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## CHAPTER 8

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# Reproductive benefits of a warming climate differ between barnacle geese breeding in the low and high Arctic

Thomas K. Lameris, Margje E. de Jong, Maarten J. J. E. Loonen, Michiel P. Boom, Henk P. van der Jeugd, Konstantin E. Litvin, Bart A. Nolet, Jouke Prop

### ABSTRACT

The Arctic is subject to rapid climate warming, advancing the onset of the Arctic spring with potentially broad consequences for all organisms. Populations of migratory Arctic-breeding birds are often thought of running the risk of suffering from deleterious effects of a phenological mismatch. Alternatively, as the Arctic breeding season is short, an advancement of the onset of spring could relieve current time constraints on the birds' reproductive cycle, and improve conditions for successful breeding. The impacts of earlier springs on reproductive output of migratory birds may mainly depend on the extent to which they advance their laying dates. We studied to what extent barnacle geese in different parts of the Arctic adjust their laying dates to earlier seasons, and whether earlier and longer Arctic breeding seasons are enhancing reproductive success. We hypothesized that bird populations towards the North pole would be more time constrained. Therefore we expected that – if any positive effects accrued to climate warming – birds in the high Arctic would respond stronger to an earlier onset of spring and benefit more from earlier springs than birds at lower latitudes. We determined the onset of the spring by date of snowmelt, as derived from MODIS satellite imagery. We collected data on egg laying date, clutch size, nest success and number of hatchlings in one colony in the low Arctic (Russia) and two colonies in the high Arctic (Svalbard) between 2000 – 2016. During this period, the onset of spring advanced by 0.65 days per year due to an earlier spring thaw in all colonies, while geese advanced their laying dates with 0.43 days per year. Geese adjusted laying dates to yearly variations in snowmelt at pre-breeding and breeding sites, but did not adjust laying dates proportionally. In early snowmelt years, geese produced larger clutches but only slightly more hatchlings. In the high Arctic, where geese could avoid predation by nesting early, geese experienced higher nesting success in earlier springs, but not in the low Arctic. In the low Arctic, geese appeared to be more susceptible to phenological mismatches as they nested relatively late, on average 6.6 days after the date of snowmelt. We conclude that climate warming leads to potential benefits for barnacle geese nesting in the high Arctic, but less so for geese in the low Arctic.

## Introduction

Earth's climate has warmed rapidly in the past decades, resulting in warmer and earlier springs (Schwartz et al. 2006; Stocker et al. 2013). As a reaction, many migratory bird species have advanced their arrival on the breeding grounds (Jonzén et al. 2006) as well as their laying dates (Crick et al. 1997). A general concern is that this advance does not fully compensate any forward shifts of seasonal food abundance peaks (Thackeray et al. 2010; Gienapp et al. 2014). This inability to optimise timing of reproduction may lead to a so-called phenological mismatch (Both & Visser 2005) with potential negative consequences for fitness (Visser & Both 2005; Post et al. 2008; Doiron et al. 2015) but see (Reed et al. 2013a). However, an advancement of laying dates may also relieve current time constraints on the birds' reproductive cycle (Tomotani et al. 2016) with positive effects on reproductive success (Dickey et al. 2008; Van Oudenhove et al. 2014).

Especially in seasonal environments where the breeding season is short, migratory birds are on a tight schedule to raise their offspring and prepare for their return journey to the wintering grounds (Tomotani et al. 2017). Under an advancement of egg laying dates under climate warming, birds become less time-constrained as the length of their breeding season increases (Halupka et al. 2008). In earlier and warmer springs birds may be able to increase reproductive success (Moltofte et al. 2007), especially in the first stages of reproduction (Van Oudenhove et al. 2014). Earlier seasons may provide better conditions for foraging as food becomes available earlier (Lameris et al. 2017b), allowing more individuals to initiate nesting (Syroechkovskiy et al. 1991; Madsen et al. 2007; Dickey et al. 2008), birds to lay a larger clutch (Rowe et al. 1994; Van Oudenhove et al. 2014), and more pairs to hatch their clutch successfully (Prop & de Vries 1993). Climate warming thus may have positive effects on reproductive success by reducing time constraints, as well as negative effects by a phenological mismatch. As these opposing effects can take place within a single species (Dickey et al. 2008; Van Oudenhove et al. 2014), it may be difficult to make predictions on the eventual demographic effects of climate change (Miller-Rushing et al. 2010; Dunn & Møller 2014).

Opposite effects of climate change on fitness components may be particularly strong in the Arctic region, which is facing the most rapid climate warming on the planet (Stocker et al. 2013). Climate warming has advanced optimal conditions for reproduction (Post et al. 2008; Doiron et al. 2013), and in reaction animals have advanced their breeding season as well (Høye et al. 2007; Liebezeit et al. 2007). However, also in the Arctic at least some species do not advance enough to avoid phenological mismatches, leading to reductions in offspring survival (Clausen and Clausen 2013; Doiron et al. 2015; Chapter 7). On the other hand, animals breeding in the Arctic are typically constrained in time by a short breeding season, which is tightly delineated by the moment of snowmelt in spring and snowfall in autumn. This is illustrated by juvenile brent geese *Branta bernicla* found frozen in the ice with apparently nothing wrong but not fully grown flight feathers (Barry 1962).

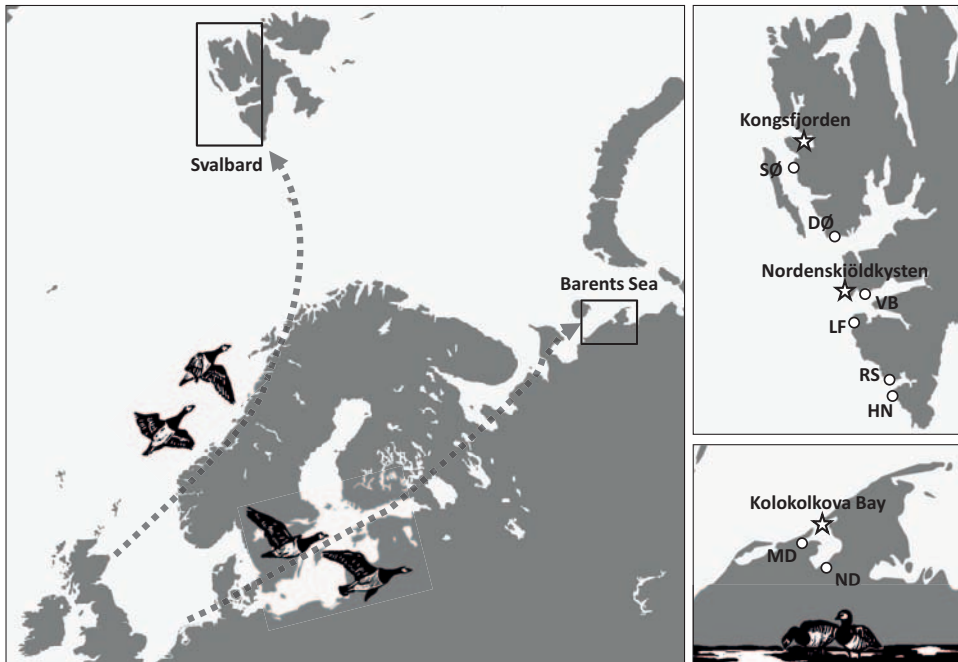
Climate warming has likely led to an increase in the length of the breeding season as the onset of spring is rapidly advancing with earlier snowmelt (Derksen & Brown 2012), but also as snow starts to fall later in the season (Callaghan et al. 2011). An increase in summer temperatures may also ameliorate conditions for chick growth and survival (Meltofte et al. 2007). When the Arctic climate warms and birds are able to advance their egg laying dates according to an earlier onset of spring, this may have strong positive effects on their reproductive success.

