# Selection or plasticity? Analysing the shifting reproductive timing of Arctic-breeding barnacle geese

R. C. I. Winters (s3807045)

*29-02-2024*

MSc Ecology & Evolution, University of Groningen

Supervised by M. J. J. E. Loonen

## Abstract

In the past few decades, the Arctic has experienced an elevated temperature increase, which is characterized by advancement of snowmelt. This enhances the plant productivity and food availability for Arctic herbivores but could also cause a mismatch between peak food availability and reproductive timing. In general, there are two ways for populations to cope with environmental changes: via selection for the reproductive timing that yield the highest fitness, or by adjusting their individual hatch date to better fit the circumstances. This study focusses on how the reproductive timing of Arctic-breeding barnacle geese has shifted in the past 33 years. Additionally, the processes behind this shift, either selection or plasticity, are analysed. For this, we studied a population of barnacle geese that breed in Kongsfjorden, Svalbard, which has been monitored from 1990 onwards. During this period, snowmelt has advanced by ~3 weeks (-0.68**), while hatch date has advanced by ~2 weeks (-0.34***). Snowmelt and hatch date are strongly correlated (0.31***), but there is a lag between the advancement of snowmelt and hatch date, indicating a possible mismatch between the hatch date of goslings and optimal food availability. Individuals from this population are moderately consistent in their reproductive timing (repeatability = 0.30), and reproductive timing is likely heritable (0.00 – 0.20), indicating that selection for a specific hatch date is possible, but that changes in the population are small from generation to generation. The variation in hatch date under changing snowmelt conditions was determined to be bigger between-individuals (0.35) than within-individuals (0.18), indicating that the observed change in reproductive timing is mainly caused by selection. This suggests that there is selection for early breeding, as this improves the growth rate of goslings and decreases their chances of size-dependent predation from e.g. Arctic foxes.

## Introduction

The Arctic is a highly seasonal environment, with large variation in habitat quality over the year, creating beneficial-,but also challenging conditions for reproduction (Perrins, 1970; Verhulst & Nilsson, 2008). The rising temperatures in the Arctic spring cause snowmelt, which increases food availability, thereby stimulating Arctic-breeding birds to migrate to the High North (Lameris et al., 2018; Tulp & Schekkerman, 2008). This is most effective when timing of migration corresponds to the phenology of the environment (Kölzsch et al., 2015), for which snowmelt can be used as proxy (Lameris et al., 2018; Tulp & Schekkerman, 2008). To optimize their individual fitness, an individual should time the hatching of their nest with the peak of resource availability (Reed et al., 2013).

In the past three decades, the Arctic region has experienced a stronger temperature increase compared to other regions. This phenomenon, also known as Arctic Amplification, is caused by positive feedback mechanisms from changes in the atmospheric oceanic circulation, as well as the loss of sea ice (Førland et al., 2011). The effects of climate change on Arctic lands is mainly characterized by the advancement of snowmelt (Foster, 1989), which prolongs the snow-free season, also known as the growing season. The combination of increased temperatures and earlier snowmelt advance plant growth, thereby boosting plant productivity and increasing plant protein content (Bjorkman et al., 2015; Jia et al., 2009). This, in turn, is beneficial for the herbivore populations, as the food availability is earlier and higher throughout the summer (Layton-Matthews et al., 2020).

In general, there are two ways for populations to cope with environmental changes. First of all, individuals can adapt their behaviour in response to environmental fluctuations,

meaning they show plasticity in their behaviour. This can protect the population against phenological mismatches (Laforge et al., 2023; Wolf & Weissing, 2012). The ability to adapt to yearly variation in phenology has positive effects on both individual fitness and the overall population endurance. Plasticity in reproductive and migratory behaviour gives the population also the ability to follow climate-change induced phenological changes (Boutin & Lane, 2014). Alternatively, high variation in phenotypes between individuals in a population can act as a buffer for changing conditions (Laforge et al., 2023; Wolf & Weissing, 2012). If this phenotypic variety is conserved over an extended period of time, and individuals thus act consistently over time, they can represent a certain phenotype in the population, also referred to as high repeatability (Dochtermann et al., 2015). This consistency in the behaviour of individuals could, if the trait is heritable, give the population the chance to adapt to shifting conditions (Laforge et al., 2023; Wolf & Weissing, 2012). The range of behavioural responses that individuals and/or populations can display under different environmental conditions show both the behavioural consistency (repeatability) and the ability to adapt to environmental fluctuations (plasticity) (Dingemanse et al., 2010).

In the summer months, a population of herbivorous barnacle geese (*Branta leucopsis*) breed on the islands of Svalbard. Climate change causes need for adjustments in migration and reproduction of barnacle geese (Tombre et al., 2019). For these geese, matching their arrival in the Arctic to the phenology of their food plants is of great importance for their reproductive success (Shariatinajafabadi et al., 2014). For example, higher food abundance decreases the pre-fledging mortality, and improves the growth rates of the goslings. It also decreases the foraging time of the parents, thereby reducing their time away from the nest and positively affecting the hatching success of barnacle geese (Layton-Matthews et al., 2020). A recent study showed that clutch size and hatch success of barnacle geese were negatively impacted by later snow melt (Layton-Matthews et al., 2020). A likely explanation is a trade-off between body mass for incubation and egg production, when they cannot replenish their body stores to recover from migration before nesting (Layton-Matthews et al., 2020; Ryder, 1970).

In lower trophic levels, climate change often causes an advance of phenology, but this is not always reflected in the higher trophic levels. The result is a phenological mismatch, where the peak of food availability occurs before the hatchlings can benefit from it, thereby negatively affecting their reproductive success (Both & Visser, 2001; Visser et al., 1998). Thus, the advancing snowmelt might cause a mismatch between the arrival and hatch date of the barnacle geese and peak food availability. Thus, literature suggests that the advancement of snowmelt could both increase and decrease the fitness of barnacle geese (Layton-Matthews et al., 2020). Although there is evidence that early breeding might be advantageous for reproductive success of barnacle geese, it is still unknown if these increased survival chances trigger selection for early breeding. Alternatively, changes in hatch date could also be a reaction to environmental conditions whereby the parents show phenotypic plasticity (Perry et al., 2018).

This study aims to assess how genetic and environmental factors have an effect on the reproductive timing of Arctic-breeding barnacle geese. To determine this, the study is divided into two parts. First, the shift in hatch date is analysed to see how barnacle geese have adjusted their reproductive timing in the past 30 years. For this, I hypothesise that the hatch date has advanced over time, following to the advancement of spring phenology observed in the region. Secondly, the processes behind this shift are investigated: are the changes in reproductive timing the result of plasticity or selection? I expect that the population average hatch date has advanced mainly because of selection, driven by directional change caused by the advancement of snowmelt.

## Method

### *Study population*

A barnacle geese population breeding in proximity to the settlement of Ny-Alesund, Svalbard (78.9235° N, 11.9099° E) was studied. Individuals belonging to this population spend the winter in the United Kingdom, on the Solway Firth, and then migrate to Svalbard via a short stop-over in coastal Norway. At the end of May, they arrive on the breeding grounds, and soon after start nesting on one of the islands in the fjord (*figure 1*). The incubation period lasts for approximately 25 days, until the end of June. When the eggs hatch, most parents leave the islands and disperse around the coast of the fjord, where they will stay until fledging at the end of August. In September, the population migrates back to the UK.

