sample size ranging from 40 - 109 nests per year. Nests were located during egg-laying and locations were recorded with GPS, a unique number and a site description. Information of clutch initiation date (CID), defined as the laying date of the first egg per nest, and number of eggs were first recorded. Subsequently, all nests were monitored regularly until hatching date, defined as the date when at least one egg was hatched. Number of hatched eggs and total clutch size, which was defined as the maximum number of eggs present during the incubation period, were also recorded. In case of nest failure, the cause (i.e. abandoned or predated) was noted. At nests discovered after egg-laying, but before hatching date, the CID was estimated using the egg floatation method and controlling for total clutch size (Ackerman and Eagles-Smith, 2010). For nests discovered after hatching, the hatching date was estimated by considering nestling development, and the CID was estimated by backdating with the use of hatching date, incubation length and total clutch size. The time between consecutive egg-laying per female was assumed to be one day, and the incubation length was assumed to be 13 days (Cramp et al., 1994). All nests were further revisited once during the nestling period, 8 - 10 days after hatching date for biometric measurements (weight and tarsus). For each revisited nest, number of fledglings, total and individual nestling weight were recorded. Fledglings were defined as nestlings > 15.0 g. on day nine after hatching, based on higher pre-fledgling mortality in smaller nestlings (A. Moksnes and Y. Espmark, unpublished data). All fledglings were also ringed. Further nests visits were avoided to prevent the young from leaving the nest prematurely (Hoset et al., 2014).

### *Timing of breeding, CID<sub>10</sub>*

Previous studies have used the mean of the first registered egg in each nest to calculate an annual mean estimate of CID (e.g Fossøy et al. 2014) used to measure the population level onset of egg-laying, or breeding. However, to adjust for years with extreme values and get a more specific measure of the timing of onset of egg-laying in the population, the 10<sup>th</sup>

percentile of the recorded clutch initiation dates were used. This is further called the CID<sub>10</sub> and corresponds to the date where 10 % of the earliest recorded nests have at least one egg. In figures and analyses, CID<sub>10</sub>'s and CID's are given as a day number where day 1 is 1<sup>st</sup> of May.

### *Synchrony Index, SI*

The synchrony index (SI) (1) developed by Kempnaers (1993) is an individual based empirical measure of the temporal breeding synchrony in a bird population. The SI range from 0 - 100 %, where 0 % represents no overlapping days in egg-laying (i.e. no breeding synchrony) and 100 % represents full synchrony in egg-laying within a season (i.e. all females lay first egg on the same day) (Kempnaers, 1993), calculated as:

$$SI = \frac{1}{F} \sum_{p=1}^F \left[ \frac{\sum_{i=1}^{tp} f_{i,p}}{tp (F-1)} \right] \quad (1)$$

Where  $F$  is total number OF fertile females, which here was the annual number of recorded nests.  $f_{i,p}$  is the number of fertile females minus the focal female  $p$  on day number  $i$ , and  $tp$  is the fertile period for female  $p$ . The number of fertile days per female,  $tp$ , was here defined as the number of days from five days before clutch initiation to the penultimate egg, as used in Kempnaers (1993). The fertile period  $tp$  was calculated for each nesting female  $p$ , using CID and clutch size. Annual estimates of SI were calculated using 17 years (1998-2014) of data. To avoid pseudoreplication, individually marked females were only included once in the calculations of SI.

### *Climate data*

To investigate the impact of local and regional climate on the onset of egg-laying and breeding synchrony, a set of climate variables were applied. Regional Arctic Oscillation indexes were acquired from the National Weather Service Climate Prediction Centre, USA ([www.cpc.ncep.noaa.gov](http://www.cpc.ncep.noaa.gov)). Here, the mean Arctic Oscillation index from December-March (AO<sub>w</sub>) was applied as a measure of regional winter climate, as used in Fossøy et al. (2014). Local climate data from 1998 - 2014 were obtained from Longyearbyen Airport meteorological station, via the Norwegian Meteorological Institute ([www.eKlima.met.no](http://www.eKlima.met.no)). Annual mean temperatures (°C) in April-May and June-July were respectively used as

estimates of spring and summer temperatures. Yearly total precipitation (mm) in April-May and June-July were used as measures of precipitation-levels in spring and summer. Total precipitation (mm) from 1 November preceding year to 30 April was used as yearly measure of winter precipitation. Because precipitation events were not always classified in precipitation type, precipitation was not split in snow and rain (Fig. 3).

### ***Statistical analyses***

In total, clutch initiation dates were recorded from 1295 nests over 17 years. To restrict the analyses to the first broods, rare cases of known second broods within the same season were excluded. Additionally, pseudo-replication was avoided by excluding females registered more than once through the 17 years. In the analyses, multi-model comparisons based on an information theoretic approach using the Akaike Information Criteria corrected for small sample sizes ( $AIC_c$ ), were used (Burnham and Anderson, 2002). This implied comparisons of a set of *a priori* models fitted with maximum likelihood technique (ML) (Burnham and Anderson, 2002). The model with  $\Delta AIC_c$  value equal to nil have the highest support in the data. I also applied the  $AIC_c$  weight, which indicates the probability that the focal model is the best, given the candidate models and the data. In general, models with low  $AIC_c$  values and high  $AIC_c$  weight are considered as the models with the best fit to the data (Burnham and Anderson, 2002). The general  $\Delta AIC_c < 2$ -rule suggest that models with  $\Delta AIC_c$ , less than 2 have substantial support from the data, given the candidate models and the data (Burnham & Anderson 2002). For the multi-model comparisons, I applied the MuMIn package in R (Barton and Barton, 2014), which permits application of criteria for variables not accepted in the same models (Barton and Barton, 2014). Highly correlated variables were not accepted in the same model to avoid multi-collinearity and unstable parameter estimates. This involved correlations between variables listed in Appendix Table A1. Additionally, avoidance of over-parameterization was ensured by reducing the number of explanatory parameters to a maximum of four variables, following the principle of Parsimony, aiming for the simplest models without redundant parameters (Burnham & Anderson 2002). Following these criteria, model selection was performed based on all possible subsets from a global model including main effects only.