Here we investigate the potential positive effects of climate warming in barnacle geese *Branta leucopsis* nesting in different parts of the Arctic. Specifically, we studied to what extent barnacle geese adjust laying dates to earlier seasons, and whether earlier and longer Arctic breeding seasons are enhancing reproductive success. We focussed on the first parts of the reproductive cycle in which we expected a positive effect, the period between arrival close to the breeding grounds up to the moment of gosling hatch. We hypothesize that bird populations towards the North pole would be more time constrained as they experience an even shorter breeding season (Owen 1980; Klaassen et al. 2006). Therefore we expect that birds in the high Arctic respond stronger to an earlier onset of spring and benefit more from earlier springs in terms of reproductive success than birds at lower latitudes.

## Methods

### Study sites

Arctic-nesting barnacle Geese are divided into three flyway populations, with geese breeding in Eastern Greenland, Svalbard and along the Barents Sea coast, and wintering in the North Sea region (Madsen et al. 1999). Between 2000 – 2016 we studied barnacle geese in three breeding colonies, two located in the high Arctic (Svalbard) and one in the low Arctic (at the Russian coast of the Barents Sea): 1) on the islet Storholmen in Kongsfjorden (KF), Svalbard (78°55'N, 12°12'E); 2) on the islet Diabasøya and adjacent tundra at Nordenskiöldkysten (NSK), Svalbard (77°46'N, 13°42'E) and 3) surrounding the abandoned village of Tobseda at the Kolokolkova Bay (KB), Russia (68°35'N, 52°20'E, Figure 8.1). For logistic reasons, data collection in the different colonies took place in different years: Kongsfjorden (2000, 2001, 2003, 2005– 2016); Nordenskiöldkysten (2004, 2010 - 2016), Kolokolkova Bay (2003 – 2009, 2014, 2015). From positions of geese equipped with tracking devices (Tombre et al. 2017; Box B), we additionally determined staging sites which geese visit, before and after the breeding period (Hübner 2006). We identified 6 sites on Svalbard: from south to north; Hornsundneset (HN), Ralstrånda (RS), Lognedalsflya (LF), Vårsolbukta (VB), Daudmannsøyra (DØ), Sarsøyra (SØ); and 2 sites around the Kolokolkova Bay: Neruta river delta (ND) and Molotsnii river delta (MD); Figure 8.1). We grouped proximate staging sites which were closest to specific colonies: LF and VB for Nordenskiöldkysten, SØ for Kongsfjorden and ND and MD for Kolokolkova Bay.



**Figure 8.1:** Location of study colonies (stars) with pre- and post-breeding sites (white circles) in the high Arctic on Svalbard (right upper panel) and in the low Arctic at the Barents Sea coast (right lower panel). Dotted arrows indicate approximate migration routes. Staging site names are abbreviated: Barents Sea (ND = Neruta river delta, MD = Molotsnii river delta); Svalbard (HN = Hornsundneset, RS = Ralstrånda, LF = Lognedalsflya, VB = Vårsolbukta, DØ = Daudmannsøyra, SØ = Sarsøyra).

### Snow cover

We used the snow-free period between the moment of snowmelt (spring) and snowfall (autumn) as a proxy for the period during which geese can stay in the Arctic, as this determines the availability of forage plants (Prop & Vries 1993). Snowmelt appears to be an important driver of reproduction timing (Madsen et al. 2007) as it is thought to drive the phenology of Arctic plants (Livensperger et al. 2016) and may thus predict the moment of peak forage plant quality, to which geese should match hatching of their goslings (Chapter 7). Snowfall, on the other hand, puts a rigid end to feeding opportunities as it covers forage plants, forcing birds to leave their breeding grounds. We estimated daily snow cover for all study sites (table S1) for the period during which the day length was long enough to collect data at all sites (26 February – 30 September), for the years 2000 – 2016 using satellite images of the MODIS snow cover product (MOD10a2, Hall et al. 2006). To limit the effects of clouds obscuring the image, composite satellite images were generated over 8 days and, when possible, classified as snow, no snow, water or ice. A pixel (500 m resolution) was assigned as snow when classified as snow at least once during an eight day

period. With a spatial overlay of the breeding areas with the MODIS images the number of pixels classified as snow within the study site could be retrieved. Dividing this number of pixels by the total number of pixels in the breeding area resulted in the percentage of snow cover. We linearly interpolated between values from composite images to attain a daily percentage of snow cover. Even though images over 8 days were combined, we still encountered pictures with a high percentage of cloud cover obstructing reliable snow cover estimates, and we excluded images with a cloud cover exceeding 25%. From the snow cover data we extracted the date of snowmelt, which we defined as the first day of the season at which snow cover was less than 50%. Similarly, we calculated the moment of snowfall as the last day of the season at which snow cover was less than 30%. The date of 50% snow cover did often not fall before the last date at which data collection was possible. As first snow in the Arctic often co-occurs with a decrease in temperature, which conditions geese and swans probably use as a cue to depart, we consider that 30% snow cover is a good proxy for the end of the season. We calculated season length at the breeding colony as the difference between dates of snowfall and snowmelt.

### **Nesting parameters**

We determined lay date, clutch size, nest fate and number of hatchlings for as many nests as possible (table S2). The number of parameters estimated and the precise methodologies differed among breeding colonies. We collected data on egg laying dates and number of hatchlings in all colonies, data on nest fates (for nests with known laying dates) were collected in KB and NSK colonies, and data on clutch size in KB and KF colonies.

In KB colony we systematically searched for nests and checked known nests every 2 to 3 days during the laying and early incubation period (late May - late June). Eggs were marked and the number of eggs was recorded at every visit. Both in the KB and KF colony we visited nests in the early and mid-incubation period to determine final clutch size, which we determined as the total number of eggs in a nest when encountered with the same number of eggs during two subsequent visits. We excluded nests in which egg-dumping was evident (more eggs per interval than expected or additional eggs after clutch completion). We visited nests during and after hatch (mid June - late July) every 2 days to estimate day of hatch and record nest fate and number of hatchlings. We recorded nest fate as successful, predated, flooded or abandoned. A nest was considered as successfully hatched when at least one chick had hatched, which we determined either by presence of hatchlings at the nest on a visit, or presence of egg membranes and trampled sides of the nest (Davis et al. 1998). Empty nests, nests containing eggshells without membranes, were considered as predated, or considered flooded when the nest was partly under water. When we encountered a nest after the laying period containing cold eggs and without nest owners present, the nest was considered as abandoned. We recorded the number of hatchlings for all nests in which we observed 1) at least half the eggs in the process of

hatching (cracks, hatching or hatched chicks), or 2) when less than half of the eggs had successfully hatched (thus hatched chicks present) and other eggs did not show signs of hatching. For the number of hatchlings we assumed all eggs with sign of hatching as to become hatchlings.

At NSK, we observed the goose colony on an offshore island from an observation tower on the mainland, 200 meters away from the colony. Nests were monitored 6–16 h per day during the period that nesting geese were present. Nests in view of the tower were mapped on high-resolution images of the island, which enabled us to assess the breeding history of individual birds by visual observation from laying until hatching. 30–60% of the pairs was recognizable by coded leg rings (either one or both partners carrying a ring). As we did not find a difference in any of the parameters estimated between marked and unmarked pairs, all pairs were used in subsequent analyses. To avoid disturbance, the island was not visited during the incubation period and therefore clutch sizes were not determined. Nest fate was established from direct observations, and rated as successful (at least one gosling was seen at the nest and no predation of eggs or goslings was observed), predated (eggs or chicks taken by predator, most often polar bears *Ursus maritimus*), or abandoned (nest owners abandon the nest territory before the eggs hatched and prior to any predation event taking place – after nests were abandoned the eggs were usually taken by glaucous gull *Larus hyperboreus*). The number of hatchlings was recorded by visual observation of nests that successfully hatched. The first day that goslings were seen at the nest rim was taken as the date of hatch.