### *Data collection*

The Kongsfjorden population has been monitored for 33 years (1990-2023). In the beginning of June, the islands Storholmen and Prins Heinrichsøya (*figure 1*) are visited every other day to check the nests on the island (except for 1997, 2000, 2002, 2004 and 2018).
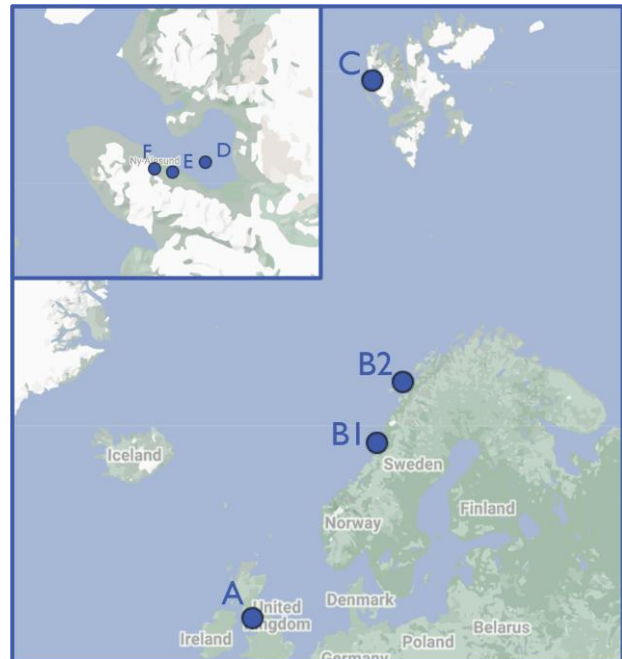


*Figure 1. Map of the migration route and breeding spots of the studied barnacle geese population. The geese spend the winter in Solway Firth (UK, location A). During their migration to Svalbard, they have a stop-over site in Helgeland, Norway (location B1) or Vesterålen also in Norway (location B2). During summer, the geese breed in Kongsfjorden, Svalbard (location C), on the islands in the fjord. Among these islands are Storholmen (location D) and Prins Heinrichsøya (location E), both of which are located nearby the town Ny-Alesund (location F).*

During these visits, the clutch size and hatch date of all nests are noted (n=4268, *see Appendix A*). In some years, chicks that were present in the nest during check-up were given an individual web tag. This web tag helps identifying the parents of the gosling if they are re-caught during the annual geese catch at the end of July.

### *Statistical analysis*

All statistical analyses were performed in R Studio (R version: 4.2.1, RStudio, 2020). The ISO dates were transformed to numerical Julian dates, with day one representing the 1st of January. The 1st of February is noted down as Julian day 32.

#### *Changing reproductive timing*

To analyse how environmental conditions have changed in the past decades, the change in snowmelt timing was analysed using a linear regression with year as a predictor for snowmelt (*Appendix B, model 1*). This data was measured on a northern hill in proximity to Ny-Ålesund. The data spans from 1993 to 2022 and indicates the first day when the reflection from the plot is less than 10 % and is provided by Marion Maturilli of the Alfred Wegener Institute in Bremerhaven. Additionally, the population change in absolute hatch date was analysed, using a linear regression with year as a predictor for hatch date (*Appendix B, model*

2). The data is then combined to compare the change in snowmelt to the change in reproductive timing (average hatch date) using a linear regression (*Appendix B, model 3*).

*Analysing the processes behind the shifting reproductive timing.*

Like mentioned in the introduction, populations can adjust to changing environments via phenotypic plasticity or selection. For selection to take place, individuals should be consistent in their reproductive timing, which can be analysed by calculating the repeatability. In this case, we are interested in when an individual reproduces compared to other individuals in the population. The relative hatch date was used instead of absolute hatch date, as this eliminates annual variation in reproductive timing from the dataset. The relative hatch date was calculated by subtracting the average hatch date of that year from the reported hatch date, thereby showing how much an individual's hatch date differed from the population mean.

$$Relative\ hatch\ date = hatch\ date_{individual} - mean(hatch\ date)_{year}$$

The repeatability will give the proportion of variance in hatch date that can be attributed to differences between individuals, and shows the upper limit for heritability (Boake, 1989; Dochtermann et al., 2015). The repeatability is based on hatch dates of individuals that occur in the dataset more than once (Boake, 1989), and is calculated over all nesting ringed females in the sampling period (Appendix A*)*. In this analysis, a model with relative hatch date as response variable and the individual (ringed female) as predictor is used (*Appendix B, model 4*). The repeatability is calculated from the variance estimates of the individuals and the residual variance, according to the following formula:

$$Repeatability = variance\ individual\ \frac{variance\ individual}{variance\ residual}$$

Heritability was calculated using mother-daughter nest data. The dataset containing nest information was combined with a dataset containing information on family-ties, based on the web-tagged goslings. This created a dataset containing all the nest information for both the mother and the daughter. For each individual the average relative hatch date is calculated. The heritability gives an estimate of the amount of phenotypic variation that can be explained by genetic variation (Dochtermann et al., 2015). A linear regression model uses the average relative hatch date of the daughter as a response variable and, the average relative hatch date of the mother as a fixed effect (*Appendix B, model 5*). The heritability can be calculated using the slope of the linear regression model. In this model, only the maternal effects are accounted for. To account for both parents the heritability is therefore doubled.

The effect of changing snowmelt conditions on hatch date is analysed by calculating the between- and within- individual variance in hatch date, using snowmelt as a predictor. The between-individual variation shows the variation in hatch date in the population. High between-individual variation would indicate that individuals are consistent in their behaviour (high repeatability), and therefore would not adjust their reproductive timing under changing snowmelt conditions (*figure 2B*). In this case, an individual represents a specific reproductive timing, and changing conditions might stimulate selection for a specific phenotype. The between-individual variance is determined by calculating the mean hatch date for each individual. The within-individual variance shows the variation in hatch date for an individual that is measured more than once. Under changing snowmelt conditions, high within-individual variation indicate that individuals adjust their reproductive timing to adapt to the changing environment (*figure 2A*). In this case, the individuals react to the changing

environment via phenotypic plasticity. The variance in hatch date was analysed using a generalised mixed-effects model, using the within- and between-individual variance as fixed effects and the individual as random effect (*Appendix B; model 6*).
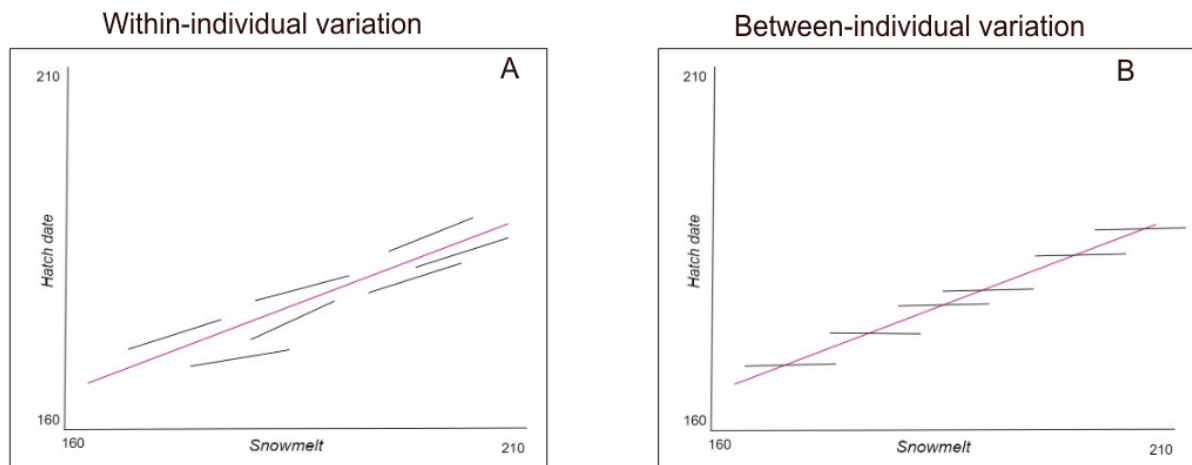


