Outflying climate change

Optimal timing of migratory geese breeding in a warming Arctic

Lameris, T.K.

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CHAPTER 7

Arctic geese tune migration to a warming climate but still suffer from a phenological mismatch

Thomas K. Lameris, Henk P. van der Jeugd, Götz Eichhorn, Adriaan M. Dokter, Willem Bouten, Michiel P. Boom, Konstantin E. Litvin, Bruno J. Ens, Bart A. Nolet

ABSTRACT

Climate warming challenges migratory organisms to advance timing of migration and reproduction. Advancement of spring migrating might be achieved by reducing stopover time, but only in capital-breeding migrants, which use stopovers not only to fuel migration but also to acquire endogenous body stores needed for reproduction. By connecting long-term tracking and reproduction data, we show that a long-distance migratory bird (barnacle goose Branta leucopsis) accelerates its 3000 km spring migration to advance arrival on its rapidly warming Arctic breeding grounds. However, as egg laying has advanced much less than arrival, they still encounter a phenological mismatch that reduces offspring survival. A shift towards using more local resources for reproduction suggests that geese first need to refuel body stores at the breeding grounds after accelerated migration. While flexibility in the use of body stores allows migrants to accelerate migration, this cannot solve the time constraint they are facing under climate warming.

Introduction

Under contemporary climate warming many animals have advanced their timing of reproduction (Parmesan & Yohe 2003), but typically advance at a slower rate than their food species (Høye et al. 2007; Thackeray et al. 2010). This can give rise to a mismatch between the moment of largest food requirements for their offspring and peak food availability (Visser & Both 2005; Doiron et al. 2015; Lameris et al. 2017b), with potentially far-reaching consequences up to population levels (Clausen & Clausen 2013). For long-distance migrants, adjustment of migration and reproduction phenology to climate warming may be hampered by their inability to predict conditions at breeding grounds at the moment of departure from the wintering grounds (Kölzsch et al. 2015). Some migratory birds, however, have shown the ability to advance arrival time by accelerating migration speed when encountering advanced phenological conditions *en route* (Ahola et al. 2004; Marra et al. 2005). A recent study suggests that a sufficient advance in arrival by acceleration of migration speed, resulting from reduced time on stopover sites, is unfeasible for long-distance migrants (Schmaljohann & Both 2017). Strong reductions in stopover time are indeed unlikely, given that this study considers stopover time only to be determined by the energy requirements for the following bout of flight. However, many long-distance migrants breeding in the polar regions also use stop-overs to acquire body stores, which they use on the breeding grounds to fuel reproduction (Klaassen et al. 2006; Drent et al. 2007; Kölzsch et al. 2016a). As these energy stores are not essential to complete their migratory journey, we hypothesize that these capital-breeding migrants have leeway to reduce stopover time and to advance arrival under climate warming by accelerating migration speed.

By combining remote sensing, bird tracking, stable isotope techniques and field observations along the entire flyway, we studied the effect of climate warming on migration and breeding phenology of barnacle geese, *Branta leucopsis*. Barnacle geese are herbivorous long-distance migrants that travel every spring from their temperate wintering and staging grounds along the North Sea coast via stop-over sites along the Baltic and Barents Sea to their breeding grounds in the Russian Arctic (Figure 7.1a). In the past decades, higher spring temperatures have caused an increasingly early onset of snowmelt in their Arctic breeding grounds (Figure S7.1; Derksen and Brown 2012; Stocker et al. 2013). The onset of snowmelt frees nesting sites of snow and triggers plant growth, which peaks in quality approximately one month after snowmelt (Figure S7.2; Doiron et al. 2015). To match the moment of gosling hatch with the peak in food quality, barnacle geese should thus aim to lay their eggs right after snowmelt (Drent et al. 2007).

Results

During six years between 2004 and 2015, we used tracking devices to study timing of spring migration in female barnacle geese nesting in colonies at the mouth of Kolokolkova Bay and on Kolguev Island (Figure 7.1a). We found that barnacle geese did not adjust their departure date from the temperate stop-over sites in the North Sea and Baltic Sea to match earlier snowmelt at the breeding grounds (Figure 7.1b; North Sea (blue line): t_{64} = -1.395, p = 0.31; Baltic Sea (yellow line): t_{67} = -0.479, p = 0.63), and in some years geese departed from the Baltic Sea only after snow had already melted in the Arctic. Nevertheless, geese arrived up to 13 days earlier at the breeding site in years with earlier snow melt (Figure 7.1b, red line: regression coefficient β = 0.51 ± 0.05 day earlier per day of earlier snowmelt, t_{53} = 10.18, p < 0.001), although not early enough to fully compensate for the earlier date of snowmelt (date of arrival ≠ date of snowmelt, t_{53} = -9.62, p < 0.001). In years with early snowmelt, barnacle geese thus accelerated migration during the second leg of their migratory flight (Figure 7.1c: β = 5.77 km/day faster per day of earlier snowmelt ± 1.25, t_{53} = -4.67, p = 0.003), spending less time refuelling at Artic stop-over sites (Figure S7.3). In 2015, the year with the earliest date of snowmelt in our dataset, some individuals performed an almost non-stop migration from the wintering grounds to the breeding grounds (Figure S4) and reached speeds of up to 500 km day^{-1}, six-fold faster than expected speeds of c. 70 km day^{-1} (including necessary stop-overs) for a bird of this size (based on allometric relationships with flight speed and fuelling rate; Nolet 2006). Geese also advanced their egg laying dates in response to earlier snowmelt (Figure 7.1b, black line: β = 0.35 day earlier per day of earlier snowmelt ± 0.03, t_{53} = 10.33, p = 0.004), but this advancement was less than the advancement in arrival date ($F_{1,91}$ = 10.39, p = 0.005) so that geese undertook a longer 'pre-breeding' period between arrival and egg-laying.