Not all nests were visited at hatch and therefore we did not acquire data on number of hatchlings for every successful nest. In order to combine nest fate and number of hatchlings into a measure of reproductive success, we calculated the total number of expected hatchlings per nest and laying date, per year and per colony, as the product of 1) fraction of hatched nests and 2) average number of hatchlings in successful nests.

### Determination of laying date

Methods to determine the date of egg laying (defined as the day at which the first egg was laid) differed between study sites. In KB, laying date was estimated by back calculation for clutches found during egg laying, assuming a laying interval of 33 hours, as follows: day of discovery when 1 egg was found; day of discovery minus 1 at 2 eggs; day of discovery minus 3 at 3 eggs; day of discovery minus 4 at 4 eggs (van der Jeugd et al. 2009). Both in KB and KF, laying dates were also back calculated from hatch date. Hatch date was estimated for clutches found in the process of hatching, hatch date was determined as follows: at least 1 egg cracked, day of observation plus 1; at least 1 egg with holes, hatching chick or chick still wet from hatching, day of observation; all chicks fluffy and no longer wet, day of observation minus 1. For back calculation we assumed a period of 29 days between lay date and hatch date (as derived from 573 nests in the KB colony between 2005 - 2015 for



which both lay and hatch date were determined). In NSK lay date was estimated as the first day during which a pair occupied a territory. Territories that were occupied for only one day were not considered in analyses.

The differing methods between study sites might affect the potential to make comparisons. In KB and NSK there is the possibility to verify laying dates by observing hatching dates, which should fall after 24 – 26 days of incubation (Dalhaug et al. 1996) and is initiated after the 3th egg is laid (which takes at least 3 days assuming 33h laying interval). We find an average interval between egg laying date and hatching date of 29 days in the KB colony and 30 days in the NSK colony (derived from 99 nests between 2010 – 2016), which gives us reason to believe that these methods are comparable. By back calculated laying dates from hatching dates as done for the KF colony, we do not take into account the laying dates of nests which do not hatch. This might influence the results, as nest failure can be higher in either early or in later laid nests (Prop & Vries 1993).

## Statistics

We tested relationships between snowmelt, laying dates and reproductive success by running generalized linear regression models (GLM) and generalized linear- mixed effect models (GLMM) with Gaussian distribution in R 3.0.2 (R Core Team, 2017), using the package “lme4” for mixed models (Bates et al. 2012). In GLMMs we added year and / or study site (all sites where we measured snow cover) as random factors. Candidate models were constructed from all possible combinations of predictor variables, including interactions which were considered ecologically meaningful. All mixed models were compared using Akaike’s information criterion (AICc; Burnham & Anderson, 2004) and we chose the model with the lowest AICc value as our final model. We tested for significance of fixed factors by comparing the final model with a reduced model in which the fixed factor was absent, using a likelihood ratio test. Besides predictor variables relating to snow cover, time and fitness components, we used predictor variables which separated high and low Arctic sites and staging and breeding sites, including ‘area’ (high or low Arctic), ‘site’ (all sites from which we gathered data on snow cover), ‘types of sites’ (southern staging sites / proximate staging sites / breeding colonies) and ‘colonies’ (the three breeding colonies under study).

First, to understand how the snow-free period differed between the high and the low Arctic and whether it changed over time, we ran GLMMs with date of snowmelt / snowfall / season length as response variable and time and area as predictor variables, with site as a random factor. To understand whether this period differed between breeding and staging sites, we ran GLMMs with date of snowmelt as an explanatory variable and types of sites as predictor variable, with site and year as random factors. We also tested correlation between snowmelt at colonies and pre-breeding sites in a GLMM, with year and area as random factors.



**Table 8.1:** Mean date of snowmelt / snowfall / mean season length ( $\pm$  SD), and change in snowmelt / snowfall / season length over time ( $\pm$  SD) for the southern and proximate staging sites (related to breeding colonies) and the breeding colonies itself.

	Colony	Southern staging site		Proximate staging site		Breeding colony	
		Mean date / length	Change, days per year	Mean date / length	Change, days per year	Mean date / length	Change, days per year
Snowmelt	KF	165 $\pm$ 7	-0.61 $\pm$ 0.33	173 $\pm$ 9	-0.78 $\pm$ 0.44	171 $\pm$ 10	-0.86 $\pm$ 0.44
	NSK	165 $\pm$ 7	-0.61 $\pm$ 0.33	169 $\pm$ 10	-0.78 $\pm$ 0.34	172 $\pm$ 9	-0.48 $\pm$ 0.43
	KB			151 $\pm$ 9	-0.53 $\pm$ 0.30	160 $\pm$ 9	-1.11 $\pm$ 0.35
Snowfall	KF	259 $\pm$ 7	0.15 $\pm$ 0.37	244 $\pm$ 10	-0.01 $\pm$ 0.51	248 $\pm$ 9	1.05 $\pm$ 0.34
	NSK	259 $\pm$ 7	0.15 $\pm$ 0.37	254 $\pm$ 11	0.62 $\pm$ 0.38	252 $\pm$ 11	0.57 $\pm$ 0.54
Season length	KB			261 $\pm$ 12	0.12 $\pm$ 0.41	252 $\pm$ 10	0.96 $\pm$ 0.46
	KF	94 $\pm$ 12	0.76 $\pm$ 0.56	72 $\pm$ 13	-0.76 $\pm$ 0.63	77 $\pm$ 15	1.91 $\pm$ 0.57
	NSK	94 $\pm$ 12	0.76 $\pm$ 0.56	86 $\pm$ 16	1.41 $\pm$ 0.52	80 $\pm$ 15	1.05 $\pm$ 0.71
	KB			110 $\pm$ 16	0.65 $\pm$ 0.54	91 $\pm$ 17	2.07 $\pm$ 0.68

Second, to understand how laying dates were affected by time and how this differed between colonies, we tested laying dates over time in a GLM with average yearly laying dates as a response variable and years as predictor variable, adding colony as a covariate. To understand how laying dates were affected by date of snowmelt, we ran GLMMs with yearly average laying date as response variable, date of snowmelt (in colonies / proximate staging sites), colony, and their interactions as predictor variables, and time as random factor. We tested whether the difference between laying dates and date of snowmelt at proximate pre-breeding sites differed between colonies by running a GLMM with this difference as explanatory variable and colony as predictor variable, and year as random factor.

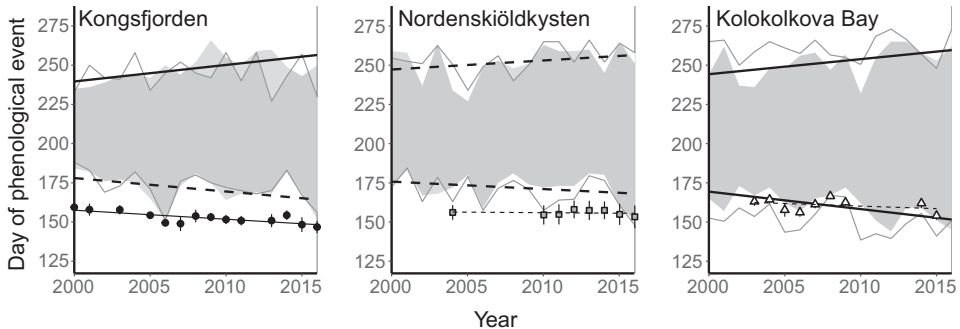
Third, we aimed to understand how laying date and date of snowmelt affected fitness components. We ran a GLMM with clutch size, number of hatchlings and the number of not-hatching eggs as explanatory variables, day of snowmelt and lay date, their interaction and colony as predictor variables, and year as a random factor. We tested the correlation between clutch size and number of hatchlings in a GLMM with year and site as random factors. We ran GLMs per colony with nest success and total expected hatchlings as explanatory variables and laying date, laying date squared (laying date<sup>2</sup>), date of snowmelt, and the interaction between date of snowmelt and laying date as predictor variables. For NSK we ran this analysis also excluding the years 2012 and 2014, when nest success was 0. We ran a similar analysis for total expected hatchlings per year (excluding date of snowmelt) to retrieve slopes per year per site. From these slopes we calculated the date at which the total expected number of hatchlings peaked for every year, which we compared with average laying date.