The statistical analyses were organized in three sections. First, I analysed whether the local and regional climatic conditions could explain the variation in the timing of onset of

breeding. I made models with the following explanatory variables;  $AO_w$ , total precipitation in April-May, mean in temperature April-May and winter precipitation. Second, I analysed to what extent the variation in breeding synchrony (SI) could be explained by local and regional climatic conditions (also including temperature and total precipitation for June-July), with  $CID_{10}$  included as a covariate in the global model. In the third section of analyses, I investigated to what extent annual reproductive success was explained by the included climate variables, as well as population level  $CID_{10}$  and breeding synchrony (SI). In this last section, predated broods were excluded to remove effects of predation on nestling survival. Based on the above criteria, the number of candidate models included in the three sections were 14, 87 and 85, respectively. Multiple linear regression models were used in all statistical analyses, using the software R version 3.1.2 (R Core Team, 2014).

## Results

### *Climate variation*

Climate variables, CID<sub>10</sub> and SI showed large interannual variation from 1998 - 2014 (see Fig. 2 and 3). The CID<sub>10</sub> ranged from 23rd of May to 8<sup>th</sup> of June in 2005 and 2010, respectively. The least synchronous breeding season was in 1999, with a SI of 22 %, and the most synchronous breeding season was in 2005, with SI estimated to 55 % (Fig. 2 and 3). The years with the lowest and the highest mean number of nestlings were 1999 and 2007 with 2.4 nestlings (SE = 0.31) and 4.0 nestlings (SE = 0.24), respectively. Additionally, there was considerable variation in mean temperatures recorded in April-May, ranging from -9.1 °C in 1998 to 0.5 °C in 2006 (Fig. 3). Much less temperature variation was recorded in June-July during the study period, ranging from 4.1 °C in 2000 to 6.5 °C in 2007 (Fig. 3). The precipitation levels recorded were generally low, in April-May ranging from 6.6 mm in 1998 to 28.1 mm in 2013, and in June-July; 3 mm in 1998 to 55 mm in 2004 (Fig. 3). Although not included in models and figures, winter precipitation ranged from 132 mm in 2010 to 53 mm in 2005 and AO<sub>w</sub> ranged from 0.8 in 2008 to -2.7 in 2010.

### *Onset of breeding*

Onset of breeding, estimated as the CID<sub>10</sub>, was best explained by a model with mean temperature April-May as the only explanatory variable (Table 1, Model 1:  $R^2 = 0.33$ ,  $P < 0.05$ ), with a negative effect (Fig. 4). The model was accompanied by an AIC<sub>c</sub> weight of 0.41, indicating a high support for the highest ranked model, given the candidate models and the data. Mean temperature in April-May was also represented in models 2 - 4, however none of which had  $\Delta AIC_c < 2$  and considerably lower AIC<sub>c</sub> weight. Thus, this result suggests that a 1 °C increase in mean spring temperature advanced the onset of egg-laying by 1.2 days (Table 1).

### *Breeding synchrony*

The annual variation in breeding synchrony, measured with SI, was best explained by a model including precipitation in April-May and CID<sub>10</sub> (Table 2, Model 1:  $R^2 = 0.55$ , Precipitation (AM):  $P < 0.01$ , CID<sub>10</sub>:  $P = 0.052$ ), both with positive effects (Fig. 5a and b). CID<sub>10</sub> was included in model 1 - 2 with  $\Delta AIC_c < 2$ . Precipitation in April-May was included



in model 1 - 4, whereas model 1 - 3 received considerable support from the data, indicated by  $\Delta AIC_c < 2$  and  $AIC_c$  weight  $> 0.2$ . The effect of precipitation was present even when accounting for the  $CID_{10}$  (Table 2). Thus, this suggests that a 1 mm increase in total precipitation in April-May increases SI by 1 %, and that one day later onset of breeding ( $CID_{10}$ ) increases SI by 0.88 % (Table 2). Additionally, in model 2, mean temperature in April-May had a positive effect (Table 2, Model 2:  $R^2 = 0.53$ , Temperature (AM):  $P = 0.144$ ) on SI, suggesting that a 1 °C increase in mean spring temperatures increased SI by 1.65 %.

### *Reproductive success*

Reproductive success was best explained by a model with positive effects of both SI and mean temperature in June-July as explanatory variables (Table 3, Model 1:  $R^2 = 0.47$ , SI:  $P = 0.069$ , Temperature JJ:  $P = 0.064$ ), both with positive effects (Fig. 6a and b). Although the effect of mean temperature in June-July was marginally non-significant, this term was also included in models 2 - 4, further indicating a positive effect on reproductive success. An increase of 1 °C in mean temperature increased mean number of fledglings by 0.32 individuals. SI, which was included in models 1,3 and 4, also had a positive effect on reproductive success (Table 3). This result suggests that an increase of 1 % in breeding synchrony, estimated by SI, increased mean number of fledglings by 0.02 individuals. Models 1 - 5 had  $\Delta AIC_c$  values below 2 (Table 3), and could be considered equally good, although models 2 - 5 had considerably lower  $AIC_c$  weight. The model containing only the intercept had lower support from the data ( $\Delta AIC_c > 3$ ), which means that the top ranked models explained a significant part of the variance in reproductive success. Model 3 and 5 included a positive effect of  $AO_w$  (Table 3).