When snow melted early, geese started laying their eggs well after the moment of snowmelt (Figure 7.1b), which resulted in an increased phenological mismatch between the moment of gosling hatch and the peak in food quality. In years with early snowmelt and a larger mismatch, goslings experienced reduced survival in the month after hatch (Figure 7.2a: β (snowmelt) = 0.0026 ± 0.0009 decrease in daily survival rate, per day of earlier snowmelt, t_{93} = -2.8, p = 0.006; β (mismatch) = 0.0032 ± 0.0012 decrease in daily survival rate, per day of increased mismatch, t_{93} = -2.6, p = 0.0134). Although geese laid slightly larger clutches in years with early snowmelt (Figure 7.2b, black line: β = 0.02 ± 0.002 eggs per day of earlier snowmelt, t_{3393} = -9.89, p < 0.001), a fecundity analysis including clutch size and survival rate over the complete 40-day period from hatching to fledging (Figure S7.5), showed that this could not compensate for declines in gosling survival rates.
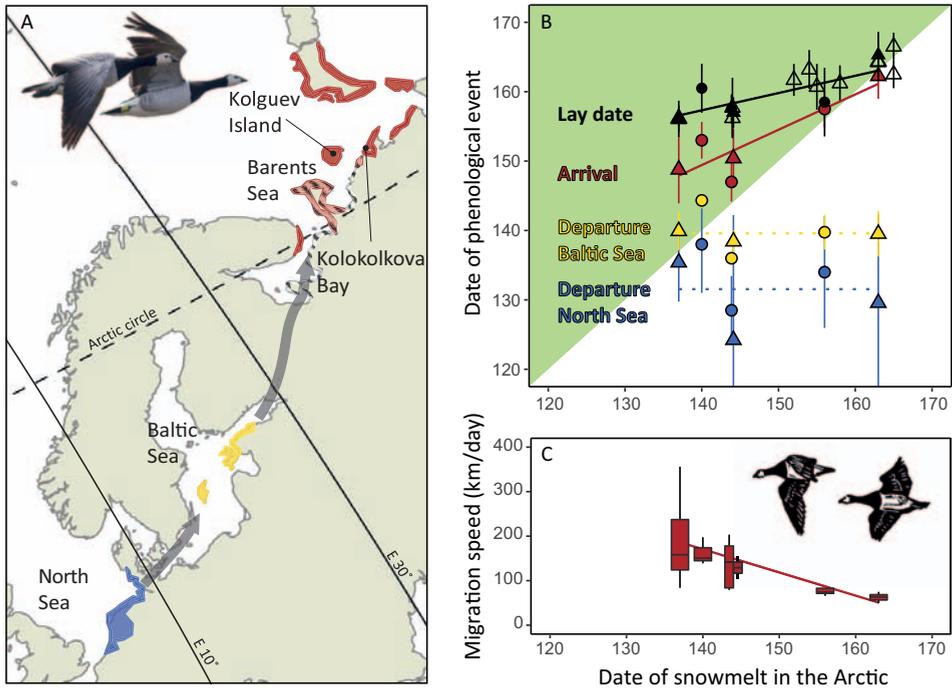
Figure 7.1: In years with early snowmelt in the Arctic breeding grounds, geese migrate faster and arrive earlier on the breeding grounds, but do not advance laying dates as much as arrival dates. (A) In spring, barnacle geese migrate from their wintering region in the North Sea (blue), via staging sites along the Baltic Sea (yellow) and the Barents Sea (diagonal grid) to their Arctic breeding grounds (red), including breeding colonies on Kolguev Island and at Kolokolkova Bay. (B) With earlier snowmelt at the Arctic breeding grounds (white-green transition), geese do not adjust departure date from the North Sea and Baltic Sea. However, birds do advance arrival at the breeding grounds, and, to a lesser extent, advance their laying dates. Circles (geese breeding at Kolguev Island) and triangles (geese breeding at Kolokolkova Bay) with standard deviations represent data from different years, closed symbols represent average laying dates of tracked birds, open triangles represent average laying dates in the whole Kolokolkova Bay colony (years 2003, 2006 – 2009, 2013 – 2014). (C) Geese speed up their migration in the second leg of their migratory flight (between the Baltic Sea and their breeding grounds) in years with earlier snowmelt.

The question arises why barnacle geese do not advance their laying dates more in years with early snowmelt to avoid a phenological mismatch, especially as they arrive on the breeding grounds much earlier. While geese are generally able to breed shortly after arrival by drawing from capital body stores accumulated along the flyway (Klaassen et al. 2006; Hahn et al. 2011), they seem limited to do so in years with early snowmelt. We argue that this is the result of their accelerated migration, which compromises accumulation of body stores during stopovers. After accelerated migration geese have to postpone laying relative to arrival as they need to replenish body stores during pre-breeding (i.e. after arrival) first,

and thus become more reliant on a local 'income' of resources for reproduction (Klaassen et al. 2006; Williams et al. 2017). Geese spent their pre-breeding time mostly grazing (47% of the time), nearly as much as on stop-over sites (59% of the time; Figure 7.3a), as shown by time-budgets derived from accelerometer data (Shamoun-Baranes et al. 2012). Moreover, geese which arrived relatively early on the breeding grounds in 2015, compensated for the lost time on stop-overs by spending a longer period pre-breeding (Figure 7.3a).
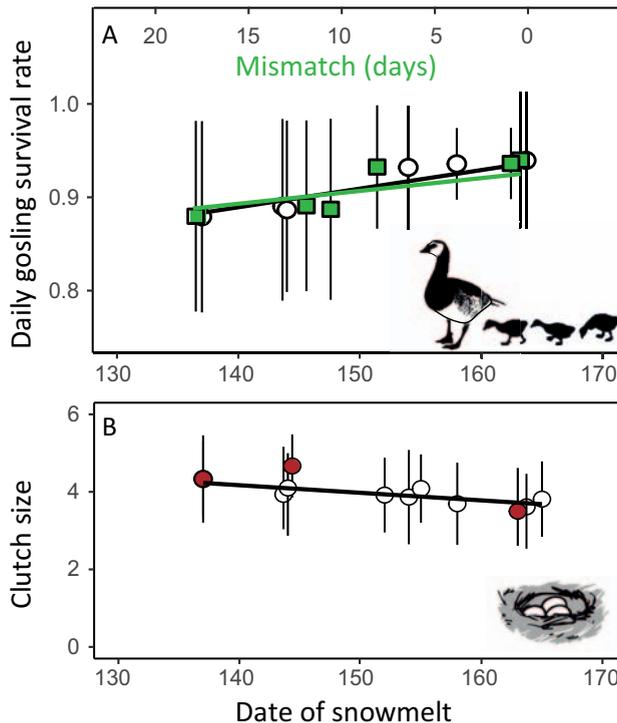
Figure 7.2: **As a result of a mismatch between gosling hatch and peak quality of food, goslings suffer from reduced survival in years with earlier snowmelt, for which a slightly larger clutch size in these years cannot compensate.** (A) When date of snowmelt is earlier in the Kolokolkova Bay (white circles, black line), barnacle geese experience a larger mismatch between laying date and snowmelt (green squares, green line), leading to reduced daily survival rates of goslings. (B) In years with earlier snowmelt, average clutch size of tracked birds (red circles) and the whole colony (white circles) is smaller. Data points include standard deviations.