## Results

### Patterns of snowmelt and snowfall

The date of snowmelt occurred on average 16 days later in the high Arctic as compared to the low Arctic sites ( $F_{2,182} = 82.0$ ,  $p < 0.001$ , table 1). Between 2000 and 2015, the date of snowmelt advanced at similar rates in the high and the low Arctic, with 0.65 days per year ( $F_{1,181} = 82.0$ ,  $p < 0.001$ ). In the high Arctic colonies date of snowmelt was on average  $7 \pm 2$  days later than at the southernmost pre-breeding site HN ( $F_{1,46} = 6.0$ ,  $p = 0.006$ ), but did not differ from proximate pre-breeding sites ( $3 \pm 5$  days later in NSK relative to LF and VB;  $1 \pm 4$  days earlier in KF relative to SØ;  $F_{1,80} = 1.7$ ,  $p = 0.337$ ). In the low Arctic colony date of snowmelt was  $9 \pm 7$  days later compared to proximate pre-breeding sites ( $F_{1,46} = 48.5$ ,  $p < 0.001$ ). Date of snowmelt in the colonies was closely related to date of snowmelt on both the most southern ( $\beta: 0.89 \pm 0.19$ ,  $F_{1,29} = 22.8$ ,  $p = 0.002$ ) and proximate pre-breeding sites ( $\beta: 0.73 \pm 0.07$ ,  $F_{1,46} = 133.7$ ,  $p < 0.001$ ). The date of snowfall was  $5 \pm 3$  days earlier in the high Arctic than in the low Arctic ( $F_{1,182} = 3.1$ ,  $p = 0.131$ ). Between 2000 and 2015, date of autumn snowfall moved back in time at all sites at 0.40 days per year ( $F_{1,182} = 8.0$ ,  $p = 0.007$ ). As a

result of earlier spring snowmelt and later autumn snowfall, the snow-free period became longer over the years ( $\beta = 1.7 \pm 0.4$  days longer season per year,  $F_{1,46} = 7.2$ ,  $p < 0.001$ ), in total 25.5 days over the course of 15 years. This period was on average 13 days longer in the low Arctic ( $F_{1,46} = 10.2$ ,  $p < 0.001$ ).



**Figure 8.2:** Annual snow-free periods (indicated by grey area) for each of the barnacle goose colonies during 2000–2016. Linear trends over the years of dates of snow melt and snow fall are indicated by dashed black lines. Dates of snow melt and snow fall at the pre- and post-breeding sites are indicated by grey lines. Average lay dates ( $\pm$  SD) are indicated by symbols and associated error bars, linear trends by solid black lines.

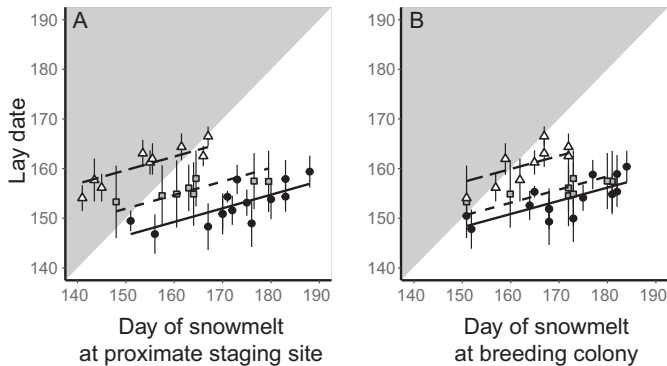
### Timing of reproduction

Both in the high and the low Arctic, barnacle geese advanced their egg laying dates at  $0.43 \pm 0.12$  days per year ( $F_{1,28} = 9.4$ ,  $p = 0.005$ ). Laying dates were positively related to snowmelt at proximate pre-breeding sites ( $\beta = 0.27 \pm 0.04$ ,  $F_{1,25} = 32.2$ ,  $p < 0.001$ , Figure 8.3a) and in colonies ( $\beta = 0.26 \pm 0.05$ ,  $F_{1,25} = 27.9$ ,  $p < 0.001$ , Figure 8.3b). The interaction between snowmelt and colonies Models containing only snowmelt at proximate pre-breeding sites gained higher support (Table S8.3), suggesting that this was a more important factor determining laying dates. We performed subsequent analyses with snowmelt on proximate pre-breeding sites. Surprisingly, laying date was inversely related to latitude, with geese in the high Arctic sites laying the earliest, and geese in the low Arctic laying up to 12 days later ( $F_{1,25} = 45.4$ ,  $p < 0.001$ , Figure 8.2). As a result, lower Arctic geese also laid their eggs closer to snowmelt (KB:  $7 \pm 3$  days after snowmelt, KF:  $20 \pm 2$  days before snowmelt, NSK:  $8 \pm 3$  days before snowmelt,  $F_{1,26} = 93.6$ ,  $p < 0.001$ , Figure 8.3a). The number of nests, as a measure of nesting effort, was not affected by snowmelt ( $F_{1,10} = 0.36$ ,  $p = 0.561$ ).

### Clutch size and number of hatchlings

Clutch size declined with laying date ( $\beta = 0.02 \pm 0.006$  egg per earlier laying date,  $F_{1,1908} = 11.7$ ,  $p < 0.001$ , Figure 8.4a), and was larger in years with earlier snowmelt ( $\beta = 0.04 \pm 0.006$  egg per earlier date of snow melt,  $F_{1,1908} = 43.0$ ,  $p < 0.001$ , Figure 8.4b). However, hatching

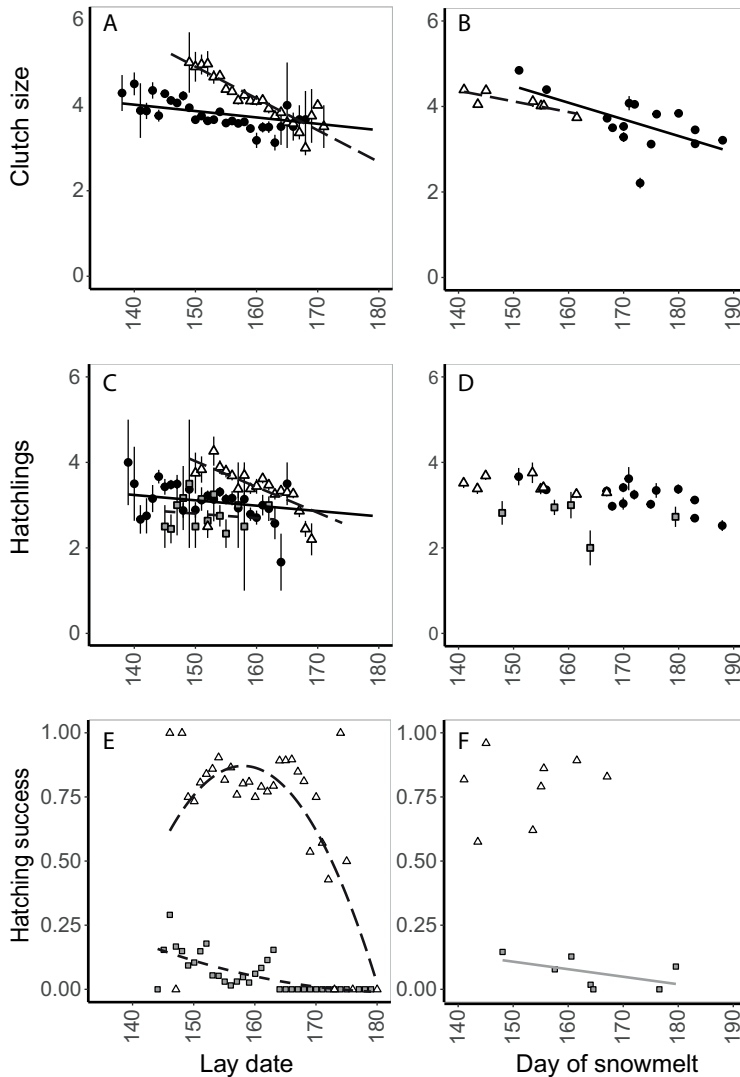
success of eggs (measured number of hatching goslings divided by clutch size) decreased with earlier snowmelt when correcting for lay dates ( $\beta = 0.07 \pm 0.02$  decrease in hatching success per earlier day of snowmelt,  $\chi^2 = 15.5$ ,  $p < 0.001$ ). The number of hatchlings was strongly correlated with clutch size ( $\beta = 0.79 \pm 0.02$ ,  $F_{1,1908} = 1446.9$ ,  $p < 0.001$ ), and declined with laying date ( $\beta = 0.04 \pm 0.005$  hatchling per earlier laying date,  $F_{1,2300} = 49.5$ ,  $p < 0.001$ , Figure 8.4c) but not with date of snowmelt ( $F_{1,2300} = 0.7$ ,  $p = 0.420$ , Figure 8.4d).