## Discussion

The present correlational study suggested that the observed variation in onset of breeding among years, breeding synchrony and reproductive success in a population of snow buntings in Svalbard, were all influenced by local climate parameters. The results demonstrated that elevated local mean temperatures in April and May advanced the timing of breeding (Table 1, Fig. 4). Further, the results indicated that breeding synchrony was higher in years with late onset of breeding ( $CID_{10}$ ) and high levels of spring precipitation (Table 2, Fig. 5a and b). Additionally, the results indicated that synchronous breeding, including high mean temperatures in June and July, had positive effects on reproductive success in the population, which was measured as annual mean number of fledglings (Table 3, Fig. 6a and b). Although there was no clear directional trend in the local mean temperatures during the study period (Fig. 3), this study indicates that the expected warmer spring and summer seasons can potentially have effects on the reproductive success and the future population dynamics of the population of snow buntings nesting in the High Arctic.

In the study population,  $CID_{10}$  was as predicted earlier in years with higher mean temperatures in April and May (Table 2, Fig. 4). Advanced laying dates associated with elevated spring temperatures was also found in the focal snow bunting population by Fossøy et al. (2014) and has been reported from several studies of other bird populations in temperate (Visser and Lessells, 2001, Dunn, 2004), boreal (Vatka et al., 2011) and Arctic areas (Grabowski et al., 2013, Liebezeit et al., 2014). Accordingly, this may suggest that elevated spring temperature is an important cue for timing of breeding in the study population. For instance, warm spring conditions in the Arctic may induce earlier snowmelt, which can advance the availability of nest sites (Jensen et al., 2014, Madsen et al., 2007), and mediate phenological activities at lower trophic levels, such as vegetation growth (Elmendorf et al., 2012) and insect emergence (Høye and Forchhammer, 2008). In general, insectivorous birds are expected to be more sensitive to temperature fluctuations, because their prey abundance is often weather dependent (Høye and Forchhammer, 2008). In this study however, there were no data available on snowmelt and snow bunting prey abundance from the study site, so it was not possible to document the importance of these factors.

It has also been suggested that higher spring temperatures may affect timing of breeding in birds directly through reduced thermoregulatory costs for the parents, as was documented

experimentally in great tits in The Netherlands (Visser et al., 2009). Snow bunting parents are under high stress before energy demanding clutch production (Visser and Lessells, 2001, Walker et al., 2015), which makes thermoregulation important in the period before breeding. Additionally, similar studies on different bird species have found long-term phenological shifts towards earlier breeding corresponding to elevated spring temperatures (Liebezeit et al., 2014). In this study however, inspection of Fig. 3 indicated that there was no clear trend of advancement in CID<sub>10</sub>, neither the mean temperature in April-May over the 17 years of study.

The finding that breeding synchrony (SI) was higher in years with higher levels of total precipitation in April and May was not expected and can be interpreted in different ways (Table 2). Based on the below-zero mean temperatures in April and May (except year 2006, Fig. 3), I assumed that the precipitation in April and May mainly falls as snow. This indicated that snowy conditions in spring made females breed more synchronously. In the High Arctic, the total levels of precipitation are in general low compared to other latitudes (AMAP, 2011). For instance, at the study site, the annual total precipitation in April and May combined, which were used in the models, ranged from 7 - 28 mm from 1998 - 2014 (Fig. 3). Thus, these low precipitation levels indicated that breeding synchrony could be influenced by other environmental factors associated with precipitation, which made snow buntings collectively delay processes related to egg-laying, resulting in a narrower, more synchronized breeding season. This is supported by the synchronizing effect of a late CID<sub>10</sub>, which was influenced by colder springs (Table 1 and 2, Fig. 4 and 5a). For instance, if the increased spring precipitation resulted in a higher snow cover, delayed snowmelt could influence both food and nest resources. Høye and Forchhammer (2008) found that timing of snowmelt was the most important predictor of arthropod emergence in a study of nine taxa of arthropods in the High Arctic Zackenberg, Greenland. Hence, a plausible explanation for the observed result may be that spring precipitation delayed the phenology of the insect production, which further delayed the onset of breeding as an adaptive plastic response in the snow bunting population, resulting in higher breeding synchrony.

The finding of a slightly positive effect of SI on reproductive success (Table 3, Fig. 6a) may suggest that there was an advantage of breeding in synchrony with other females in the snow bunting population. This finding is consistent with the theories that individuals breeding in synchrony experience higher reproductive success (e.g. Lack, 1968, Perrins, 1970). An

explanation could be reduced predation pressure, hence decreased individual probability of being predated (Darling, 1938, Ims, 1990). However, effects of predation were beyond the scope of this study, so predated nests were as mentioned excluded from the analyses, and could therefore not explain this result. Alternatively, the positive fitness effect of synchronous breeding may be caused by plasticity in timing of breeding to match peaks in insect production. Accordingly, at the population level, this would result in a positive relationship between synchronization of egg-laying and reproductive success (e.g. Møller et al., 2007, Charmantier et al., 2008). From my study it is however not clear if the snow bunting females time their breeding in order to be synchronous or if they are breeding in synchrony because of collective responses to favourable environmental conditions. In this study, I have found that years with high degree of breeding synchrony also had higher population level reproductive success. However, if individuals breeding in synchrony have higher reproductive success, the breeding synchrony may be adaptive (Westneat, 1992). It may also be that the population breeds in synchrony simply because there is a short window of opportunity for rearing young (Findlay and Cooke, 1982).