**Figure 2.** *Schematic overview of the individual response in hatch date for changing snowmelt conditions. Figure A shows the individual response (black lines) to changing snowmelt conditions, when there is high within-individual variation. In this case, the individuals adjust their hatch date to match snowmelt. Alternatively, figure B displays the individuals' response to changing snowmelt conditions when the between-individual variation is high. Under these circumstances, the individual does not modify their reproductive timing to the changing conditions, and there might be selection for the best-suited hatch date.*

## Results

### *Changing reproductive timing*

The climate-change induced temperature increase in the Arctic has led to an advancement of snowmelt by ±0.68 days a year (p-value: 0.004, n: 30; *figure 3, Appendix C1)*, indicating that the snow melts roughly three weeks earlier than in the 1990s.
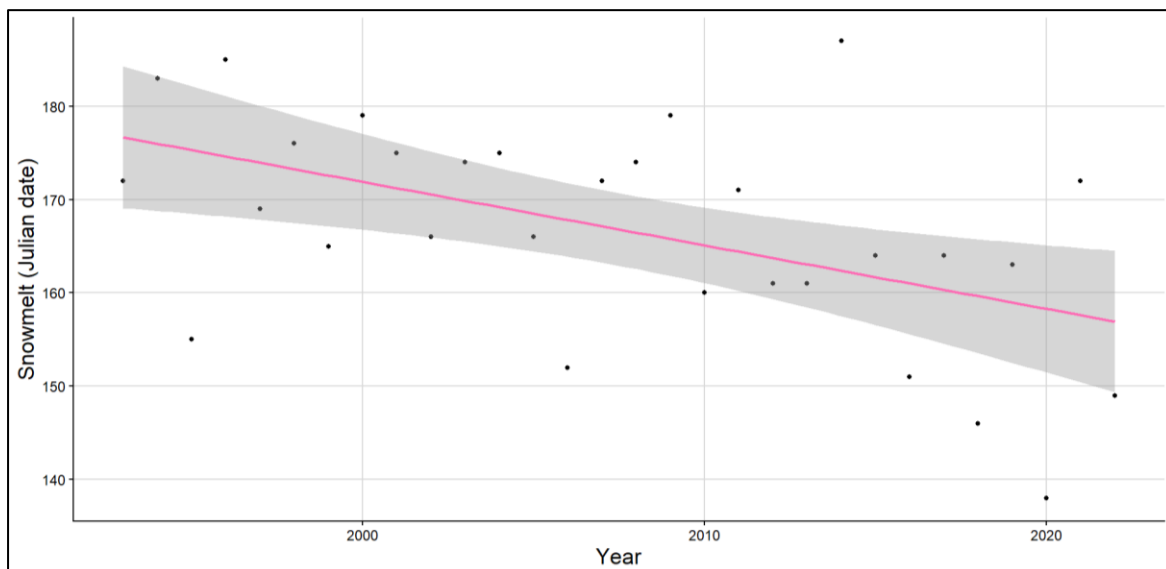


**Figure 3.** *The changes in first snow-free day over time. The x-axis shows the timespan of measurements (1990-2022), while the y-axis shows the Julian date on which the plot was completely snow-free for the first time that year (135-190). The regression line (pink) shows a significant negative correlation between snow melt and time, with a slope of - 0.68**.*

As a result of earlier snowmelt, the Kongsfjorden population has advanced their hatch date by ±2 weeks, or on average ±0.34 days a year between 1990 and 2023 (p-value: <0.001, n: 4348 ; *figure 4, Appendix C2*).
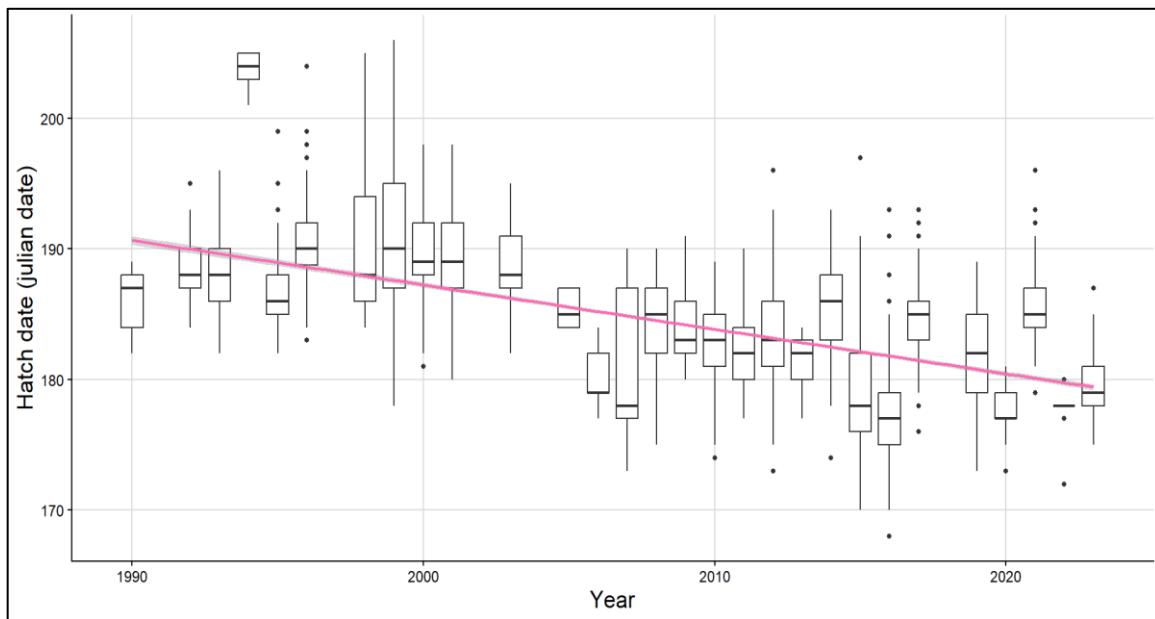


*Figure 4.* *The shift in hatch date of barnacle geese nests from the islands of Storholmen and Prins Heinrich in Kongsfjorden, Svalbard (n=4348). The x-axis shows the years in which sampling has taken place (ranging from 1990-2023), while the y-axis represents the Julian hatch date, ranging from day 170 (19th of June) to 200 (18th of July). The regression line (pink) has a slope of -0.34\*\*\*, showing a significant negative correlation between year and hatch date.*