**Figure 8.3:** (A) Relationship between yearly average laying dates (shown with standard deviations) and date of snowmelt at proximate staging sites; (B) relationship between yearly average laying dates and date of snowmelt in breeding colonies. Lines show linear regressions, symbols and line types correspond to the three study sites: Kongsfjorden (black dots, solid lines), Nordenskiöldkysten (grey squares, dotted lines) and Kolokolkova Bay (white triangles, dashed lines).

### Nest success

In the high Arctic (NSK), nest success was zero in two years as all nests were predated by polar bears (2012 and 2014). When excluding these years (see Methods), nest success was higher for nests laid on earlier dates (lay date:  $\beta = -0.11 \pm 0.03$ ,  $F_{1,162} = 41.4$ ,  $p < 0.001$ ; lay date squared  $\beta = -0.034 \pm 0.013$ ,  $F_{1,162} = 12.6$ ,  $p < 0.001$ ; Figure 8.4e), but only in years with early snowmelt (interaction lay date and snowmelt:  $F_{1,162} = 6.7$ ,  $p = 0.010$ , Figure 8.4e, f). As a result, the expected number of hatchlings peaked in early laid nests in years with an early snowmelt, while the number was invariably low in years with late snowmelt (Figure 8.5). In the low Arctic, hatching success and expected number of hatchlings was highest on intermediate dates (lay date:  $\beta = 0.49 \pm 0.12$ ,  $F_{1,143} = 3.2$ ,  $p = 0.076$ ; lay date  $^2$ :  $\beta = -0.002$ ,  $F_{1,143} = 15.8$ ,  $p < 0.001$ , Figure 8.4e) and was not affected by date of snowmelt ( $F_{1,143} = 1.5$ ,  $p = 0.221$ ; Figure 8.4f). When comparing peak date of expected number of hatchlings with average laying dates, we find that in the high Arctic site, geese appeared to nest too late relative to the date of peak expected success in years with earlier snowmelt, while in the low Arctic site, geese generally appeared to nest in sync with the date of peak expected success (Figure 8.5, Figure S8.1).



**Figure 8.4:** Clutch size (A; B), number of hatchlings (C; D) and hatching success (E; F) for different lay dates (all years combined, A; C; E) and in years differing in the date of snowmelt at proximate pre-breeding sites (B; D; F). Lines show linear regressions, symbols and colours correspond to the three study sites: Kongsfjorden (black dots, solid lines), Nordenskiöldkysten (grey squares, dotted lines) and Kolokolkova Bay (light grey triangles, dashed lines). In E, the expected number of hatchlings is depicted for KB for all years, and for NSK only for years when hatching success was above 0.

## Discussion

Barnacle geese advanced laying dates in response to earlier springs, but at a slower rate than the advance in date of snowmelt. In these earlier springs, geese benefitted from improved foraging conditions prior to breeding, as they were able to lay larger clutches. However, this did not result in more hatching goslings, as hatching success of eggs decreased in earlier springs. Nest success was positively affected by earlier springs in the high Arctic, where early nesting geese could avoid nest predation, but not in the low Arctic, where both early and late nests suffered from nest predation. Overall, high Arctic geese gained reproductive benefits from earlier springs, but low Arctic geese did not. As a matter of fact, early springs may make low Arctic geese more prone to suffer from phenological mismatches, as they nest later relative to the onset of spring than their high-Arctic counterparts. Negative and positive effects of climate warming may importantly differ for birds nesting in high and low Arctic regions.

### Advance of egg laying in high- and low-Arctic

During the past 15 years, Arctic-breeding barnacle geese advanced egg laying by 0.43 days per year, coinciding with an advancement of the onset of spring (date of snowmelt) on the breeding grounds by 0.65 days per year. Although this suggests that geese keep track of earlier springs on the long term, geese show a much smaller response (with a slope of 0.27, Figure 8.3) in adjusting laying dates to yearly variations in the onset of spring. Egg laying dates of birds have been repeatedly shown to advance under climate warming in temperate regions (Crick et al. 1997; Parmesan & Yohe 2003), and more recently also for Arctic migrants (Høye et al. 2007; Saalfeld & Lanctot 2017). The strong correlation between the date of snowmelt and egg laying dates suggests that barnacle geese indeed advance their egg laying dates as a reaction to an earlier date of snowmelt in the Arctic, but seem to advance at a slower rate than the onset of spring (Barry 1962; Prop & Vries 1993; Lindberg et al. 1997; Bêty et al. 2003). Birds typically advance egg laying dates slower than the advance of their food peaks (Gienapp et al. 2014), as they may face constraints which limit them adequate adjustments of laying date. Long-distance migrants such as barnacle geese may be constrained to advance laying as they do not arrive earlier at their breeding grounds (Both & Visser 2001). However, barnacle geese breeding in the low Arctic have been found to advance their arrival under earlier springs (Chapter 7). After arrival, geese may also need time to build up body stores locally before laying (Prop & Vries 1993; Prop et al. 2003; Hahn et al. 2011) and an advance in egg laying may be constrained by local feeding opportunities (Prop & Vries 1993; Hübner 2006; Hübner et al. 2010). This is also stressed by our finding that laying dates correlate with date of snowmelt at proximate staging sites, it is difficult to separate the effects of date of snowmelt at staging sites and in the breeding colony. Potentially, timing of egg-laying is primarily determined by the

moment of snowmelt at pre-breeding site, as this determines food availability, and fine-tuned by date of snowmelt in the breeding colony, which allows nest initiation (Hübner et al. 2010).

Surprisingly, average dates of laying in the three study colonies were inversely related to latitude, with geese in the most northern colony laying eggs earlier than in the southern colony. This is in contrast to the general finding in birds that the onset of egg laying is later at higher latitudes (Owen 1980). There may be several mechanisms which allow high Arctic geese to lay earlier than their low Arctic conspecifics. First of all, high and low Arctic geese may differ in the amount of endogenous body stores which they carry with them to the breeding grounds. In the high Arctic, earliest nesting geese draw heavily from endogenous body stores for egg production (Hahn et al. 2011), which allows them to breed shortly after arrival. In the low Arctic, the earliest nesting geese use much more local resources for egg production (Pokrovskaya et al. 2011; Chapter 7), suggesting that nesting only takes place after geese have accumulated body stores close to the breeding grounds. Additionally, earlier laying dates in the high-Arctic can be attributed to the ability of geese to benefit from low-quality mosses and woody plants in the absence of high-quality graminoids, which are thought to be the reason why herbivores like geese are able to occupy most northern parts of the tundra (Prop & Vulink 1992). These low-quality plants form a substantial part of the phytomass in the high Arctic tundra system and are among the food plants available as soon as snow melt starts (Prop & Vries 1993; de Fouw et al. 2016), giving geese a chance to exploit food resources as soon as the first spots of the tundra become uncovered from snow and well before the onset of the growth of more nutritious graminoids. In the coastal low-Arctic occupied by barnacle geese, an early surge of low-quality food is lacking and geese depend entirely on the development of high-quality food (van der Graaf et al. 2004, 2006), which starts growing only after snow has already melted (Prop & Vries 1993).