Data on stable isotope signals in hatchling down feathers (which represent the stable isotope signal of the egg; (Hahn et al. 2011)) collected in the same year, revealed that when spending more time pre-breeding, geese increasingly relied on local resources for egg production (Figure 7.3b: after 8.1 days pre-breeding, $\beta = 0.09 \pm 0.01$ increase in local
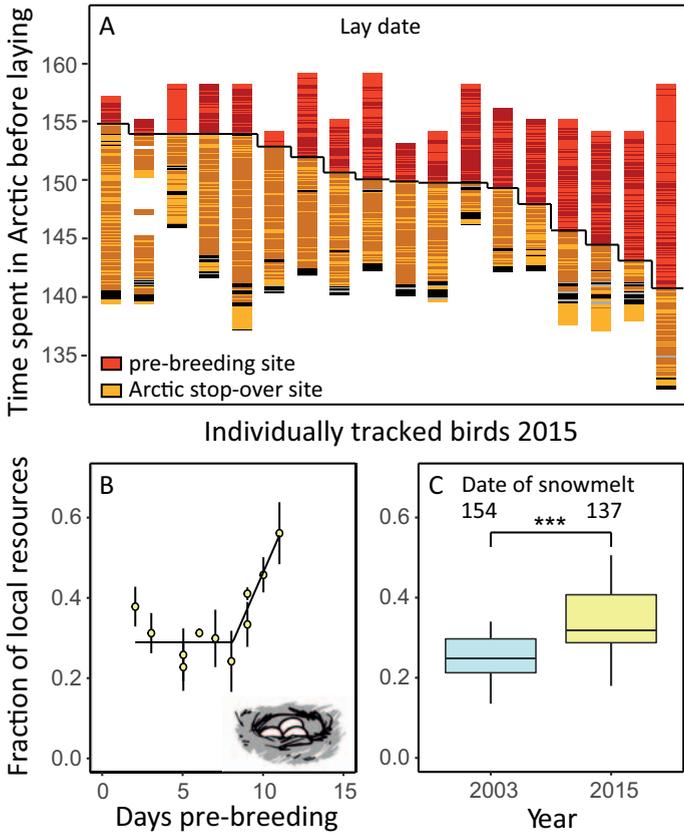
Figure 7.3: **Geese that spent little time at Arctic stop-over sites compensated for this by increasing their pre-breeding time, which made them more reliant on local resources for egg production.** (A) Time budgets in the Arctic between departure from the Baltic Sea and laying dates, show that in 2015 geese that spent little time at Arctic stopover sites (orange) balanced this by spending more time pre-breeding (red). Darker shades of orange / red show time spent grazing, black shows flying and grey shows short stopovers. Individuals were sorted by the day of arrival at the breeding site. (B) Geese which spent longer than 8 days pre-breeding used a larger fraction of local resources for egg production in 2015. (C) The fraction of local resources used for egg production was significantly greater in a year with early snowmelt (2015) than one with later snowmelt (2003).

resources per day spent pre-breeding, t = 6.66, p = 0.001). The use of local resources is more pronounced in years with early snowmelt, as becomes clear from a comparison with a year of late snowmelt (2003, when also stable isotope data was collected), in which geese used much fewer local resources for egg production than in 2015 (Figure 7.3c: 2015: 35 ± 13; 2003: 23 ± 7; t = -4.518, df = 60, p < 0.001). Alternative to our proposition that geese need the pre-breeding period to refuel before they can start laying in years with early snowmelt, geese may use an extended pre-breeding period after early arrival to gain extra

body stores to produce a larger clutch (Rowe et al. 1994). Since we found clutch size to be only slightly larger in years with early snowmelt (Figure 7.2b), a longer pre-breeding period is better explained by the need to recover body condition before laying (Figure S7.6). When snow melts early, the time necessary for fuelling rather than arrival time constrains Arctic-breeding barnacle geese to advance laying dates. This is analogous to the situation in recently established temperate-breeding populations of barnacle geese, which suffer from a phenological mismatch as they are unable to accumulate enough body stores early in the season (van der Jeugd et al. 2009).

Discussion

Under early snowmelt in the Arctic, we show that barnacle geese are able to accelerate migration and thereby advance arrival up to 13 days. This advancement is in line with data presented for geese in the study by Schmaljohann and Both (2017); their method, which calculates potential advancement from a general relationship between migration speed and stopover duration, results in a relative advancement in arrival of 16 days for geese, given the acceleration in migration speed we observed in the final 1500 km of migration. While such an adjustment in migration speed may not be possible for smaller migrants, geese may be able to achieve it because their flexibility in using either capital or income resources for reproduction (Klaassen et al. 2006; Williams et al. 2017) allows them to adjust the extent of stopover site use. But despite a strong advance in arrival (which may be beneficial for the acquisition of territories; Kokko 1999), geese do not advance their lay dates enough to fully avoid a mismatch in years with early snowmelt, and therefore suffer from reduced reproductive success. For capital breeders, the main limitation for advancing laying dates may not be spring arrival (Both & Visser 2001), but the time needed to acquire resources during spring migration to fuel reproduction. Although acceleration of migration provides flexibility to make small advancements in arrival and laying date, stronger shifts in laying date require an advancement of the moment of body store deposition. This goes hand in hand with an advancement in migration departure from the wintering grounds, which also forms the main limitation for advancements in smaller migrants, which are unable to accelerate migration (Schmaljohann & Both 2017). While geese do not appear to be limited by food resources at temperate staging grounds to advance body store deposition (Lameris et al. 2017c), the moment of departure from the wintering range seems currently unaffected by the timing of snowmelt on the breeding grounds. In some years, geese even departed after snow had already melted at their Arctic breeding grounds. Spring phenology on temperate and Arctic sites along the flyway are not correlated and, as many other long-distance migrants, geese presumably lack reliable cues to correctly adjust timing of departure from the wintering area to conditions on the breeding grounds (Gwinner 1996; Kölzsch et al. 2015). Little variation in departure

dates as observed for many Arctic long-distance migrants (Duriez et al. 2009; Clausen & Clausen 2013) suggests the use of photoperiod cues (Rees 1982), which yields an inflexible timing of migration departure. While this may have been, on average, optimal under yearly fluctuations in Arctic climatic conditions, it will constrain further advancement of arrival and laying date under rapid climate change in the Arctic. In the near future, such constraints may limit the possibility for successful reproduction in migratory Arctic species which in turn is likely to impact their populations. Whether these migrants can adapt their cue sensitivity to match their migration timing with changing climatic conditions will be a pivotal question in a rapidly warming Arctic (McNamara et al. 2011).