The finding of a positive effect of mean temperature in June-July on reproductive success supports the suggestion that temperature may be an important cue for egg laying in the focal population. This is also in consistence with Hoset (2004), who found that higher ambient temperatures increased the parental feeding rate, which resulted in higher reproductive success in the focal population. Other studies in the Arctic have also documented a positive effect of high summer temperatures on reproductive output e.g. in a population of greater snow geese (*Chen caerulescens atlantica*) nesting in the Canadian Arctic (Dickey et al., 2008). Milder conditions during breeding season may result in reduced thermoregulatory costs for the altricial nestlings and their feeding parents (Visser et al., 2009), and higher summer temperatures may lead to higher abundance and activity for a range of invertebrates, as reported from the High Arctic Greenland (Høye and Forchhammer, 2008).

Interestingly, these results indicated that years with warmer springs had earlier onset of breeding and less synchronous breeding, which was associated with reduced reproductive success in the population. This is in agreement with Hoset et al. (2009), who found that early breeders in the focal population had lower reproductive success, also supported by the results of Fossøy et al. (2014), where lowest mean number and weight in the earliest hatched snow bunting nestlings.

The findings of this study indicate that future environmental changes may alter fecundity rates during the breeding season for the snow bunting population. With expected warmer springs in the High Arctic (Høye et al., 2007), snow buntings responding to higher temperatures may result in a future shift towards earlier breeding phenology in the population. For instance, advancement in clutch initiation dates have been observed in other High Arctic nesting birds, for instance; dunlin (*Caladris alpina*), ruddy turnstone (*Arenaria interpres*) and sanderling (*Caladris alba*), with a change of 0.40 – 1.0 days per year from 1995 - 2005 (Meltofte et al., 2007). A potential consequence of altered laying dates relative to the insect phenology is trophic mismatch, which has been documented to reduce reproductive success in populations of great tit in Hoge Veluwe, The Netherlands (Visser et al., 1998, Reed et al., 2013). Snow buntings, as well as their prey on lower trophic levels may be exposed to environmental changes of which they are not adapted (Høye and Forchhammer, 2008). It is therefore of high importance to understand responses to environmental changes on different trophic levels in this High Arctic ecosystem.

### **Conclusion**

As one of few studies investigating climatic effects and fitness consequences of population-level breeding synchrony in the High Arctic, this long term study found that local mean temperature before and during the nesting season was important for timing of breeding and reproductive success, suggesting that temperature at the nesting ground may be an important cue for timing of breeding. The findings also suggested that years with late onset of breeding and high spring precipitation increased breeding synchrony, which in turn had a slight positive effect on the population-level reproductive success. However, there are many questions unanswered. Future prospects of this study should therefore investigate the interaction between insect and snow bunting phenology.

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## Tables

**Table 1:** Top ranked models by AIC<sub>c</sub> model selection for analysis of the timing of onset of breeding with the CID<sub>10</sub> as response variable, which is explained in the Methods section. Table shows parameter estimates ( $\beta$ ), standard error ( $\pm$ SE) for intercept and explanatory variables. AIC<sub>c</sub> values,  $\Delta$ AIC<sub>c</sub> values and AIC<sub>c</sub> weight ( $w_i$ ) are reported for all candidate models. AO<sub>w</sub> = Arctic Oscillation index winter, Precipitation winter = total precipitation in November-April, precipitation (AM) = total precipitation in April-May, Temperature (AM) = mean temperature in April-May. Criteria for composition of candidate models are specified in the Methods section. The number of candidate models ranked in this section was 14.

Rank	Intercept	Explanatory variables				Model selection criteria		
		AO <sub>w</sub>	Precipitation winter	Precipitation (AM)	Temperature (AM)	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	$w_i$
1	25.41 $\pm$ 2.71				-1.22 $\pm$ 0.45	102.7	0.00	0.414
2	26.45 $\pm$ 2.91	1.07 $\pm$ 1.10			-1.08 $\pm$ 0.47	105.0	2.34	0.128
3	22.66 $\pm$ 4.02			0.15 $\pm$ 0.16	-1.30 $\pm$ 0.46	105.1	2.47	0.120
4	29.11 $\pm$ 5.37		-0.04 $\pm$ 0.04		-1.13 $\pm$ 0.47	105.4	2.72	0.106
<b>Null model</b>	32.18 $\pm$ 32.54					106.4	3.75	0.063