### **Climate change effects on fitness components**

Under an earlier onset of spring breeding propensity is known to increase in Arctic geese (Madsen et al. 2007; Dickey et al. 2008). Fewer barnacle geese indeed seem to nest in years with a late onset of spring (Syroechkovskiy et al. 1991), but we did not find an effect of the onset of spring on the number of recorded nests.

Barnacle geese increased their clutch size with earlier lay dates and with an earlier date of snowmelt. A seasonal decline in clutch size is common in geese and birds in general (Crick et al. 1993; Rowe et al. 1994; Dalhaug et al. 1996). This is thought to result from a decrease in offspring value as the season progresses, which would drive late laying birds to invest less in reproduction (Drent & Daan 1980; Rowe et al. 1994). As laying dates advanced, larger clutches can be expected from the strong relationship between laying date and clutch size (Winkler et al. 2002). In earlier and warmer springs, larger clutches

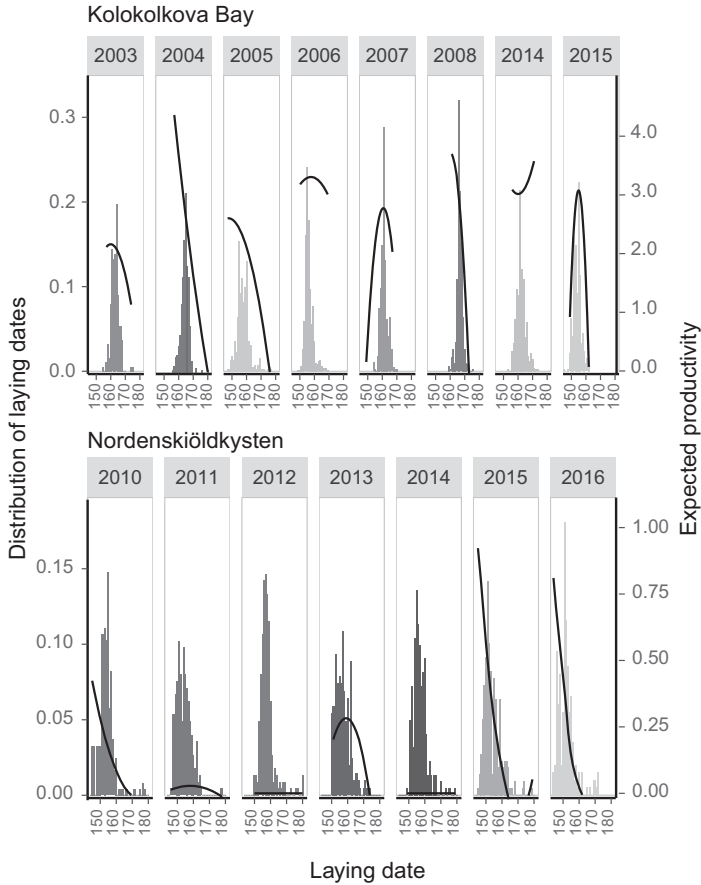


have often been found in other species of geese (Barry 1962; Dalhaug et al. 1996; Bêty et al. 2003; Van Oudenhove et al. 2014). If geese do not proportionally advance their laying dates with local snowmelt, local forage plants become available to them prior to breeding in early seasons (Prop & Vries 1993). As they can use extra income to lay a larger clutch, a delay of laying dates relative to the date of snowmelt may be an optimal decision to increase reproductive output (Rowe et al. 1994).

Despite a positive effect of earlier springs on clutch size, we did not find an increase in the number of hatchlings in earlier springs. Due to a decrease in hatching success in earlier seasons, the number of hatchlings did not differ between early and late springs. A decrease in hatching success can be caused by factors on the population level, if nests with large clutches have an increased chance of being depredated in early years, or on the level of the individual nest, when single egg predation or the number of unfertilized eggs (Cooke et al. 1995) is proportional to the clutch size (thus larger clutches losing more eggs). Single egg predation by glaucous gulls is common in both colonies in which we measured clutch size (Tombre & Erikstad 1996; Dorofeev et al. 2013), and a proportional chance of egg predation with clutch size might indeed be possible.

Nesting success was strongly associated with laying date, with more successful nests at intermediate laying dates in the low Arctic and at early laying dates in the high Arctic. In the low Arctic, nesting success was not influenced by earlier springs, but in the high Arctic, nesting success was higher in earlier springs. During the study period, failure of nests in Arctic geese was primarily caused by nest predation, mostly by glaucous gulls (van der Jeugd et al. 2003), but also by Arctic foxes *Vulpes lagopus* (Jensen et al. 2014) and polar bears (Prop et al. 2015). In the low Arctic, geese which settle before the peak in laying dates may experience an increased predation pressure, as they are one of the few birds which have started nesting by this time (Findlay & Cooke 1982). Birds which settle after the peak may similarly experience higher predation pressure, or may be birds of lower quality which are more prone to nest predation or to abandon their nest. In the high Arctic, nesting success of early laid nests of barnacle geese was relatively low in the past, explained by the potentially small fat reserves of early laying geese which allowed less time for nest attendance and protection (Prop & Vries 1993; Spaans et al. 2007). Currently, we find early laid nests to be the most successful, which is likely caused by the arrival of a new predator moving southwards under climate warming (Prop et al. 2015). Since the 2000s, the most important predators are polar bears which enter the colony from mid-June onwards to predate substantial numbers of nests in the colony (Prop et al. 2015). Early laid nests have a chance to hatch in time and escape predation, explaining why nesting success is positively affected by earlier lay dates and an early onset of spring, when birds are able to nest relatively early. As such, the window during which nests successfully hatched did not become longer, and especially late nests experienced a very low nesting success in the high Arctic. At the same time, polar bears are advancing the date at which

they first enter the colonies (Prop et al. 2015), and it is thus the question whether geese are able to advance their laying dates enough to keep escaping predation pressure.



**Figure 8.5:** Distribution of laying dates (bars) in Kolokolkova Bay and Nordenskiöldkysten by year. The timing of snow melt is indicated by intensity of shading of the bars (dark grey – late snowmelt, light grey – early snowmelt). Black lines result from linear models of expected number of hatchlings.

### Selection for earlier laying

When organisms do not advance their reproduction phenology at the same rate as their food under climate warming, there can be strong selection pressure for earlier breeding, especially in earlier seasons (van Noordwijk et al. 1995; Both & Visser 2001; Gienapp et al. 2014). On the other hand, earlier seasons may allow more time for adults to prepare for breeding and for offspring to grow, causing selection pressure to be lower in earlier seasons (Tomotani et al. 2016). For geese and other large bird species with long lifespans,

adjustment of phenology under rapid climate warming is more importantly determined by phenotypic plasticity via social learning (Visser 2008; Mueller et al. 2013; Teitelbaum et al. 2016) than through genetic change, and these birds may optimize migration and reproduction timing by learning (Madsen 2001; Agostini et al. 2017). The framework of selection pressure can help us to understand whether geese advance laying dates enough in relation to the climate warming (e.g. Clermont et al. 2017). As we only investigated reproductive success up to gosling hatch, our measure of reproductive success is mostly affected by nest and single egg predation, and does not take into account a potential phenological mismatch that acts primarily on the growing goslings, and hence on fledging success and subsequent gosling survival. In the low Arctic colony, we find little difference between years in selection pressure (as found also by van der Jeugd et al. 2009), suggesting that the ability of geese to synchronize laying dates with peak expected hatching success is not affected by snowmelt. In the high Arctic colony NSK, peak reproductive success always occurred early in the season. While this is the result of extremely high predation pressure of polar bears as discussed above, a similar pattern can be expected when seasons are extremely short. Consistent pressure for earlier breeding under a short season may drive the continuous advance of laying dates in the other high Arctic colony (KF).