Methods

Date of snowmelt and food quality

We used the date of 50% snowmelt as a proxy for the optimal moment of nesting, i.e. nesting on this date results in the highest fitness. The optimal moment of nesting is suggested to be determined by the moment of peak food quality, which is highly important for chick growth (Doiron et al. 2015). From field and modelled data combined (see supplementary materials), we show that the peak in nitrogen concentration occurred 24.8 ± 5.1 days after the day of 50% snowmelt (Figure S7.1), which is similar to results of a study at another Arctic site (Doiron et al. 2015). As the complete laying and incubation period totals around 30 days (van der Jeugd et al. 2009), geese which start laying at snowmelt will have hatching eggs shortly after the moment of peak food quality, and profit from optimal conditions for gosling growth.

Snow cover data

We estimated snow cover during spring for the years 2000 – 2015 for the breeding locations Kolguev Island (69°10'N, 49°07'E) and Kolokolkova Bay (68°35'N, 52°20'E). As geese used several breeding locations on Kolguev Island (Kondratyev et al. 2013), we estimated snow cover for the whole island. For Kolokolkova Bay snow cover was estimated for the colony itself (described in van der Jeugd et al. 2003). We estimated snow cover using satellite images of the MODIS snow cover product (MOD10a2, (Hall et al. 2006). To limit the distortion by clouds, composite satellite images are generated over eight days and, when possible, classified as snow, no snow, water or lake ice. A pixel (500m resolution) is assigned as snow when it was classified as snow at least once during the eight days over which the image is composed. With a spatial overlay of the breeding areas with the MODIS images the number of pixels classified as snow within the breeding area could be retrieved. Dividing this number of pixels by the total number of pixels inside the breeding area resulted in the percentage of snow cover. Snow cover disappearance was a homogeneous process, and the midpoint of snowmelt thus correlates well with onset and

complete snowmelt. To be able to estimate the midpoint of snowmelt (day at which the snow cover had decreased to 50%), the snow cover estimates between 26th of February and 1st of July were linearly interpolated between points to attain a daily percentage of snow cover. We excluded images with a cloud cover of more than 25%.

Timing of migration, reproduction and clutch size

We determined timing of migration and lay dates from spring migration tracks and observations in the field. We collected spring migration tracks from birds nesting at Kolokolkova Bay in 2004, 2005 and 2015, and from birds nesting on Kolguev Island in 2009 – 2011. In our main study site at the Kolokolkova Bay we equipped geese with tracking devices in 2003, 2004 and 2014. In the summer of 2003 and 2004 we equipped 54 female geese with geolocators (9 g) attached to legrings. Geolocators were retrieved in 2004 and 2005 which resulted in 31 spring migration tracks (23 in 2004 and 8 in 2005). Positions were determined from geolocator data using the program 'Multitrace' (see Eichhorn et al. 2006 for details). In addition, in 2004, 16 female barnacle geese were caught during moult and implanted with PTT satellite transmitters (30 g; Eichhorn 2005), from which we retrieved 4 spring migration tracks for 2005. In the summer of 2014 we captured 40 female barnacle geese on their nests and attached UvA-BiTS GPS-loggers (19 g; Bouten et al. 2013) with Teflon backpack harnesses (Lameris et al. 2017a). In the summer of 2015 we remotely downloaded data from these loggers which resulted in 24 spring migration tracks. An analysis including data form both geolocators and GPS-loggers is feasible, as we found that migration timing and speed of birds with GPS-loggers did not differ from a control group equipped with geolocators (Chapter 4). In the winter of 2008 and 2009, 15 female barnacle geese were captured using canon nets on their wintering grounds in the north-western part of the province of Frysland, the Netherlands (53°37'N, 6°13'E) and fitted with PTT satellite transmitters (30 g) using cordura-nylon backpack harnesses (Ens et al. 2008); 4 of them migrated to breeding grounds on the island of Kolguev between 2009 – 2011 (de Boer et al. 2014), which resulted in a total of 9 migration tracks included in this analysis.

For every spring migration track we determined the day of departure from the North Sea region (first location where longitude > 10˚; Figure 7.1) and the day of departure from the Baltic Sea region (first location where longitude > 30˚). We determined the nesting site in the breeding colony either visually (Kolokolkova Bay) or based on PTT locations (Kolguev Island). The nesting sites in Kolguev Island were determined as an area of < 200 m where at least 75% of the daily PTT locations were located for a period of more than 10 days in late May / June. Date of arrival on the nesting site was then determined as the first day at which a bird arrived within 5 km from the nesting site. For birds equipped with geolocators, the day of arrival could not be estimated from the geolocation data during midnight sun, and for these birds the day of arrival was determined as the first

day the bird was observed in the colony (7.4 km²), based on observations of colour rings which were conducted for at least 5 h daily between end of May – mid June (K.E. Litvin, personal communication). Although arrivals before the first date of observation cannot be excluded, this was unlikely as no geese were observed to be present in the colony at the start of the observation period. Day of arrival using this method could be estimated for 16 birds in 2004 and 2 birds in 2005. Migration speed in km day^{-1} was eventually calculated as the great circle distance (km) between the average point where birds departed from the Baltic Sea region (61°18' N, 30°00'E) and the nesting site for every individual bird, divided by the time in days between departure from the Baltic Sea and arrival at the nesting site (i.e. excluding the period of fuelling in the Baltic Sea region).

Lay dates were determined in the field for birds nesting at the Kolokolkova Bay and determined from PTT locations for birds nesting at Kolguev Island. In Kolokolkova Bay between 2003 – 2009 and 2013 – 2015, we determined lay dates by active searching nests, in which we marked the eggs, and checking known nests every 2 to 3 days between late May and end of June, following methods described in (van der Jeugd et al. 2009). Clutch size was recorded when the number of eggs found in the nest did not change between visits. Using this method, lay date and clutch size was recorded for most focal birds with tracking devices in the Kolokolkova Bay, including 21 birds in 2004, 8 birds in 2005 and 18 birds in 2015. We observed lay date and clutch size for other birds in the colony yearly for >200 nests per year, from which average lay dates and clutch sizes per year were calculated. For birds nesting on Kolguev Island we defined the lay date of the bird as the first day when more than 75% of the PTT locations were at the nesting site (see previous paragraph).