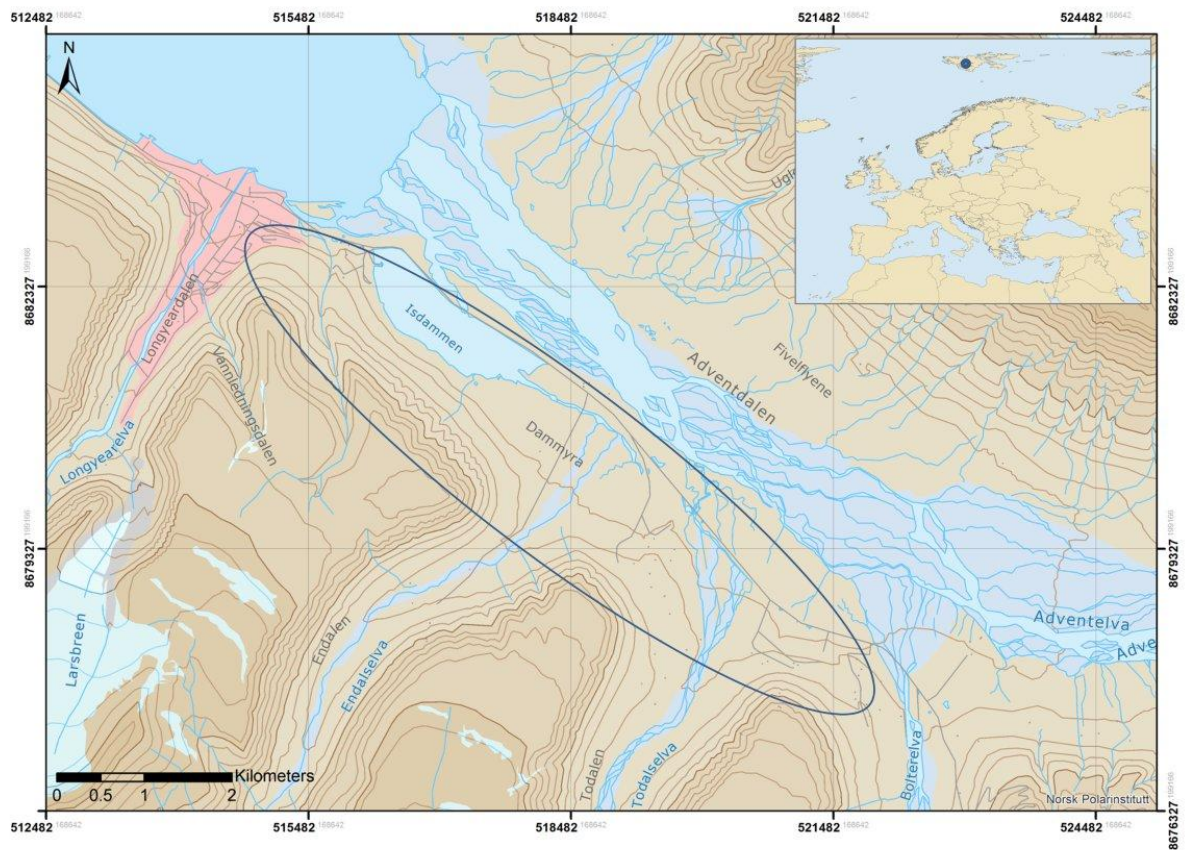
**Table 2:** Top ranked models by the AIC<sub>c</sub> model selection for analysis of breeding synchrony, with SI as response variable, which is explained in the Methods section. Table shows parameter estimates ( $\beta$ ), standard errors ( $\pm$ SE) for intercept and explanatory variables. AIC<sub>c</sub> values,  $\Delta$ AIC<sub>c</sub> values and AIC<sub>c</sub> weight ( $w_i$ ) are reported for all candidate models. AO<sub>w</sub> = Arctic Oscillation index winter, CID<sub>10</sub> = 10<sup>th</sup> percentile of Clutch Initiation Date for each year, Precipitation winter = total precipitation in November-April, Precipitation (AM) = total precipitation in April-May, Temperature (AM) = mean temperature in April-May. Precipitation winter and Precipitation (AM) were specified not to be included in the same models. The number of candidate models ranked in this section was 87.

Rank	Intercept	Explanatory variables				Model selection criteria		
		AO <sub>w</sub>	CID <sub>10</sub>	Precipitation (AM)	Temperature (AM)	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	$w_i$
1	-1.68± 13.83		0.88±0.41	1.01 ± 0.31		127.5	0.00	0.375
2	-5.17± 13.37		1.34±0.49	0.88 ± 0.31	1.65± 1.06	128.7	1.22	0.204
3	25.61± 5.65			1.07 ± 0.34		128.7	1.25	0.200
4	-7.60± 15.11	-2.13±2.17	1.03±0.44	1.03 ± 0.31		130.4	2.91	0.088
<b>Null model</b>	42.93 ±43.43					134.4	6.91	0.008