### Sensitivity to mismatches

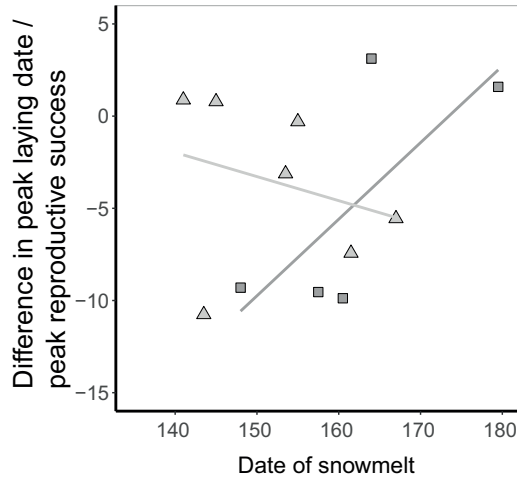
We find that while high-Arctic geese start laying eggs well before the date of snowmelt on pre-breeding sites and in the colony, low-Arctic geese start laying only after the date of snowmelt. This may have important consequences for their sensitivity to a phenological mismatch. Phenology of plants in the Arctic is importantly determined by snowmelt (Livensperger et al. 2016; Semenchuk et al. 2016). While forage plants respond directly to snowmelt, sprouting right after snow has melted (Livensperger et al. 2016), geese show a much slower advancement in their adjustment of laying dates, which may result in a phenological mismatch between peak forage plant quality and the moment of gosling hatch (Doiron et al. 2015). It has indeed been found that low-Arctic barnacle geese suffer from a phenological mismatch in early springs which reduces gosling survival (Chapter 7). For high-Arctic barnacle geese, goslings may still hatch prior to the peak in forage plant quality, as laying dates fall well before the date of snowmelt.

### Conclusions

While the heterogeneity of climate warming effects has been recognized (Gilg et al. 2012), high Arctic communities are often considered to be especially vulnerable to climate warming by disruption of trophic interactions (Høye et al. 2007; Post et al. 2009). In contrast, here we show that climate warming may potentially have stronger negative effects on reproductive success of low-Arctic barnacle geese in comparison to high-Arctic geese, as low Arctic birds do not benefit from earlier springs in the number of

hatching goslings, and in fact run a greater risk of facing a phenological mismatch as they nest late in comparison to the date of snowmelt. In the high Arctic barnacle geese are able to breed much earlier as they can profit from low quality food available before all snow has melted, and seem to even benefit from increased nesting success in earlier springs, as has been found before in high Arctic snow geese *Anser caerulescens* (Dickey et al. 2008; Van Oudenhove et al. 2014). For both high and low Arctic barnacle geese, the potential reproductive benefits of reproducing early in the season appear to be rather limited as hatching success decreased in all colonies with earlier seasons. Combined with the increased risk of facing phenological mismatches with potential strong reductions of fitness, negative effects of climate warming for Arctic bird populations predominate.

## Supplementary material



**Figure S8.1:** Difference between average laying date and peak date of reproductive success (measured as expected hatchlings) for different dates of snowmelt at proximate pre-breeding sites, for the high Arctic (NSK: dark grey squares) and the low Arctic (light grey triangles).

**Table S8.1:** Pre-breeding sites and colonies for which snow cover data was determined, including size of the sites in pixels as used for MODIS and in km<sup>2</sup>. As snow cover could not be estimated for the island of Storholmen, we used two adjacent sites (totalling 16 km<sup>2</sup>).

Area	Area type	Number of pixels	Surface area (km <sup>2</sup> )	Longitude	Latitude
Kolokolkova Bay (KB)	Breeding	168	42	68°35'51.60"N	52°20'12.45"E
Nordenskiöldkysten (NSK)	Breeding	361	90.25	77°47'18.59"N	14°5'51.05"E
Kongsfjorden (KF)	Breeding	64	16	78°57'42.19"N	12°4'9.87"E
				78°50'57.97"N	11°50'19.14"E
Molotsnii delta (MD)	Staging	320	80	68°30'1.49"N	52°0'58.65"E
Neruta delta (ND)	Staging	370	92.5	68°17'4.35"N	52°16'39.79"E
Hornsundneset (HN)	Staging	78	19.5	76°52'1.13"N	15°34'56.68"E
Ralstrända (RS)	Staging	83	20.75	77°1'24.45"N	15°11'35.85"E
Lognedalsflya (LF)	Staging	90	22.5	77°30'4.56"N	13°56'5.96"E
Vårsolbukta (VB)	Staging	73	18.25	77°46'2.70"N	14°15'18.91"E
Daudmannsøyra (DØ)	Staging	113	28.25	78°12'44.16"N	13°25'44.25"E
Sarsøyra (SØ)	Staging	84	21	78°45'23.00"N	11°40'10.35"E

**Table S8.2:** Number of nests for which data was available on laying date, nest fate, clutch size and number of hatchlings, grouped per colony and year.

Colony	Year	Laying date	Nest fate	Clutch size	Hatchlings
NSK	2010	336	336		19
NSK	2011	225	225		4
NSK	2012	317	317		
NSK	2013	226	226		12
NSK	2014	289	289		
NSK	2015	225	225		17
NSK	2016	236	236		22
KF	2000	158		131	46
KF	2001	282		246	159
KF	2003	113		23	
KF	2005	25		25	21
KF	2006	73		71	42
KF	2007	71		73	32
KF	2008	128		116	83
KF	2009	142		135	95
KF	2010	170		156	102
KF	2011	172		126	73
KF	2012	214		212	119
KF	2013	136		107	54
KF	2014	220		195	118
KF	2015	295		260	130
KF	2016	312		274	170
KB	2003	153	153	76	37
KB	2004	355	355	220	161
KB	2005	344	344	170	86
KB	2006	553	553	404	147
KB	2007	316	316	122	85
KB	2008	446	446		109
KB	2014	450	450	450	252
KB	2015	380	380	276	114

**Table S8.3:** Generalized linear mixed models for date of snowmelt, date of snowfall, season length, laying date, amount of nests, clutch size, number of hatchlings, and hatching success of eggs. Models include random effects of year (Y) and site (S). Coefficient values are given for fixed effects, and models are ordered from lowest to highest  $AIC_c$  values.