In addition, for birds equipped with PTT satellite transmitters (2009 – 2011) and GPS-loggers (2015) we determined the time birds spent on stopover sites. We considered a bird to be on a stopover when it resided in an area with a maximum size of 10 by 10 km (as birds can travel from roosting to foraging sites within a stopover) for at least 6 h. We then calculated the total time birds spent on stopover sites between departure from the Baltic and arrival at the breeding site (Figure S7.3). For birds tracked with GPS-loggers in 2015 we also calculated a daily average position between 15th of April and 5th of June (at which all geese had arrived in the breeding colony), and calculated the great circle distance between their position and the breeding colony in the Kolokolkova Bay (Figure S7.4).

Gosling survival

In the breeding colony at the Kolokolkova Bay in 2003 – 2007 and 2015, we estimated daily gosling survival from series of observations of colour-banded adults with accompanying goslings after hatch. Prior to hatch we calculated expected hatch dates from nest initiation dates (see above), and then visited nests during expected hatch (early – mid July) to determine hatch date and to count the number of goslings on the nest. As long as the

parents were still on the nest, we assumed that goslings would successfully hatch from eggs with holes or cracks. During the post-hatching period (mid July – mid August), we determined brood size of colour-banded pairs of geese from a hide using a spotting scope. In this way we were able to collect multiple observations from 110 families with known hatch dates (2003 = 6; 2004 = 12; 2005 = 21; 2006 = 17; 2007 = 16; 2015 = 28) during an average period of 11.2 ± 11.9 days. We calculated overall survival for every family using the 'Mayfield method', i.e. dividing the total number of goslings lost between observations (functional mortality rate) by the number of days between observations (exposure; Mayfield 1961). For every family we determined the mismatch as the difference in days between laying date (hatch date – incubation and laying period of 30 days; van der Jeugd et al. 2009) and date of snowmelt for that year. We then calculated an average daily survival rate and average mismatch for every year. We found snowmelt and mismatch to be the most important predictors explaining gosling survival (Table S7.3 and S7.4). We modelled the expected number of fledglings (Figure S7.5) using a fecundity analysis (Lameris et al. 2016), as $F = Y*S$, in which Y is the clutch size and S is the survival for the complete period of gosling hatch until fledgling, averaging 40 days (van der Jeugd et al. 2009), calculated as $S = s^{40}$.

Time budgets

For 18 barnacle geese which were fitted with UvA-BiTS GPS-loggers (Bouten et al. 2013) and initiated breeding in 2015, we classified behaviour from tri-axial accelerometer data to calculated time budgets for the spring of 2015. A tri-axial accelerometer measures movement acceleration (g-force) with respect to the earth's gravitational field in three directions: surge (x), sway (y) and heave (z; Shamoun-Baranes et al. 2012). We calibrated a machine-learning model to classify behaviours from these accelerometer data. We trained and validated the model with a dataset of accelerometer data of filmed behaviours from 8 barnacle geese kept in captivity at our research facilities in Wageningen, the Netherlands in April 2014 (approved by Animal Welfare Committee, protocol NIOO 14.01). We used this dataset to annotate the behavioural classes inactive, active and grazing. When a goose was sitting or standing still for a period longer than 1 s we annotated inactive behaviour. When a goose was walking (head up, not faster than 5 km/h for longer than 1 s) we annotated active behaviour. When a goose was foraging actively, with its head down and biting off grass tillers, for a period longer than 1 s, we annotated grazing behaviour. In all other cases (e.g. other behaviours or transition between behaviours) we did not annotate the data. We annotated the behavioural class of flying for accelerometer data collected during spring migratory flights of free-living geese, for which we annotated 'flying' when a goose was moving faster than 20 km/h and clear flapping in the z-axis were visible.

To calibrate the machine learning model we randomly split the dataset of annotated behaviours (945 samples: 796 inactive, 57 active, 44 grazing, 48 flying) for training (0.4)

and testing (0.6). The model was set up to use bouts of 10 accelerometer measurements. We selected features to use for the model by comparing model accuracy of a 'pruned tree' model for different combinations of features. Features retained in the final model were overall dynamic body acceleration, mean pitch (angle of the body along the z-axis), and mean absolute derivative of the acceleration of the x- and y-axis. We then ran a random forest model with 50 trees with the selected features. The final model correctly classified 0.99 of all behaviours (N = 931), ranging from 0.86 (grazing) to 1.00 (flying). This resulted in a Kappa statistic of 0.95. We than ran the machine learning model to annotate all accelerometer data associated with every GPS-fix in our dataset for the spring of 2015.

To determine the fraction of time birds spent grazing at different staging sites, we calculated time budgets for every individual goose at every staging site (North Sea, Baltic Sea, Russian Arctic, breeding site); for the breeding site we calculated separate time budgets for the pre-breeding period (arrival – lay date) and the first part of the breeding period (lay date – 14 days after lay date). For the North Sea, we started calculating time budgets from the 15th of April onwards, when local pre-migratory fuelling rates are close to the peak (Eichhorn et al. 2012). We excluded periods of migratory flight (flights of >15 minutes in NE direction), and only considered stopover sites (see definition above) where a bird remained for at least 6 h.

Stable isotope analysis

In July 2003 and 2015 we collected down feathers from 1-2 day old goslings in the nest, and stored these in paper bags. We determined laying dates for these nests as described above. In addition, we collected goose dropping in April and May 2002-2006 on the wintering grounds (pastures and salt marshes at Schiermonnikoog Island, the Netherlands) and in June 2004 on the breeding grounds (saltmarshes at the breeding colony at the Kolokolkova Bay). Goose droppings consist of undigested plant material that provides a representative isotopic signature of the diet (Hahn et al. 2011; Eichhorn et al. 2012).