Snowmelt and reproductive timing are significantly positively correlated, where the one-day advancement of snowmelt leads to an earlier average hatch date of ±0.31 days (p-value: <0.001, n: 26 ; *figure 5, Appendix C3*). The strong correlation between hatch date and snowmelt suggests that the population has adjusted their reproductive timing as a response to the snowmelt conditions.
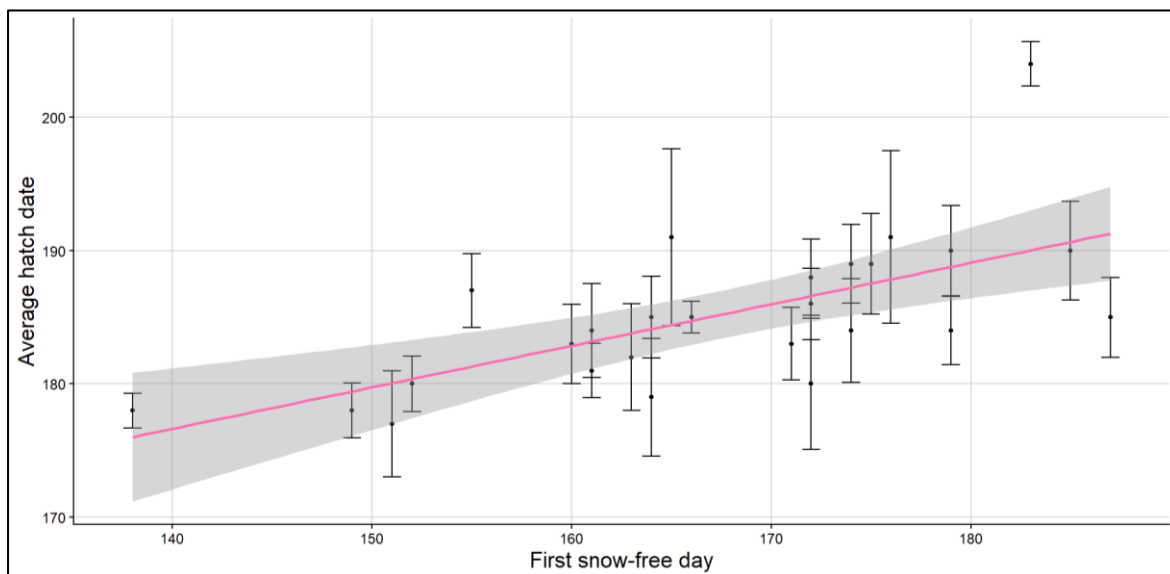


*Figure 5.* *The correlation between the average hatch date per year (y-axis) and the first snow-free day (x-axis). The error bars represent the standard deviation of hatch date per year. The pink regression line has a slope of 0.31\*\*\*. The y-axis ranges from Julian date 170 (18th of June) to 200 (19th of July). The x-axis is also in Julian date, ranging from 140 (20th of May) to 180 (29th of June).*

### Analysing the processes behind the shift in reproductive timing.

The repeatability of the relative hatch date was determined to be 0.30 (*table 1*), indicating that 30% of the variance in hatch date comes from variation between individuals. As stated before, the repeatability was calculated from the variance estimates of the ID of the females ($\tau_{oo\ female}$ ; *table 1*) and the residual variance ($\sigma^2$ ; *table 1*), as stated in the formula below.

$$Repeatability = variance\ ID_{female}\ \frac{variance\ ID_{female}}{variance\ residual} = 3.71\frac{3.71}{8.46} = 0.30$$

*Table 1. Overview of the results from the Linear Mixed-Effects Model comparing the identity of the female ($ID_{female}$) to predict the relative hatch date. The table shows the estimates, confidence intervals (CI) and p-value (p) for all predictors used in the model. The $\sigma^2$ represents the residual variance, while $\tau_{oo\ female}$ states the individual variance. The intraclass correlation (ICC) also shows the repeatability. In total there were 2149 observations from 860 females used in the model ($N_{female}$).*

| Predictors | Estimates | CI | p |
|---|---|---|---|
| (Intercept) | 0.16 | -0.03 – 0.34 | 0.103 |
| **Random Effects** | | | |
| $\sigma^2$ | 8.46 | | |
| $\tau_{oo\ female}$ | 3.71 | | |
| ICC | 0.30 | | |
| $N_{female}$ | 886 | | |
| Observations | 2276 | | |

A model comparing the average relative hatch date of mother-daughter pairs showed a positive correlation, with a slope of 0.10 (p-value: 0.214, n: 170; *figure 6; Appendix C4*). The slope of this model can be used to calculate the heritability, according to the following formula: $Heritability = 2\ x\ slope = 2\ x\ 0.10 = 0.20$. However, as the slope is not significant, the heritability can range from 0.00 to 0.20. However, this suggests that reproductive timing is heritable in barnacle geese, and therefore that selection might take place.
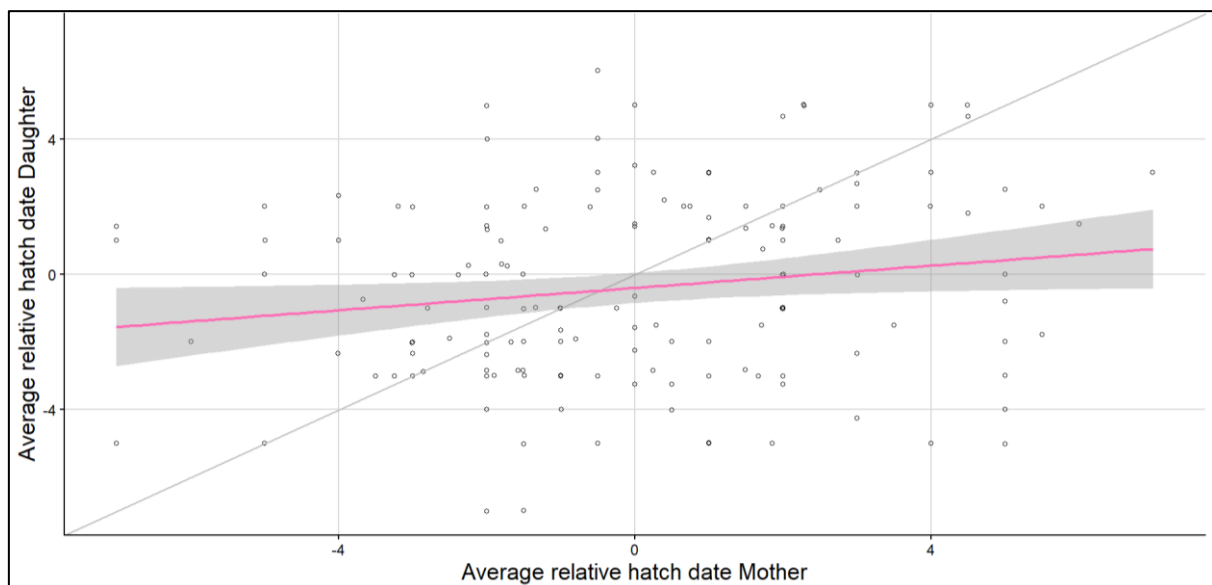


*Figure 6. The correlation between the average relative hatch date of the mother (x-axis) and the average relative hatch date of the daughter (y-axis). The regression line (pink) has a slope of 0.10 and is not significant.*

The within- and between individual variance in hatch date in relation to snowmelt is calculated to analyse how individuals have adjusted their reproductive timing in response to changing snowmelt conditions. A Generalized Linear Mixed-Effects model comparing within- and between-individual variation in hatch date under different snowmelt conditions showed that the confidence intervals of the between-individual variation and the within-individual variation do not overlap, indicating that they are significantly different from each other. There is both an effect of within-individual variation and between-individual variation, as the confidence intervals of both predictors do not overlap with zero (*table 7*). The variance in absolute hatch date within-individuals was 0.18 (p-value: <0.001 ; *table 2*), while the between-individual variance was estimated to be 0.35 (p-value: <0.001 ; *table 2*). As the between-individual variation is higher than the within-individual variation, that the population-wide change in reproductive timing is mainly caused by variation between individuals.