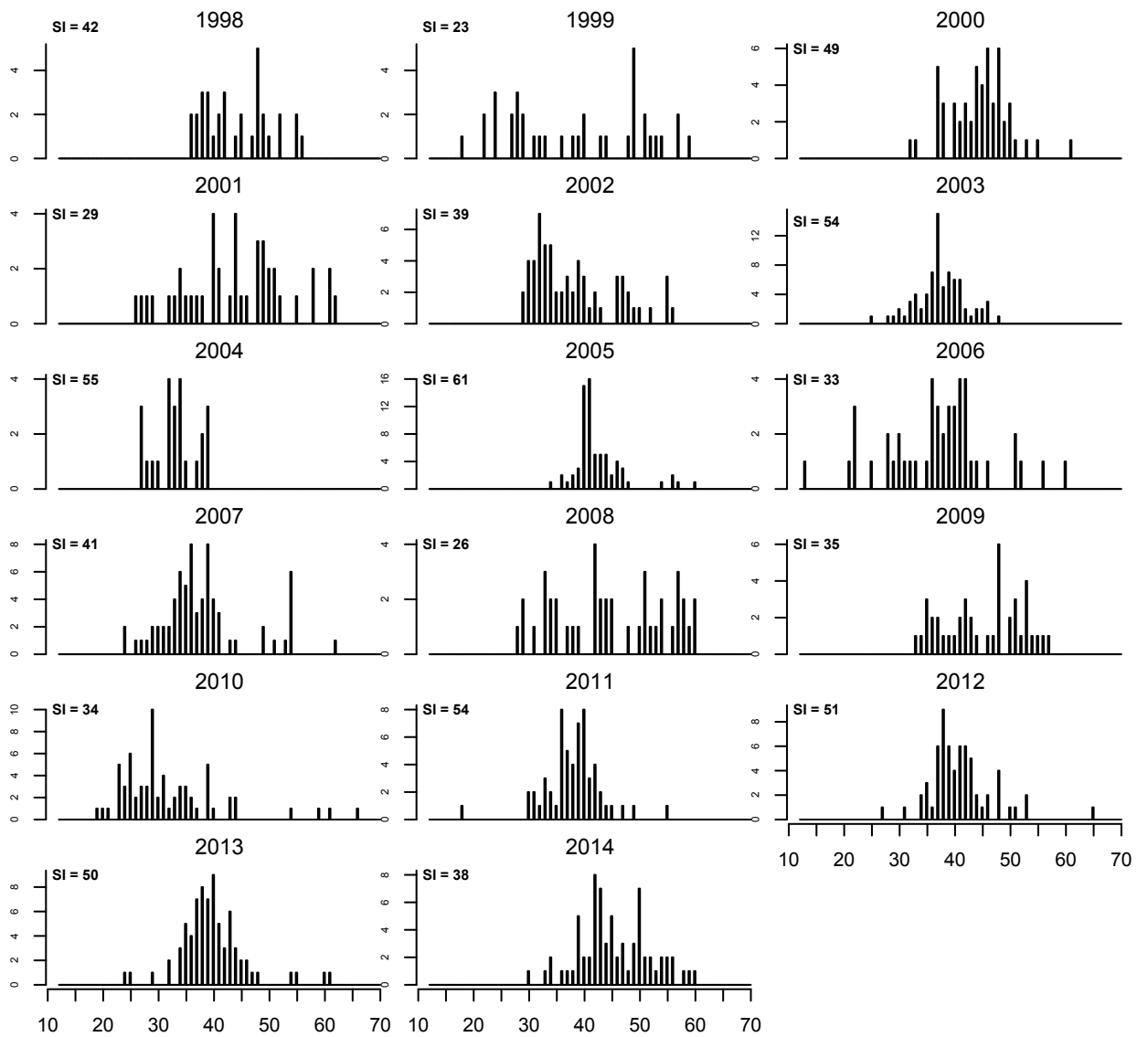
**Table 3:** The five top ranked models by the AIC<sub>c</sub> model selection for analysis of reproductive success, with mean number of fledglings as response variable. Table shows parameter estimates ( $\beta$ ), standard errors ( $\pm$ SE) for intercept and explanatory variables. AIC<sub>c</sub> values,  $\Delta$ AIC<sub>c</sub> values and AIC<sub>c</sub> weight ( $w_i$ ) are reported for all candidate models. SI = synchrony index (%), which is explained in the Methods section. AO<sub>w</sub> = Arctic Oscillation index winter, Precipitation (AM) = total precipitation in April-May, Temperature (AM) = mean temperature in April-May, Temperature (JJ) = mean temperature in June-July. Precipitation winter (Table 1) and Precipitation (AM) were specified to not be included in the same model. The number of candidate models ranked in this section was 85.

Model Rank	Intercept	Explanatory variables				Model selection criteria		
		SI	AO <sub>w</sub>	Precipitation (AM)	Temperature (JJ)	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	$w_i$
1	0.89 $\pm$ 0.82	0.02 $\pm$ 0.01			0.32 $\pm$ 0.16	22.3	0.00	0.238
2	1.15 $\pm$ 0.90				0.41 $\pm$ 0.17	22.9	0.60	0.177
3	0.83 $\pm$ 0.77	0.02 $\pm$ 0.01	0.15 $\pm$ 0.09		0.35 $\pm$ 0.15	23.0	0.66	0.172
4	2.38 $\pm$ 0.41	0.02 $\pm$ 0.01				23.1	0.74	0.165
5	1.06 $\pm$ 0.84		0.17 $\pm$ 0.10		0.45 $\pm$ 0.16	23.1	0.77	0.162
6	1.13 $\pm$ 0.87			0.02 $\pm$ 0.02	0.35 $\pm$ 0.17	24.4	2.04	0.086
<b>Null model</b>	3.35 $\pm$ 3.38					25.7	3.32	0.023