We determined the discrimination factor from droppings to down feathers by a comparison of $\delta15N$ and $\delta13C$ values of samples collected in a colony of resident Barnacle geese in the South-West of the Netherlands (51˚78'N,4˚13'E) in the spring of 2015. As these geese are resident and spend most of the three months prior to egg laying in the breeding colony, we inferred that they would not shift in diet in this period, and discrimination was the sole factor causing a difference in the signal of the endogenous food sources for egg production and the signal of exogenous food sources. We sampled droppings on 8 locations shortly prior to nest initiation (mid-April). In 6 nests we collected 1 to 3 eggs in the fourth week of incubation, when embryos had already developed down feathers. Eggs were boiled and stored in a freezer, after which we collected down feathers from these embryos in the lab. Prior to analyses, feather samples were cleaned in a chloroform / methanol mixture (2:1) to remove any contamination. Dropping samples were oven dried at 60˚C and grinded to 1 mm particles using a bead mill (QIAGEN TissueLyser II).

Subsamples of 0.5 – 1 mg material were then analysed in 6mm diameter metal cups for δ15N (‰ difference from the 15N/14N ratio in atmospheric N2) and for δ13C (‰ difference from 13C/12C ratio in Vienna PeeDee limestone) in a C:N analyser (Flash EA 1112 analyzer from Thermo Fisher Scientific Inc. Waltham, USA). The resulting discrimination factor from droppings to down feathers was 0.73 ± 0.49 for δ15N and 1.08 ± 0.29 for δ13C.

For gosling down feathers from the breeding area at the Kolokolkova Bay, we estimated the proportion of down feather tissue originating from endogenous versus exogenous resources by calculating the median probability that a down feather originated from two sources (wintering grounds versus the breeding grounds). We used the Bayesian mixing modelling tool SIAR (Parnell & Jackson 2013), which takes into account the uncertainties in isotopic composition as well as discrimination factors between different tissues (Caut et al. 2009; see above).

Statistics

We tested the effect of day of snowmelt on departure from the North Sea, departure from the Baltic Sea, arrival on the breeding grounds and on lay date by running linear mixed models using the package "lme4" in R 3.0.2 (R Development Core Team 2014), and determined the best model using AIC_c values (Burnham & Anderson 2002). We fitted year as a random factor and included fixed factors snowmelt and area (Kolokolkova Bay or Kolguev Island), but found that area was never present in the highest ranking model (Table S7.1). We tested whether arrival differed from the date of snowmelt by comparing a model of arrival date over snowmelt with a slope of 1. To compare the slopes of arrival and lay date over snowmelt we used a dummy variable representing either arrival or lay date, and tested whether this was a significant factor in a linear mixed model on a dataset of both arrival and lay dates, including also snowmelt and area as a fixed factor, and year as a random factor. We tested the effect of date of snowmelt on clutch size by running linear mixed models in which we fitted year as a random factor and included day of snowmelt as a fixed factor (Table S7.2). We tested the effect of date of snowmelt on gosling survival by running linear models in which we included day of snowmelt and hatch date as fixed factors (Table S7.3). We tested the effect of mismatch on gosling survival by running linear mixed models in which we fitted year as a random factor and mismatch and hatch date as fixed factors (Table S7.4). As the fraction of local resources used for egg production over days spent pre-breeding showed an abrupt increase, we ran a segmented linear mixed model on the data, which included two separate linear regression factors (before and after a breaking point) for resources over days pre-breeding and nest as a random factor. First, we determined the breaking point which led to the maximum likelihood estimates for all parameters in the model, which we than used to calculate a final best model (Table S7.5). We compared the fraction of local resources between the years 2003 and 2015 using a t-test.

Acknowledgments

Supplementary material

1. Methods

To investigate whether date of 50% snowmelt is a good proxy for the optimal date of nesting, we related our snowmelt data to data on peak food quality at our study site Kolokolkova Bay. We used nitrogen concentration as proxy for forage quality, because it relates directly to protein content and correlates well with digestibility (Prop & Deerenberg 1991). In 2003, 2014 and 2015 we biweekly measured the nitrogen concentration in the main forage plant Carex subspathacea for barnacle geese at the breeding site in Kolokolkova Bay (van der Graaf et al. 2006), and from these data determined the day of peak nitrogen concentration. In addition, we measured nitrogen concentration in an experimental setup where plants were exposed to +1.5°C warming, and from these data we constructed a model to calculate the day of peak nitrogen concentration from temperature data (see Lameris et al. 2017a for full methods). We used this model to calculate the day of peak nitrogen concentration for the years 2004 – 2009 and 2013.

Table S7.1: Generalized linear mixed models for departure date, arrival and laying date including a random effect of year (Y). Coefficient values and standard are given for fixed effects, and models are ordered from lowest to highest AICc values. Models for laying dates were run separately for birds for which we also had tracking data ("tracked birds"), and the average laying date of the breeding colony at the Kolokolkova Bay ("colony birds") over the period 2003 - 2015. Snowmelt is included in the best models for arrival and laying date, but not for departure dates (only a small negative effect in a model within 2Δ AICc, potentially caused by a larger proportion of geese not staging in the Baltic in recent years with earlier snowmelt, (Eichhorn et al. 2009).

	Intercept	Area (A)	Date of snowmelt (DSM)	degrees of freedom	Log likelihood	AIC$_c$	Δ AIC$_c$
Departure North Sea							
~(Y)	131.37			3	-246.0	498.4	0.00
~DSM + (Y)	156.75		-0.17 ± 0.12	4	-245.5	499.6	1.24
~ A + (Y)	134.05	-2.88		4	-245.7	500.1	1.70
~A + DSM + (Y)	158.41	-2.88	-0.16 ± 0.13	5	-245.2	501.5	3.10
Departure Baltic Sea							
~(Y)	139.58			3	-166.5	339.3	0.00
~ A + (Y)	140.44	-1.00		4	-166.0	340.6	1.34
~DSM + (Y)	141.80		-0.01 ± 0.03	4	-166.3	341.3	2.04
~A + DSM + (Y)	142.56	-0.99	-0.01 ± 0.03	5	-165.9	342.8	3.47
Arrival breeding site							
~DSM + (Y)	78.07		0.51 ± 0.05	4	-150.3	309.4	0.00
~A + DSM + (Y)	77.52	0.58	0.51 ± 0.05	5	-150.2	311.7	2.29
~(Y)				3	-157.3	321.0	11.63
~ A + (Y)	152.70	1.15		4	-157.2	323.3	13.91
Laying date (tracked birds)							
~DSM + (Y)	108.00		0.35 ± 0.03	4	-131.1	271.00	0.00
~A + DSM + (Y)	107.80	0.41	0.35 ± 0.03	5	-131.0	273.30	2.33
~(Y)				3	-135.3	277.10	6.07
~ A + (Y)	158.80	0.67		4	-135.3	279.30	8.36
Laying date (Colony birds)							
~DSM + (Y)	111.11		0.32 ± 0.05	4	17.4	44.80	0.00

Table S7.2: Generalized linear mixed models rate for clutch size, with year (Y) as a random factor. Coefficient values are given for fixed effects, and models are ordered from lowest to highest AIC_c values.