*Table 2. Overview of the results from the Generalized Linear Mixed-Effects Model comparing the within-individual variation and the between-individual variation in hatch date with changing snowmelt conditions. The table shows the estimates, confidence intervals (CI) and p-value (p) for all predictors used in the model. The $\sigma^2$ represents the residual variance, while $\tau_{00\ female}$ states the individual variance. In total there were 2149 observations from 860 females used in the model ($N_{female}$).*

| Predictors | Estimates | CI | p |
|---|---|---|---|
| (Intercept) | 126.38 | 120.73-132.04 | **<0.001** |
| Within Individual | 0.18 | 0.16 – 0.19 | **<0.001** |
| Between Individual | 0.35 | 0.32 – 0.38 | **<0.001** |
| **Random Effects** | | | |
| $\sigma^2$ | 12.08 | | |
| $\tau_{00\ female}$ | 8.27 | | |
| ICC | 0.41 | | |
| $N_{female}$ | 860 | | |
| Observations | 2149 | | |

## Discussion

In the following part, the advancement of hatch date of the Kongsfjorden barnacle geese population over the past 30 years (*figure 2*) is discussed. The individual response to changing conditions is analysed, as well as whether the population has adapted to the advancement of snowmelt via selection or plasticity.

### *Advancement of snowmelt and reproductive timing*

The first part of this study focussed on analysing the change in the reproductive timing of Arctic-breeding barnacle geese from 1990-2023. Both snowmelt (± 21 days) and population-average hatch date (± 14 days) have advanced over the past 30 years. The reproductive timing of barnacle geese was positively correlated with the moment of snowmelt. However, the population is not adjusting as rapidly as snowmelt is advancing.

Although there has been an overall advancement of reproductive timing, there is still a lot of variation in hatch date between the years, which are mainly caused by annual weather

conditions. In relatively cold years, when the snowmelt is later in the season, geese follow the trend by nesting later (barnacle geese: Layton-Matthews et al., 2020; pink-footed geese: Madsen et al., 2007). However, they do initiate nesting when the snow has not yet fully melted (Lindberg et al., 1997; Nolet et al., 2019).

Annual weather conditions are the main cause for variation in reproductive timing, but other factors might also influence the trend in hatch date in our dataset. For example, in 1994, the fjord was covered in sea ice for an extended period (M.J.J.E Loonen, *Personal communication,* 2023). This enabled Arctic foxes (*Vulpes lagopus*) to cross the fjord and scavenge the breeding islands, where they predated on the barnacle geese nests. The only hatched nests of that year are broods that started after ice-break-up. A more recent threat to the hatch-success are the growing numbers of polar bears (*Ursus maritimus*) visiting the breeding islands (Prop et al., 2015). The loss of sea ice has caused polar bears to become stuck on Svalbard, where they must seek other food sources, such as bird eggs (Layton-Matthews et al., 2020; Prop et al., 2015). Polar bears can predate on a substantial amount of geese nests (Prop et al., 2013, 2015; Robert F. Rockwell et al., 2011), as observed in 2022, when only three of the originally 173 nests on Storholmen survived until hatching after polar bear visitations (M.J.J.E Loonen, *Personal communication,* 2023; Loonen, 2022). Such events have severe impacts on the reproductive success of the geese.

The difference in advancement of snowmelt and reproductive timing causes a mismatch between plant phenology and hatching of the eggs. This result is in line with earlier research, which has stated that organisms from higher trophic levels show a weakened response to environmental changes than organisms from lower in the food chain (Both & Visser, 2001; Visser et al., 1998). The results of this study contradict the findings from a recently published paper on directional change in spring phenology in Zackenberg, Greenland. The study by Schmidt *et al.* (2023), found that the advancement of phenology decreased after expanding the timeframe. In this case, the reduced directional change was suggested to be the result of the plasticity in the response of individuals to local environmental conditions (Schmidt et al., 2023). The Kongsfjorden barnacle geese population does not show the same trend, as directional change is still visible after a period of 30 years. On Svalbard, barnacle geese show more variation in reproductive timing in recent years, while there was a strong advancement in hatch date in the 2000s (*Appendix D*). Strong directional change in this period might have forced the population to adjust its reproductive timing beyond their phenotypic plasticity range, causing irreversible changes in reproductive timing. To better understand what has caused the change in hatch date in the Kongsfjorden population, the processes behind the advancement of reproductive timing are discussed in the next section.

### *Analysing the processes behind the advancement of reproductive timing*

This part focusses on the question whether the advancement of reproductive timing observed in the study population is caused by selection or plasticity. The repeatability represents the contribution of individuality on the variation in reproductive timing and was determined to be 0.30. This repeatability indicates that 30% of the variation can be attributed to learned, inherited, imprinted or developed traits (Dochtermann et al., 2015; Jesmer et al., 2018; Stamps & Groothuis, 2010; Stuber et al., 2022), and thus that individuals are moderately consistent in their reproductive timing compared to the rest of the population. As the repeatability contains the inherited trait, it forms the upper limit for heritability (Dochtermann et al., 2015). The heritability of reproductive timing indicates that 0-20% of the variance in reproductive timing can be allocated to traits inherited from their parents. This suggests that the population likely has potential to undergo selection, as changes in hatch date

of the whole population can only occur over multiple generations (Boake, 1989; Laforge et al., 2023). Subsequently, timing of reproduction can be transmitted from generation to generation, which could eventually lead to an evolutionary response (Vander Wal et al., 2022). The speed of this evolutionary response is determined by the heritability, so in this case the phenotypic change between generations will be small (Boake, 1989).

Although a significant part of the variation in hatch date (30%) can be attributed to individual traits, 70% of the variation remains unexplained. This fraction of variance might come from a variety of factors, such as predation pressure, migration initiation, weather conditions in the stopover sites in Norway, and from spatial variation in environmental conditions, such as snowmelt. The variation in individual hatch date in response to changing snowmelt conditions was mainly caused by differences between-individuals, indicating that the population adjusts its reproductive timing via selection.

Both snowmelt and reproductive timing have advanced over the past 30 years. Therefore, it is to be expected that selection would work in favour for individuals that usually breed early. Still, selection would not take place if the early breeders do not have a fitness advantage over individuals that breed later in the season. Although concrete numbers on the survival of goslings dependent on their relative hatch date have not been analysed, one can make an estimate on what reproductive timing strategy would yield the highest number of goslings.

For barnacle geese, matching hatching eggs to the peak of protein concentrations in the plants is favourable for the survival of goslings. However, this is becoming increasingly mismatched due to the changing environmental conditions (Doiron et al., 2015). Late born goslings experience a reduction in protein content in their food (Richman et al., 2015), which slows their growth compared to early born chicks (Cooch et al., 1991). This slower growth also extends the period in which the goslings are vulnerable to size-dependent predation from e.g. glaucous gulls (*Larus hyperboreus*), great skuas (*Stercorarius skua*) and Arctic foxes (Samelius & Alisauskas, 2011).