# Figures

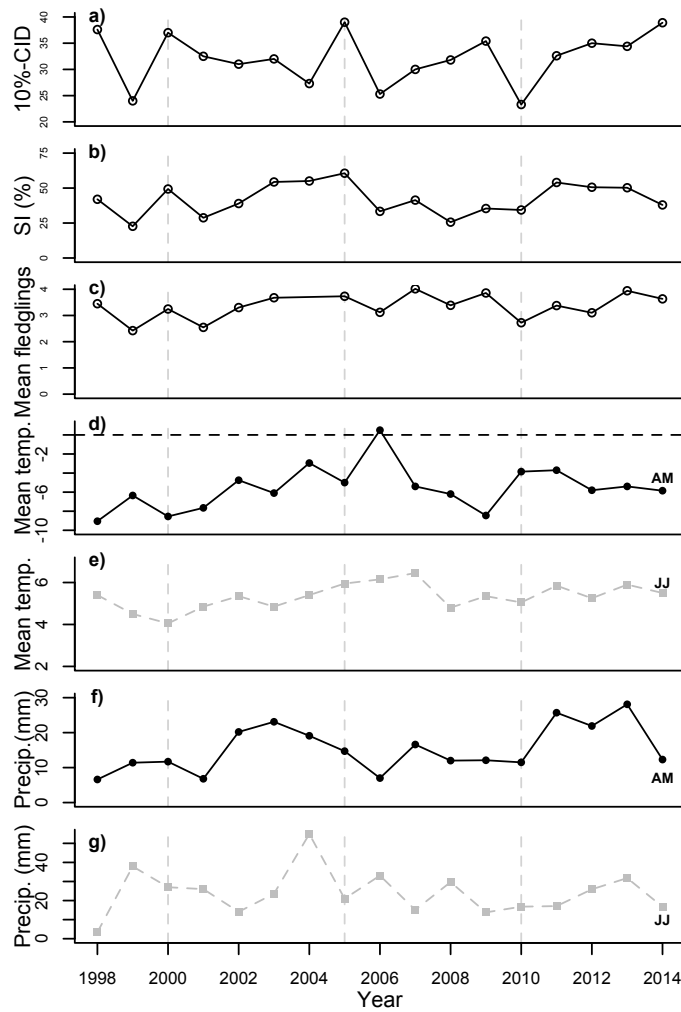


**Fig. 1:** Geographical location of the study site in the Adventdalen valley, Spitsbergen, Svalbard ( $78^{\circ} 13'N$ ,  $15^{\circ}38'E$ ), with nesting site of the study population of snow buntings indicated with blue ellipse. The map is in UTM33 format, made in ArcMap 10.1, and is obtained from the Norwegian Polar institute.

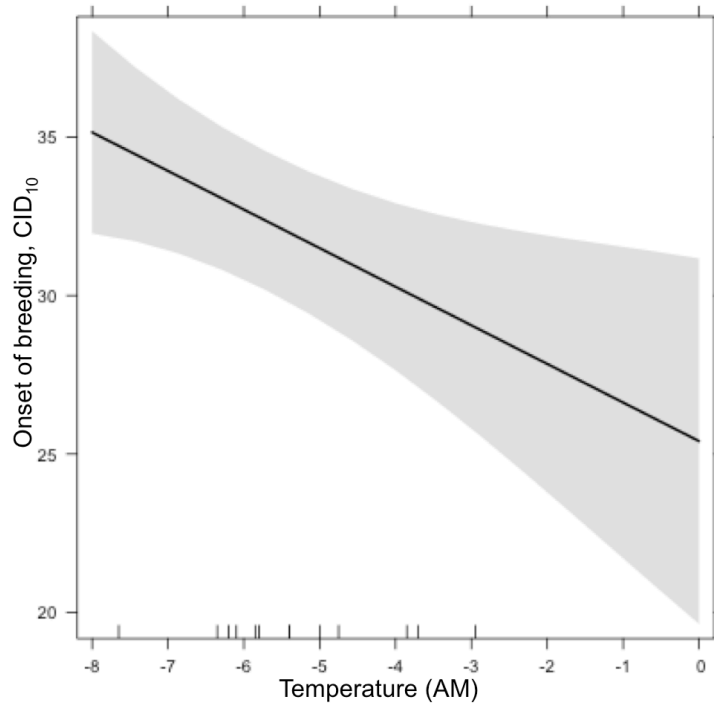


**Fig. 2:** Frequency histograms showing the distribution of clutch initiation dates in all monitored snow bunting nests per season from 1998-2014, with the corresponding Synchrony Index (SI) showing percentage of breeding synchrony in the upper left corner. The clutch initiation date is indicated on the x-axis by a day number in the breeding season, where day 1 = 1<sup>st</sup> of May. For information about SI, see Methods section.