Clutch size	Intercept	Date of snowmelt (DSM)	degrees of freedom	Log likelihood	AIC_c	ΔAIC_c
~DSM + (Y)	6.917	-0.020	4	-4934.0	9876.1	0.0
~ (Y)	3.929		3	-4939.3	9884.6	8.5

Table S7.3: Generalized linear models for gosling daily survival over date of snowmelt. Coefficient values are given for fixed effects, and models are ordered from lowest to highest AIC_c values. The best model includes only day of snowmelt.

Gosling survival	Intercept	Date of snowmelt (DSM)	Day of hatch (DH)	degrees of freedom	Log likelihood	AIC_c	ΔAIC_c
~DSM	0.516	0.003		3	99.35	-192.4	0.0
~DH + DSM	0.456	0.003	0.0004	4	99.36	-190.3	2.2
~ DH	-0.016		0.005	3	97.69	-189.1	3.3

Table S7.4: Generalized linear mixed models for gosling daily survival over mismatch. Coefficient values are given for fixed effects, and models are ordered from lowest to highest AIC_c values. The best models include mismatch and day of hatch.

Gosling survival	Intercept	Mismatch (M)	Day of hatch (DH)	degrees of freedom	Log likelihood	AIC_c	ΔAIC_c
~M + (Y)	0.937	-0.003		4	98.67	-188.9	0.0
~M + DH + (Y)	0.380	-0.003	0.003	5	99.36	-188.0	0.8
~ DH + (Y)	-0.016	0.005		4	97.69	186.9	1.9

Table S7.5: Segmented linear mixed models for fraction of local resources used for egg production, with nest (N) included as a random factor. Coefficient values are given for the two fixed effects, days pre-breeding before (1) and after (2) the breaking point, which was determined to lie at 8.1 days pre-breeding (see statistics section for methods). Models are ordered from lowest to highest AIC_c values. The best model includes only days pre-breeding after the breaking point as fixed factor.

| Fraction of local resources	Intercept	Days pre-breeding 1 (PB1)	Days pre-breeding 2 (PB2)	degrees of freedom	Log likelihood	AIC_c	ΔAIC_c
~PB2 + (N)	0.285		0.092	6	35.3	-55.1	0.0
~PB1 + (N)	0.373	-0.036		6	30.0	-44.6	10.5
~PB1 + PB2 + (N)	0.273	0.004	0.098	10	33.0	-35.1	20.0
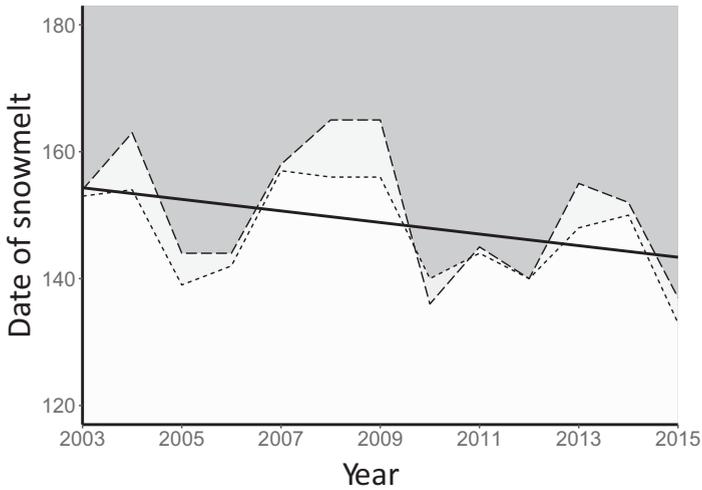
Figure S7.1: Date of 50% snowmelt has advanced by almost 1 day per year between 2003 – 2015 in Kolokolkova Bay (solid line) and Kolguev Island (dashed line), shown by the black solid line ($y = -0.91x + 1981.23$, $R^2 = 0.14$, t = one-tailed p = 0.028).). For visualization, light grey background indicates that on one site snowmelt has passed 50% and dark grey indicates that this applied to both sites.
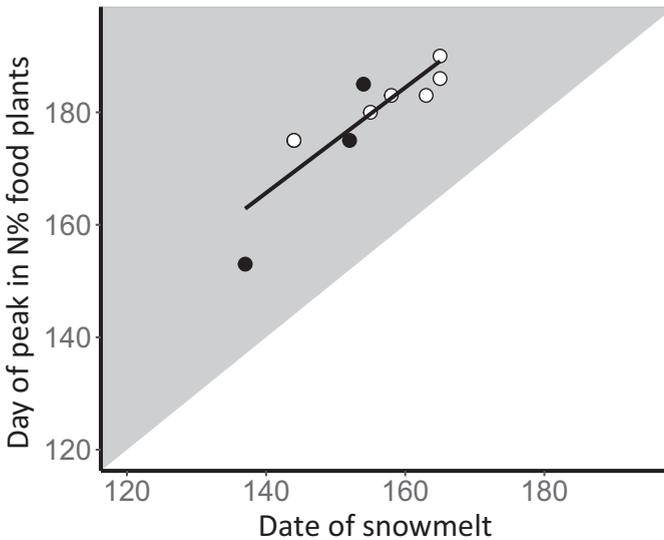