Yearly differences in the geese's reproductive success come, among others, from fluctuations in Arctic fox abundances. The Arctic fox is the main top-down regulator of the barnacle geese population, as they predate on their eggs and goslings (Gauthier et al., 2004; Layton-Matthews et al., 2020; Loonen et al., 1998). An extreme example would be the result from the rain-on-snow event that occurred in the winter of 1993/94, and caused a mass die-off event for Svalbard reindeer (*Rangifer tarandus platyrhynchus*). This led to elevated levels of food availability for the Arctic fox, thereby increasing their reproductive success for two years. This, in turn, had detrimental effects on the survival of barnacle goslings in the following years (Fuglei et al., 2003; Layton-Matthews et al., 2023). In general, the Arctic foxes predate on the smallest goslings, as they are easier to catch. Early hatched goslings have had more time to grow, thereby decreasing their chances of being predated upon (Layton-Matthews et al., 2020). Like mentioned before, polar bears have an increasing impact on the hatching of eggs. Observations by Lameris *et al.,* (2019) and Rockwell & Gormezano (2009), suggest that the early-initiated clutches might escape predation, as these nests have the chance to hatch before polar bear visitations.

## Conclusion

This study investigated the shifting reproductive timing of Arctic-breeding barnacle geese, as well as the processes behind this change. The population-average hatch date has advanced over the past 33 years, but individuals show a weak response to snowmelt, which has

resulted in a mismatch between hatch date and the peak in food availability. Reproductive timing is likely to be heritable in barnacle geese, which makes selection for a specific hatch date possible. However, heritability is relatively low, indicating that changes will be small from generation to generation (i.e. slow evolution). The population-wide shift in hatch date in response to changing snowmelt conditions is mainly caused by selection for individuals that reproduce early in the season. However, there is still some plasticity in the individual response to changing snowmelt conditions.

While some effects of reproductive timing on the reproductive success have been mentioned in this article, there are still many factors that were not covered. Although we made presumptions on which goslings have the highest survival, the survival of goslings compared to their relative hatch date has not been studied yet. Age corrected body mass and body size are good predictors of gosling survival, so further research should focus on analysing the weight of goslings or their survival in relation to hatch date. This study used the snowmelt data that is measured north of Ny-Ålesund. The ground has a slight exposure to the north, and the adjacent mountain can produce local shading when the sun has a low height above the horizon. The snowmelt conditions on the islands seem to differ from this location, and therefore this data only shows the trend in snowmelt, but not the exact availability of nesting sites on the breeding island. Using satellite data to analyse the timing of snowmelt on Storholmen would significantly improve the analysis. Alternatively, temperature or the number of days-above-zero could also be used as an indicator of environmental conditions. Of course, reproductive timing is determined by more than just genetics and environmental conditions. The body condition of the adult geese and their arrival time are both heavily impacted by the conditions encountered during their migration, which should also be taken into consideration.

## Acknowledgements

## Bibliography

Bjorkman, A. D., Elmendorf, S. C., Beamish, A. L., Vellend, M., & Henry, G. H. R. (2015). Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades. *Global Change Biology*, *21*(12), 4651–4661. https://doi.org/10.1111/gcb.13051

Boake, C. R. B. (1989). Repeatability: Its role in evolutionary studies of mating behavior. *Evolutionary Ecology*, *3*(2), 173–182. https://doi.org/10.1007/BF02270919

Both, C., & Visser, M. E. (2001). Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, *411*(6835), 296–298. https://doi.org/10.1038/35077063

Boutin, S., & Lane, J. E. (2014). Climate change and mammals: evolutionary versus plastic responses. *Evolutionary Applications*, *7*(1), 29–41. https://doi.org/10.1111/EVA.12121

Cooch, E. G., Lank, D. B., Dzubin, A., Rockwell, R. F., & Cooke, F. (1991). Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. *Ecology*, *72*(2), 503–512. https://doi.org/10.2307/2937191

Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology and Evolution*, *25*(2), 81–89. https://doi.org/10.1016/j.tree.2009.07.013

Dochtermann, N. A., Schwab, T., & Sih, A. (2015). The contribution of additive genetic variation to personality variation: heritability of personality. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1798). https://doi.org/10.1098/RSPB.2014.2201

Doiron, M., Gauthier, G., & Lévesque, E. (2015). Trophic mismatch and its effects on the growth of young in an Arctic herbivore. *Global Change Biology*, *21*(12), 4364–4376. https://doi.org/10.1111/gcb.13057

Førland, E. J., Benestad, R., Hanssen-Bauer, I., Haugen, J. E., & Skaugen, T. E. (2011). Temperature and Precipitation Development at Svalbard 1900–2100. *Advances in Meteorology*, 1–14. https://doi.org/10.1155/2011/893790

Foster, J. L. (1989). The Significance of the Date of Snow Disappearance on the Arctic Tundra as a Possible Indicator of Climate Change. *Arctic and Alpine Research*, *21*(1), 60–70. https://doi.org/10.1080/00040851.1989.12002710

Fuglei, E., Øritsland, N. A., & Prestrud, P. (2003). Local variation in arctic fox abundance on Svalbard, Norway. *Polar Biology*, *26*(2), 93–98. https://doi.org/10.1007/s00300-002-0458-8

Gauthier, G., Bêty, J., Giroux, J.-F., & Rochefort, L. (2004). Trophic Interactions in a High Arctic Snow Goose Colony. *Integrative and Comparative Biology*, *44*(2), 119–129. https://academic.oup.com/icb/article/44/2/119/674152

Jesmer, B. R., Merkle, J. A., Goheen, J. R., Aikens, E. O., Beck, J. L., Courtemanch, A. B., Hurley, M. A., McWhirter, D. E., Miyasaki, H. M., Monteith, K. L., & Kauffman, M. J. (2018). Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science*, *361*(6406), 1023–1025. https://doi.org/10.1126/SCIENCE.AAT0985/SUPPL_FILE/AAT0985-JESMER-SM.PDF

Jia, G. J., Epstein, H. E., & Walker, D. A. (2009). Vegetation greening in the canadian arctic related to decadal warming. *Journal of Environmental Monitoring*, *11*(12), 2231–2238. https://doi.org/10.1039/B911677J

Kölzsch, A., Bauer, S., de Boer, R., Griffin, L., Cabot, D., Exo, K. M., van der Jeugd, H. P., & Nolet, B. A. (2015). Forecasting spring from afar? Timing of migration and predictability of phenology along different migration routes of an avian herbivore. *Journal of Animal Ecology*, *84*(1), 272–283. https://doi.org/10.1111/1365-2656.12281

Laforge, M. P., Webber, Q. M. R., & Vander Wal, E. (2023). Plasticity and repeatability in spring migration and parturition dates with implications for annual reproductive success. *Journal of Animal Ecology*, *92*(5), 1042–1054. https://doi.org/10.1111/1365-2656.13911

Lameris, T. K., de Jong, M. E., Boom, M. P., van der Jeugd, H. P., Litvin, K. E., Loonen, M. J. J. E., Nolet, B. A., & Prop, J. (2019). Climate warming may affect the optimal timing of reproduction for migratory geese differently in the low and high Arctic. *Oecologia*, *191*(4), 1003–1014. https://doi.org/10.1007/s00442-019-04533-7

Lameris, T. K., van der Jeugd, H. P., Eichhorn, G., Dokter, A. M., Bouten, W., Boom, M. P., Litvin, K. E., Ens, B. J., & Nolet, B. A. (2018). Arctic Geese Tune Migration to a Warming

Climate but Still Suffer from a Phenological Mismatch. *Current Biology*, *28*(15), 2467-2473.e4. https://doi.org/10.1016/J.CUB.2018.05.077

Layton-Matthews, K., Hansen, B. B., Grøtan, V., Fuglei, E., & Loonen, M. J. J. E. (2020). Contrasting consequences of climate change for migratory geese: Predation, density dependence and carryover effects offset benefits of high-arctic warming. *Global Change Biology*, *26*(2), 642–657. https://doi.org/10.1111/gcb.14773

Layton-Matthews, K., Vriend, S. J. G., Grøtan, V., Loonen, M. J. J. E., Sæther, B. E., Fuglei, E., & Hansen, B. B. (2023). Extreme events, trophic chain reactions, and shifts in phenotypic selection. *Scientific Reports*, *13*(1), 1–9. https://doi.org/10.1038/s41598-023-41940-6

Lindberg, M. S., Sedinger, J. S., & Flint, P. L. (1997). Effects of spring environment on nesting phenology and clutch size of Black Brant. *Condor*, *99*(2), 381–388. https://doi.org/10.2307/1369944

Loonen, M. J. J. E. (2022). *Polar bear kills seal*. https://www.arcticstation.nl/weblog.php?nr=2295

Loonen, M. J. J. E., Tombre, I. M., & Mehlun, F. (1998). Development of an arctic barnacle goose colony: Interactions between density and predation. *Norsk Polarinstitutt Skrifter*, *200*, 67–79.