	Intercept	Country (C)	Year (Y)	Interaction (C*Y)	degrees of freedom	Log likelihood	$AIC_c$	$\Delta AIC_c$
<b>Snowmelt (SM)</b>								
SM ~ C + Y + (S)	1468	16.03	-0.65		5	-666.9	1344	0
SM ~ C + Y + C*Y + (S)	1605	-171.2	-0.72	0.09	6	-666.8	1346.1	2.0
SM ~ Y + (S)	1480		-0.65		4	-676.0	1360.1	16.1
SM ~ C + (S)	154	16.03			4	-679.8	1367.9	23.8
<b>Snowfall (SF)</b>								
SF ~ C + Y + (S)	-544	-5.38	0.40		5	-698.6	1407.5	0.0
SF ~ Y + (S)	-548		0.40		4	-700.0	1408.2	0.7
SF ~ C + Y + C*S + (S)	-548	-0.25	0.40	-0.003	6	-698.6	1409.6	2.1
SF ~ C + (S)	258	-5.38			4	-702.2	1412.7	5.2
<b>Season Length (SL)</b>								
SL ~ C + Y + (S)	-3280	-13.06	1.68		5	-202.2	415.7	0.0
SL ~ C + Y + C*Y + (S)	-4072	1175.50	2.07	-0.59	6	-201.9	417.7	2.0
SL ~ Y + (S)	-3289		1.68		4	-205.5	420	4.2
SL ~ C + (S)	91	-13.06			4	-211.1	431	15.3



Table S8.3: Continued

Laying date (LD)										
Intercept	Site (S)	Snowmelt (SM)	Snowmelt breeding (SMP)	Interaction (S*SM)	Interaction (S*SMP)	degrees of freedom	Log likelihood	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	
LD ~ SMP + S + (Y)	107	12.06	0.27			6	-66.5	148.5	0.0	
LD ~ SM + S + SMP + SMP*S + (Y)	109	29.18	0.03	0.29		9	-62.6	151.7	3.2	
LD ~ SM + S + SMP + (Y)	107	4.48	0.01			7	-66.5	151.9	3.4	
LD ~ SM + S + SMP + SM*S + (Y)	105	30.01	0.06	0.28		9	-63.7	154.0	5.5	
LD ~ SM + S + (Y)	108	9.06	0.27			6	-69.6	154.6	6.1	
LD ~ SM + S + SMP + SM*S + SMP*S + (Y)	116	30.66	0.24	-0.4	0.5	11	-61.5	158.8	10.3	
LD ~ S + (Y)	154	7.13				5	-78.3	169.0	20.4	
LD ~ SM + (Y)	133		0.14			4	-89.2	187.9	39.4	
LD ~ SMP (Y)	157		0.00			4	-90.5	190.6	42.1	

Total clutch size (TC)

Total clutch size (TC)										
Intercept	Laying date (LD)	Site (S)	Snowmelt pre-breeding (SMP)	Interaction (LD*SMP)	degrees of freedom	Log likelihood	AIC <sub>c</sub>	ΔAIC <sub>c</sub>		
TC ~ LD + S + SMP + LD*SMP + (Y)	83.4	-0.47	-0.13	0.003	7	-2526.6	5067.2	0.0		
TC ~ LD + S + SMP + (Y)	14.1	-0.02	-0.41		6	-2542.3	5096.7	29.5		
TC ~ LD + SMP + (Y)	12.5	-0.03	-0.03		5	-2544.8	5099.5	32.3		
TC ~ S + LD + SMP + (Y)	11.4		-0.63		5	-2548.1	5106.2	39.0		
TC ~ SMP + (Y)	7.5		-0.02		4	-2557.1	5122.1	54.9		
TC ~ S + LD + (Y)	8.4	-0.03	0.60		5	-2564.8	5139.6	72.4		
TC ~ S + (Y)	3.7		0.39		4	-2576.1	5160.2	93.0		
TC ~ LD + (Y)	4.0	0.00			4	-2595.5	5199.1	131.9		

**Table S8.3:** Continued

Number of hatchlings (TH)									
	Intercept	Laying date (LD)	Site (S)	Snowmelt pre-breeding (SMP)	Interaction (LD*SMP)	degrees of freedom	Log likelihood	AIC <sub>c</sub>	Δ AIC <sub>c</sub>
TH ~ LD + S + (Y)	9.4	-0.04	0.97			6	-3499.0	7010.0	0.0
TH ~ LD + S + SMP + SMP*LD + (Y)	30.9	-0.18	0.97	-0.13	0.001	8	-3497.1	7010.2	0.2
TH ~ LD + S + SMP + (Y)	9.5	-0.04	0.92	0.00		7	-3498.7	7011.5	1.5
TH ~ LD + SMP + (Y)	10.0	-0.02		-0.02		5	-3513.1	7036.2	26.2
TH ~ S + SMP + (Y)	5.9		-0.53	-0.02		6	-3514.5	7041.1	31.0
TH ~ SMP + (Y)	5.6			-0.01		4	-3522.0	7052.0	42.0
TH ~ S + (Y)	3.2		0.7			5	-3522.7	7055.4	45.4
TH ~ LD + (Y)	5.0	-0.01				4	-3535.5	7079.0	68.9

Difference clutch / hatchlings (DCH)									
	Intercept	Laying date (LD)	Site (S)	Snowmelt pre-breeding (SMP)	Interaction (LD*SMP)	degrees of freedom	Log likelihood	AIC <sub>c</sub>	Δ AIC <sub>c</sub>
DCH ~ LD + S + SMP + SMP*LD + (Y)	52.1	-0.31	-0.33	-0.31	0.002	7	-2417.7	4849.5	0.0
DCH ~ S + SMP + (Y)	4.1		-0.44	-0.02		5	-2428.4	4866.9	17.4
DCH ~ LD + S + SMP + (Y)	3.3	0.01	-0.55	-0.02		6	-2427.5	4867.0	17.6
DCH ~ SMP + (Y)	1.5			-0.01		4	-2436.8	4881.6	32.1
DCH ~ LD + SMP + (Y)	2.5	-0.01		-0.01		5	-2436.2	4882.4	32.9
DCH ~ S + (Y)	0.6		0.02			4	-2439.9	4887.9	38.4
DCH ~ LD + (Y)	0.5	0.00				4	-2440.0	4888.0	38.5
DCH ~ LD + S + (Y)	0.7	0.00	0.03			5	-2439.9	4889.9	40.4

**Table S8.3:** Continued

Amount of nests (NN)							
	Intercept	Site (S)	Snowmelt pre-breeding (SMP)	degrees of freedom	Log likelihood	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>
NN ~ S + (Y)	201	184.6		4	-86.4	184.9	0.0
NN ~ S + SMP + (Y)	441	159.5	-1.43	5	-86.2	189.1	4.3
NN ~ (Y)				3	-92.0	192.3	7.4
NN ~ SMP + (Y)	1739		-9.10	4	-90.3	192.6	7.7

**Table S8.4:** Generalized linear models for nest success and total number of expected hatchlings, run separately for Kolokolkova Bay (KB) and Nordenskiöldkysten (NSK). Covariates include laying date, laying date squared and the date of snowmelt at proximate staging site. Also the interaction between laying date and date of snowmelt is included in the model concerning nest success at NSK. Given are degrees of freedom, sum of squared, mean square, F – statistic and P value.

Nest success KB						
	degrees of freedom	Sum Squares	Mean Square	F	P	
laydate	1	0.24	0.24	3.2	0.076	
Snowmelt staging	1	0.11	0.11	1.5	0.221	
Laydate ^ 2	1	1.10	1.10	14.6	<b>0.000</b>	
Residuals	143	10.80	0.08			
Total number of hatchlings KB						
	degrees of freedom	Sum Squares	Mean Square	F	P	
laydate	1	12.57	12.57	10.4	<b>0.002</b>	
Snowmelt staging	1	10.12	10.12	8.4	<b>0.005</b>	
Laydate ^ 2	1	18.79	18.79	15.6	<b>0.000</b>	
Residuals	110	132.32	1.20			
Nest success NSK						
	degrees of freedom	Sum Squares	Mean Square	F	P	
laydate	1	0.30	0.30	41.4	<b>0.000</b>	
Snowmelt staging	1	0.01	0.01	0.8	0.379	
Laydate ^ 2	1	0.09	0.09	12.6	<b>0.001</b>	
interaction laydate x snowmelt staging	1	0.05	0.05	6.7	<b>0.011</b>	
Residuals	162	1.17	0.01			
Total number of hatchlings NSK						
	degrees of freedom	Sum Squares	Mean Square	F	P	
laydate	1	2.26	2.26	34.7	<b>0.000</b>	
Snowmelt staging	1	0.09	0.09	1.4	0.241	
Laydate ^ 2	1	0.74	0.74	11.4	<b>0.001</b>	
Residuals	159	10.33	0.06			