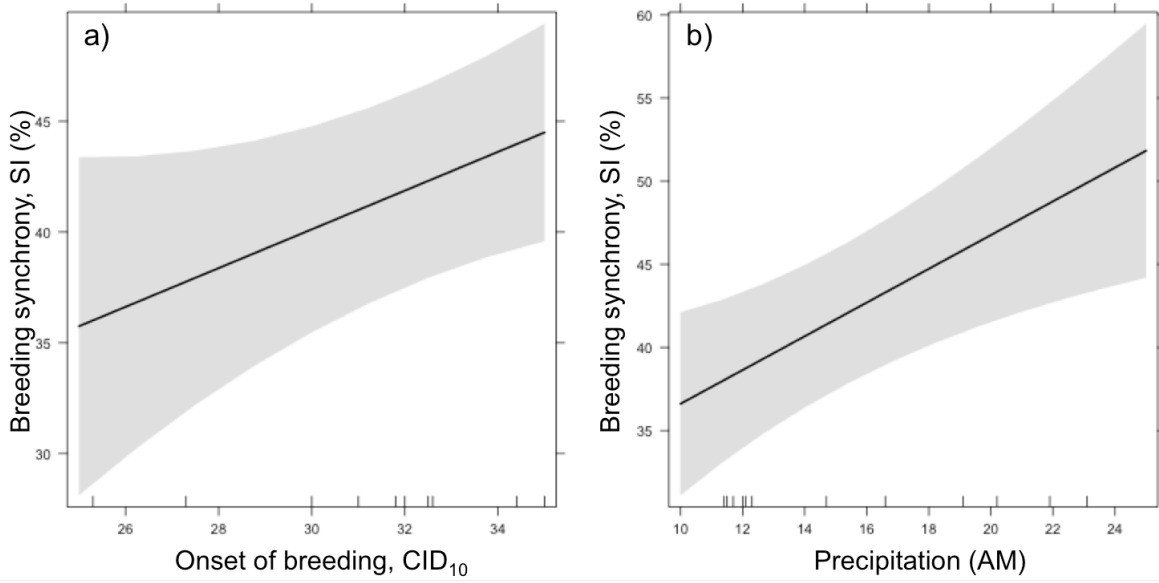




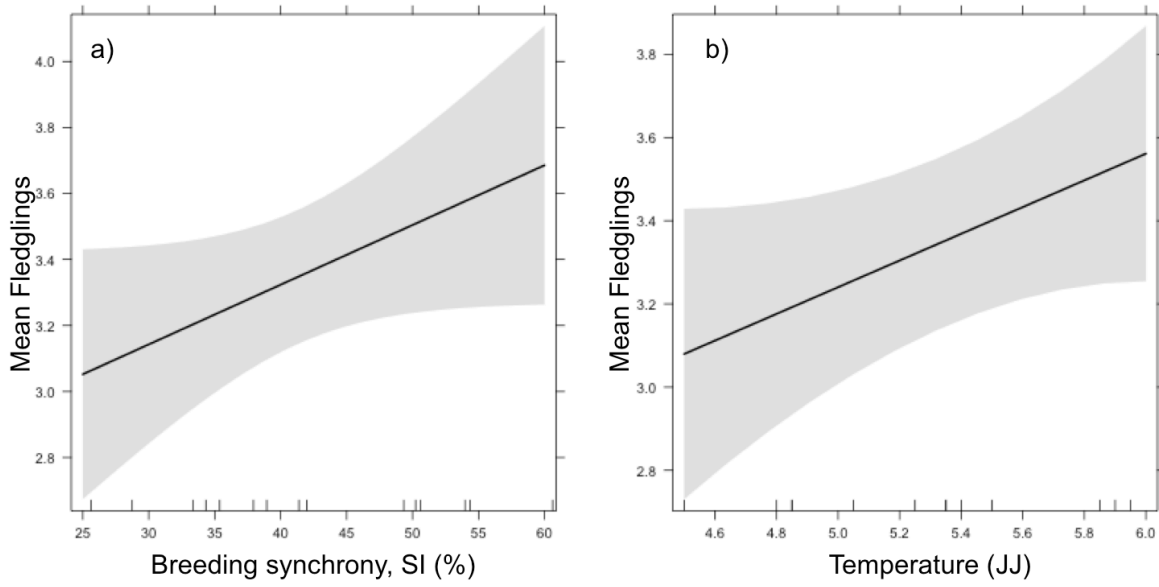
**Fig. 3:** Time series (1998 - 2014) with annual values of a)  $CID_{10}$ , b) Synchrony Index, SI (%), c) Mean fledglings = population level mean number of fledglings, d) Temperature (AM) = mean temperature in April-May, e) Temperature (JJ) = mean temperature in June-July, f) Precipitation (AM) = total precipitation in April-May and g) Precipitation (JJ) = Total precipitation in June-July. The  $CID_{10}$  and the Synchrony Index (SI) are explained in the Methods section.



**Fig. 4:** Effect plot of estimates from Table 1, model 1, showing negative effect of onset of breeding, CID<sub>10</sub>, as a response to Temperature (AM), mean temperature in April-May.



**Fig. 5:** Effect plots of estimates from Table 2, model 1, showing positive effects on breeding synchrony, SI (%), as a response to a) onset of breeding, CID<sub>10</sub>, and b) the total precipitation in April-May.



**Fig. 6:** Effect plots of estimates from Table 3, model 1, showing positive effects on reproductive success, measured in mean number of fledglings, as a response to a) breeding synchrony (SI) and b) mean temperature in June-July.

## Appendix

**Table A1:** Pearson's correlation coefficients between local climate and breeding variables with test statistics ( $P < 0.05^{**}$ ,  $P < 0.001^{***}$ ).  $CID_{10}$  and SI are explained in the Methods section. Mean fledglings = mean number of fledglings per year, Temperature (AM) = mean temperature in April-May, Precipitation (AM) = total precipitation in April-May, Temperature (JJ) = mean temperature in June-July. Precipitation (JJ) = total precipitation in June-July. Precipitation winter = total precipitation in November-April.  $AO_w$  = Arctic Oscillation index winter.

	$CID_{10}$	SI	Mean Fledglings	Temperature (AM)	Precipitation (AM)	Temperature (JJ)	Precipitation (JJ)	Precipitation winter	$AO_w$
$CID_{10}$	1.00								
SI	0.44	1.00							
Mean fledglings	0.56	0.55	1.00						
Temperature (AM)	-0.57 *	0.10	-0.08	1.00					
Precipitation (AM)	0.09	0.63 **	0.43	0.25	1.00				
Temperature (JJ)	0.04	0.28	0.55	0.52	0.25	1.00			
Precipitation (JJ)	-0.44	0.04	-0.38	0.40	0.15	-0.19	1.00		
Precipitation winter	-0.30	0.20	0.01	0.24	0.47	-0.01	-0.06	1.00	
$AO_w$	0.37	0.03	0.32	-0.30	0.08	-0.09	-0.11	-0.20	1.00