Madsen, J., Tamstorf, M., Klaassen, M., Eide, N., Glahder, C., Rigét, F., Nyegaard, H., & Cottaar, F. (2007). Effects of snow cover on the timing and success of reproduction in high-Arctic pink-footed geese Anser brachyrhynchus. *Polar Biology*, *30*(11), 1363–1372. https://doi.org/10.1007/s00300-007-0296-9

Nolet, B. A., Schreven, K. H. T., Boom, M. P., & Lameris, T. K. (2019). Contrasting effects of the onset of spring on reproductive success of Arctic-nesting geese. *The Auk*, *137*(1), 1–9. https://doi.org/https://doi.org/10.1093/auk/ukz063

Perrins, C. M. (1970). the Timing of Birds' Breeding Seasons. *Ibis*, *112*(2), 242–255. https://doi.org/10.1111/j.1474-919X.1970.tb00096.x

Perry, B. W., Schield, D. R., & Castoe, T. A. (2018). Evolution: Plasticity versus Selection, or Plasticity and Selection? *Current Biology*, *28*(18), R1104–R1106. https://doi.org/10.1016/J.CUB.2018.07.050

Prop, J., Aars, J., Bårdsen, B. J., Hanssen, S. A., Bech, C., Bourgeon, S., de Fouw, J., Gabrielsen, G. W., Lang, J., Noreen, E., Oudman, T., Sittler, B., Stempniewicz, L., Tombre, I., Wolters, E., & Moe, B. (2015). Climate change and the increasing impact of polar bears on bird populations. *Frontiers in Ecology and Evolution*, *3*(33). https://doi.org/https://doi.org/10.3389/fevo.2015.00033

Prop, J., Oudman, T., Van Spanje, T. M., & Wolters, E. H. (2013). Patterns of predation of Pink-footed Goose nests by polar bear. *Ornis Norvegica*, *36*, 38–46. https://doi.org/10.15845/on.v36i0.439

Reed, T. E., Jenouvrier, S., & Visser, M. E. (2013). Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *Journal of Animal Ecology*, *82*(1), 131–144. https://doi.org/10.1111/J.1365-2656.2012.02020.X

Richman, S. E., Leafloor, J. O., Karasov, W. H., & Mcwilliams, S. R. (2015). Ecological implications of reduced forage quality on growth and survival of sympatric geese. *Journal of Animal Ecology*, *84*(1), 284–298. https://doi.org/10.1111/1365-2656.12270

Rockwell, R. F., & Gormezano, L. J. (2009). The early bear gets the goose: Climate change, polar bears and lesser snow geese in western Hudson Bay. *Polar Biology*, 32(4), 539–547. https://doi.org/10.1007/S00300-008-0548-3/FIGURES/4

Rockwell, Robert F., Gormezano, L. J., & Koons, D. N. (2011). Trophic matches and mismatches: Can polar bears reduce the abundance of nesting snow geese in western Hudson Bay? *Oikos*, 120(5), 696–709. https://doi.org/10.1111/j.1600-0706.2010.18837.x

RStudio, T. (2020). RStudio: Integrated Development for R. In *RStudio, Inc., Boston, MA* (Vol. 42, p. 14). PBC. http://www.rstudio.com/

Ryder, J. P. (1970). A Possible Factor In The Evolution Of Clutch Size In Ross' Goose . *Wilson Bull*, 82(1), 5–13.

Samelius, G., & Alisauskas, R. T. (2011). Diet and growth of glaucous gulls at a large Arctic goose colony. *Https://Doi-Org.Proxy-Ub.Rug.Nl/10.1139/Z99-091*, 77(8), 1327–1331. https://doi.org/10.1139/Z99-091

Schmidt, N. M., Kankaanpää, T., Tiusanen, M., Reneerkens, J., Versluijs, T. S. L., Hansen, L. H., Hansen, J., Gerlich, H. S., Høye, T. T., Cirtwill, A. R., Zhemchuzhnikov, M. K., Peña-Aguilera, P., & Roslin, T. (2023). Little directional change in the timing of Arctic spring phenology over the past 25 years. *Current Biology : CB*, 33(15), 3244–3249. https://doi.org/10.1016/j.cub.2023.06.038

Shariatinajafabadi, M., Wang, T., Skidmore, A. K., Toxopeus, A. G., Kölzsch, A., Nolet, B. A., Exo, K. M., Griffin, L., Stahl, J., & Cabot, D. (2014). Migratory herbivorous waterfowl track satellite-derived green wave index. *PLoS ONE*, 9(9), 1–11. https://doi.org/10.1371/journal.pone.0108331

Stamps, J. A., & Groothuis, T. G. G. (2010). Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4029–4041. https://doi.org/10.1098/RSTB.2010.0218

Stuber, E. F., Carlson, B. S., & Jesmer, B. R. (2022). Spatial personalities: a meta-analysis of consistent individual differences in spatial behavior. *Behavioral Ecology*, 33(3), 477–486. https://doi.org/10.1093/BEHECO/ARAB147

Tombre, I. M., Oudman, T., Shimmings, P., Griffin, L., & Prop, J. (2019). Northward range expansion in spring-staging barnacle geese is a response to climate change and population growth, mediated by individual experience. *Global Change Biology*, 25(11), 3680–3693. https://doi.org/10.1111/gcb.14793

Tulp, I., & Schekkerman, H. (2008). Has Prey Availability for Arctic Birds Advanced with Climate Change? Hindcasting the Abundance of Tundra Arthropods Using Weather and Seasonal Variation. *Arctic*, 61(1), 48–60.