Figure S7.2: Measured and modelled day of peak nitrogen concentration in sprouts of the grass *Carex subspathacea* in the Kolokolkova Bay over years differing in moment of snowmelt ($y = 0.94 \pm 0.19x + 37.82$, $R^2 = 0.76$), of which the slope (solid line) does not differ from 1 ($F_{1,8} = 0.115$, p=0.74). Measured peaks are represented as filled dots, modelled peaks as unfilled dots.
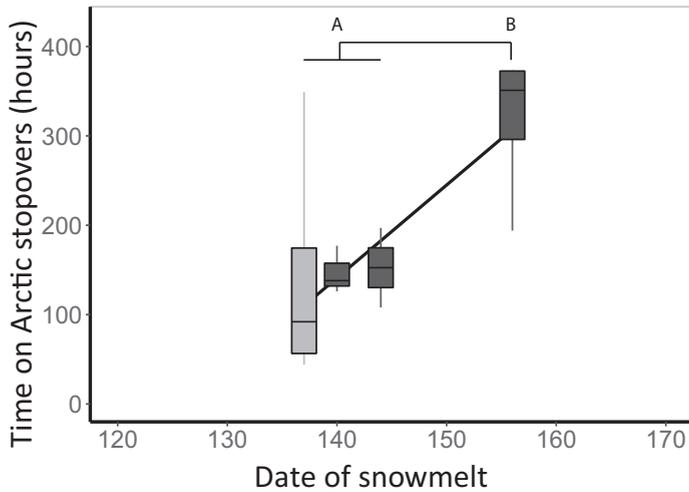
Figure S7.3: The total time in hours which birds spent on stopover sites ($y = 9.93x - 1238.52$, $R^2 = 0.37$, $t = 4.24$, $p < 0.001$) during their migration along the Barents Sea in 2009 – 2011 to Kolguev Island (dark grey) and 2015 to the Kolokolkova Bay (light grey), the letters denote groups of years which significantly differ.
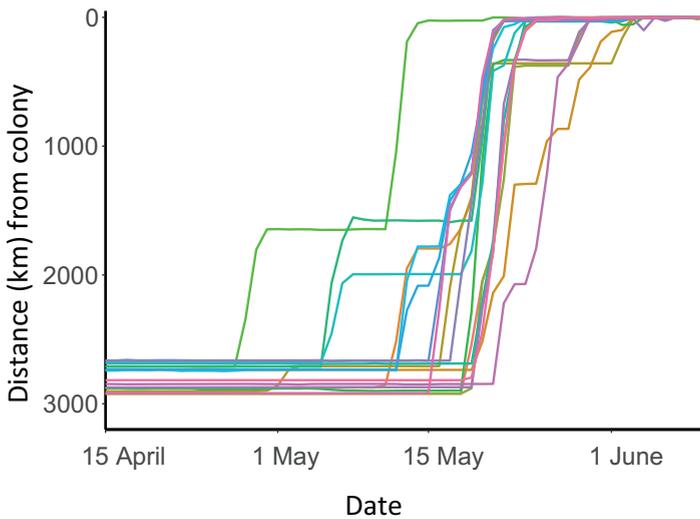
Figure S7.4: Migration schedules of the 18 nesting barnacle geese tracked with UvA-BiTS GPS-loggers in spring 2015. After a period of staging at the North Sea, most geese migrate fast to the breeding grounds without long periods on stopover sites, and some geese fly non-stop (i.e., near vertical lines).
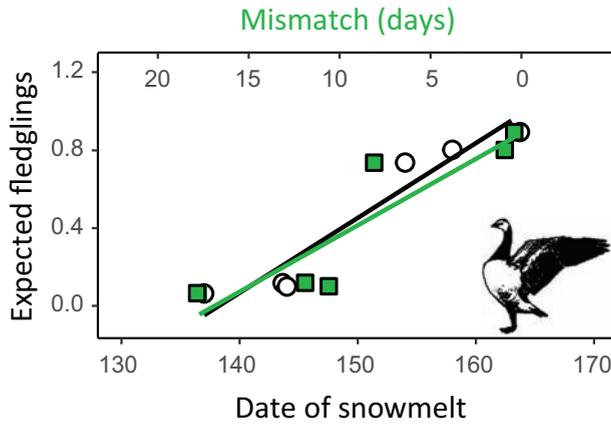
Figure S7.5: Expected fledgling survival for years differing in date of snowmelt (white circles) or the mismatch between laying date and date of snowmelt (green squares). The expected fledgling survival is calculated from the daily survival estimate and clutch size as shown in Fig. 3, taking into account a period of 40 days from hatching until fledging.
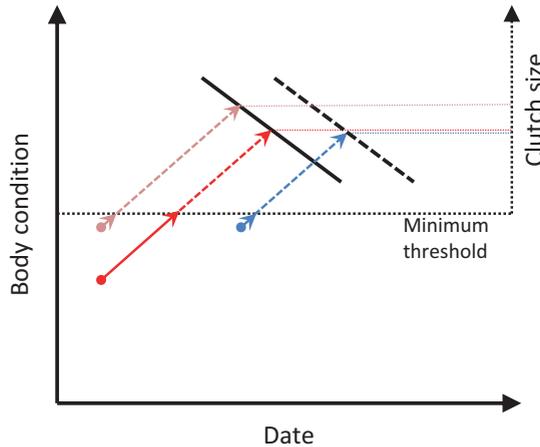
Figure S7.6: Illustration of the condition-dependent model on optimal clutch size and laying date, developed by Rowe et al. (1994), showing how geese in a year with early snowmelt (red lines) and late snowmelt (blue lines) can differ in the time which they spend pre-breeding. Geese arrive at a certain date (x-axis) with a certain body condition (y-axis), after which they gain in condition, which above a certain minimum threshold (black dotted line) can be used to produce a certain clutch size. Due to a seasonal decline in egg value because of a lower recruitment of later hatched young (Drent & Daan 1980) there exists an optimal combination of lay date and clutch size (black lines). This optimum decreases from an earlier date in years with earlier snowmelt (black solid line) than in years with a later snowmelt (black dashed line), as prospects for goslings decline with date relative to the moment of snowmelt rather than an absolute date. This results in a combination of two processes which can explain differences in lay date and clutch size in years differing in date of snowmelt. 1) If birds arrive

with a low body condition in a year with early snowmelt, they will need a longer period to reach a minimum threshold for laying (red solid line) than birds which arrive with a higher body condition when snow melts later (blue solid line). 2) The optimal combination of lay date and clutch size should fall earlier in a year with earlier snowmelt (solid line) as compared to late snowmelt (dashed line). Due to this it should be expected that geese have a similar waiting time and clutch size in years with early (red dashed line) and late snowmelt (blue dashed line) if they reach the minimum threshold condition at the same moment relative to snowmelt. If under earlier snowmelt geese would arrive relatively early, but with a high body condition (pink lines), we would expect to observe a longer waiting time as compared to a year with late snowmelt, but also a larger clutch size and likely a larger advance in laying date. We thus argue that the longer waiting time in years with early snowmelt results from geese needing to refuel up to an adequate body condition for laying, as they arrive with less body stores after a rapid migration schedule.