Vander Wal, E., Webber, Q. M. R., & Laforge, M. P. (2022). Repeatability is the first step in a broader hypothesis test: a comment on Stuber et al. *Behavioral Ecology*, 33(3), 487–488. https://doi.org/10.1093/BEHECO/ARAC005

Verhulst, S., & Nilsson, J. Å. (2008). The timing of birds' breeding seasons: A review of experiments that manipulated timing of breeding. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1490), 399–410. https://doi.org/10.1098/rstb.2007.2146

Visser, M. E., Van Noordwijk, A. J., Tinbergen, J. M., & Lessells, C. M. (1998). Warmer springs lead to mistimed reproduction in great tits (Parus major). *Proceedings of the Royal*

*Society B: Biological Sciences, 265*(1408), 1867–1870. https://doi.org/10.1098/rspb.1998.0514

Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology and Evolution, 27*(8), 452–461. https://doi.org/10.1016/j.tree.2012.05.001

# Appendix A

**Table A.** *Frequency table of the number of nests used in the statistical analyses, sorted by year. For each year the total number of nests is mentioned, as well as how many of those nests were occupied by a ringed female.*

| Year | Number of nests | Number of nests with ringed females | Year | Number of nests | Number of nests with ringed females |
|------|------|------|------|------|------|
| 1990 | 23 | 12 | 2007 | 73 | 50 |
| 1991 | 0 | 0 | 2008 | 135 | 112 |
| 1992 | 64 | 50 | 2009 | 157 | 97 |
| 1993 | 188 | 101 | 2010 | 176 | 116 |
| 1994 | 5 | 4 | 2011 | 147 | 100 |
| 1995 | 71 | 62 | 2012 | 218 | 89 |
| 1996 | 115 | 90 | 2013 | 131 | 62 |
| 1997 | 0 | 0 | 2014 | 219 | 93 |
| 1998 | 35 | 22 | 2015 | 302 | 129 |
| 1999 | 107 | 79 | 2016 | 312 | 141 |
| 2000 | 154 | 98 | 2017 | 272 | 132 |
| 2001 | 299 | 179 | 2018 | 0 | 0 |
| 2002 | 0 | 0 | 2019 | 253 | 106 |
| 2003 | 113 | 73 | 2020 | 183 | 56 |
| 2004 | 0 | 0 | 2021 | 210 | 83 |
| 2005 | 25 | 14 | 2022 | 10 | 7 |
| 2006 | 84 | 54 | 2023 | 187 | 65 |

# Appendix B

**Table B.** *Overview of the models used in the statistical analysis. For each model, the type of model, the response variable, fixed effects and random effects are stated.*

| Nr. | Model | Response variable | Fixed effect | Random effect |
|---|---|---|---|---|
| 1 | Linear Regression | Snowmelt | Year | |
| 2 | Linear Regression | Hatch date | Year | |
| 3 | Linear Regression | Average hatch date | Snowmelt | |
| 4 | Linear Mixed-effect | Relative hatch date | | Female |
| 5 | Linear Regression | Average relative hatch date daughter | Average relative hatch date mother | |
| 6 | Generalized Mixed-effect | Hatch date | Within-individual variance, between-individual variance | Female |

## Appendix C

**Table C1.** *Overview of the results from the Linear Regression Model describing change in first snow-free day over the past 30 years (1990-2022). The table shows the estimates, confidence intervals (CI) and p-value (p) for all predictors used in the model.*

| Predictors | Estimates | CI | p |
|---|---|---|---|
| (Intercept) | 1533.42 | 632.69 – 2434.15 | **0.002** |
| Year | -0.68 | -1.13– -0.23 | **0.004** |
| Observations | 30 | | |
| R²/R² adjusted | 0.26 / 0.23 | | |

**Table C2.** *Overview of the results from the Linear Regression Model using the year (fixed effect, ranging from 1990 to 2023) to predict hatch date (absolute numerical value). The table shows the estimates, confidence intervals (CI) and p-value (p) for all predictors used in the model.*

| Predictors | Estimates | CI | p |
|---|---|---|---|
| (Intercept) | 868.60 | 838.01 – 899.19 | **<0.001** |
| Year | -0.34 | -0.36 – -0.33 | **<0.001** |
| Observations | 4348 | | |
| R²/R² adjusted | 0.31 / 0.31 | | |

**Table C3.** *Overview of the Linear Regression model comparing the average hatch date to the first snow-free day. The The table shows the estimates, confidence intervals (CI) and p-value (p) for all predictors used in the model.*

| Predictors | Estimates | CI | p |
|---|---|---|---|
| (Intercept) | 133.06 | 107.40 – 158.71 | **<0.001** |
| First snow-free day | 0.31 | 0.16 – 0.46 | **<0.001** |
| Observations | 26 | | |
| ²/R² adjusted | 0.42 / 0.40 | | |

**Table C4.** *Overview of the results from the Linear Mixed-Effects Model using the average relative hatch date of the mother to predict the average relative hatch date of the daughter. The table shows the estimates, confidence intervals (CI) and p-value (p) for all predictors used in the model.*

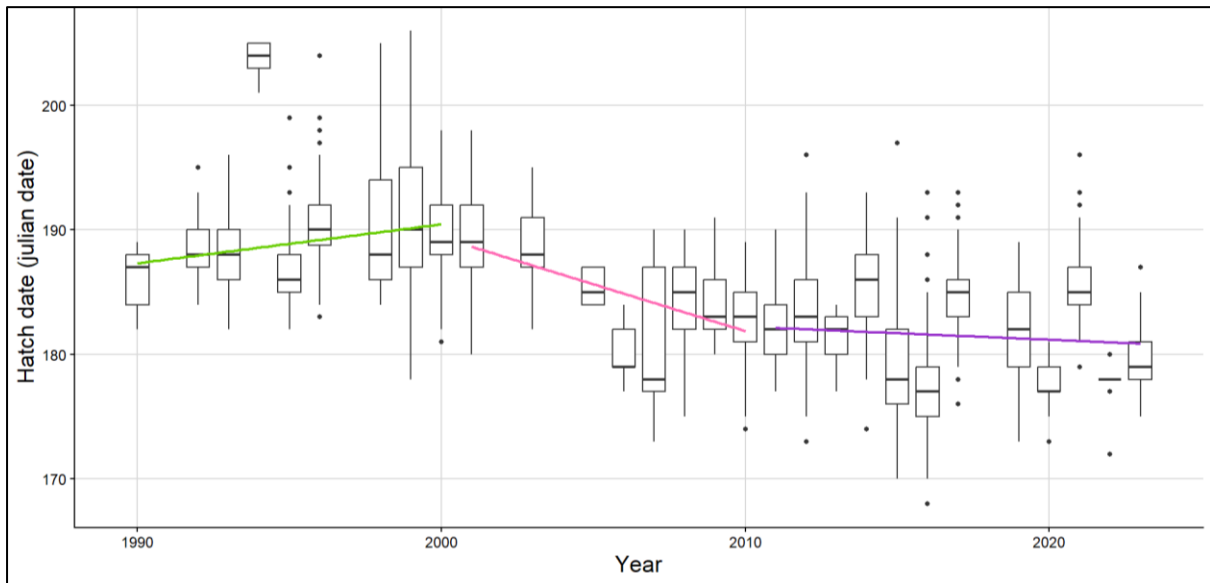| Predictors | Estimates | CI | p |
|---|---|---|---|
| (Intercept) | 0.06 | -0.39 – 0.52 | 0.785 |
| Average relative hatch date mother | 0.10 | -0.06 – 0.25 | 0.214 |
| Observations | 170 | | |
| Marginal R² / Conditional R² | 0.01/ 0.00 | | |

## Appendix D



**Figure D**. *The shift in hatch date of barnacle geese nests from the islands of Storholmen and Prins Heinrich in Kongsfjorden, Svalbard (n=4348). The x-axis shows the years in which sampling has taken place (ranging from 1990-2023), while the y-axis represents the Julian hatch date, ranging from day 170 (19th of June) to 200 (18th of July). The change in population hatch date has been divided into three periods. The first period, from 1990-2000, shows a positive significant correlation, with a slope of 0.31. Between 2001 and 2010 the hatch date has significantly advanced, with a slope of -0.75\*\*\*. The rate of change has stabilized from 2011 onwards, which shows a significant slope of -0.10.*