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Arctic Geese Tune Migration to a Warming Climate but Still Suffer from a Phenological Mismatch

Graphical Abstract



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In Brief

Spring in the Arctic is starting increasingly early under rapid climate warming. Lameris et al. show how migratory geese advance arrival on the Arctic breeding grounds in early springs. After early arrival, geese need time to refuel and do not advance their laying date as much. As a result their goslings hatch late and suffer from reduced survival.

Highlights

- In warmer springs, barnacle geese skip stopovers to advance arrival in the Arctic
- After advanced arrival, geese need time to refuel before they can start laying
- As geese advance lay dates insufficiently, their goslings survive less well



Arctic Geese Tune Migration to a Warming Climate but Still Suffer from a Phenological Mismatch

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SUMMARY

Climate warming challenges animals to advance their timing of reproduction [1], but many animals appear to be unable to advance at the same rate as their food species [2, 3]. As a result, mismatches can arise between the moment of largest food requirements for their offspring and peak food availability [4-6], with important fitness consequences [7]. For long-distance migrants, adjustment of phenology to climate warming may be hampered by their inability to predict the optimal timing of arrival at the breeding grounds from their wintering grounds [8]. Arrival can be advanced if birds accelerate migration by reducing time on stopover sites [9, 10], but a recent study suggests that most long-distance migrants are on too tight a schedule to do so [11]. This may be different for capital-breeding migrants, which use stopovers not only to fuel migration but also to acquire body stores needed for reproduction [12–14]. By combining multiple years of tracking and reproduction data, we show that a long-distance migratory bird (the barnacle goose, Branta leucopsis) accelerates its 3,000 km spring migration to advance arrival on its rapidly warming Arctic breeding grounds. As egg laying has advanced much less than arrival, they still encounter a phenological mismatch that reduces offspring survival. A shift toward using more local resources for reproduction suggests that geese first need to refuel body stores at the breeding grounds after accelerated migration. Although flexibility in body store use allows migrants to accelerate migration, this cannot solve the time constraint they are facing under climate warming.

RESULTS

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 stopover sites along the Baltic Sea and Barents Sea to their breeding grounds in the Russian Arctic (Figure 1).

Timing of Snowmelt, Peak Food Quality, Migration, and Reproduction

Snowmelt exposes the nesting sites of barnacle geese and triggers plant growth, with forage plants peaking in nitrogen concentration (as a measure of quality) 25 ± 5 days after the onset of snowmelt (Figure 2A) [6]. This peak in food quality advances with earlier snowmelt (Figure 2A; regression coefficient $\beta = 0.9 \pm 0.2$ days earlier per day of earlier snowmelt, t₈ = 5.04, p = 0.001). As the complete laying and incubation period totals around 30 days [15], barnacle geese should aim to lay their eggs right after snowmelt to match the moment of gosling hatch with the peak in food quality [13]. Although the onset of snowmelt in their Arctic breeding grounds varies between years (Figure 2B), higher spring temperatures have caused an increasingly early snowmelt in the past decades, advancing by almost 1 day per year (Figure 2B; $\beta = -0.91 \pm 0.45$, $t_{23} = -2.01$, p = 0.057) [16, 17]. During 6 years between 2004 and 2015 that differed in the date of snowmelt, we used tracking devices to study timing of spring migration in female barnacle geese nesting in colonies at the ocean inlet of Kolokolkova Bay and on Kolguev Island (Figure 1). We found that barnacle geese did not advance their departure date from the temperate stopover sites in the North Sea and Baltic Sea in years of earlier snowmelt at the breeding grounds (Figure 2C; 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. After departure from the Baltic Sea, geese showed flexible use and departure timing from Arctic stopover sites (Figure S1A), with some geese skipping Arctic stopover sites altogether (Figure S1B). As a result, geese arrived up to 13 days earlier at the breeding site in years with earlier snow melt (Figure 2C, red line; $\beta = 0.51 \pm 0.05$ day earlier per day of earlier snowmelt, $t_{53} = 10.18$, p < 0.001), but

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Figure 1. Migration Route

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.

not early enough to fully compensate for the earlier date of snowmelt (date of arrival \neq 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 2D; $\beta = 5.77$ km/day faster per day of earlier snowmelt \pm 1.25, $t_{53} = -4.67, \, p = 0.003$). Geese also advanced their egg lay dates in response to earlier snowmelt (Figure 2C, black line; $\beta = 0.35$ day earlier per day of earlier snowmelt \pm 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), such that geese undertook a longer "pre-breeding" period between arrival and egg laying.

Reproductive Output

When snow melted early, geese started laying their eggs well after the moment of snowmelt (Figure 2C), 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 hatching (Figure 3A; β [snowmelt] = 0.0026 \pm 0.0009 decrease in daily survival rate, per day of earlier snowmelt, t_{93} = $-2.8, \, p$ = 0.006; β [mismatch] = 0.0032 \pm 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 3B, black line; β = 0.02 \pm 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 S2) shows that a larger clutch did not compensate for declines in gosling survival rates.

Resource Acquisition for Egg Production

The question arises as to why barnacle geese do not advance their lay dates more in years with early snowmelt to avoid a phenological mismatch, especially as they arrive on the breeding grounds much earlier. Although geese are generally able to breed shortly after arrival by drawing from capital body stores accumulated along the flyway [18], they do not seem to be able to do so in years with early snowmelt. Accelerated migration in early springs compromises resource acquisition during stopovers in the Arctic, after which geese will need to replenish body stores during prebreeding (i.e., after arrival) first, in order not to jeopardize their own survival by drawing from the little reserves left after migration. By refueling at the breeding grounds, geese become more reliant on a local "income" of resources for reproduction [8, 12, 19]. We can show this with data on time budgets, stopover timing, and egg composition. Geese spent their pre-breeding time mostly grazing (47% of the time), nearly as much as on stopover sites (59% of the time; Figure 4A), as shown by time budgets derived from accelerometer data [20]. Moreover, geese that arrived relatively early on the breeding grounds in 2015 compensated for the lost time on stopovers by spending a longer period pre-breeding (Figure 4A). A within-year analysis on stable isotope signals in hatchling down feathers (which represent the stable isotope signal of the egg [17]) collected in 2015 revealed that when spending more time pre-breeding, geese increasingly relied on local resources for egg production (Figure 4B; after 8.1 days pre-breeding, $\beta = 0.09 \pm 0.01$ increase in local resources per day spent pre-breeding, t = 6.66, p = 0.001). A between-year comparison on data from 2015 and (a year with early snowmelt) and 2003 (a year of late snowmelt when stable isotope data were also collected) shows that the use of local resources is more pronounced in the year with early snowmelt, 2015, when geese used much more local resources for egg production than they did in 2003 (Figure 4C; 2015: 35 ± 13 ; 2003: 23 ± 7 ; t = -4.518, df = 60, p < 0.001). The increasing use of local resources when spring is early, as well as when individuals spend more time pre-breeding, matches patterns found in pink-footed geese nesting in Svalbard [21]. Instead of using the pre-breeding period to refuel after a faster migration in years with early snowmelt, geese may use this period to gain extra body stores to produce a larger clutch [22]. Since we found clutch size to be only slightly larger in years with early snowmelt (Figure 3B), a longer pre-breeding period is better explained by the need to recover body condition before laying (Figure S3). When snow melts early, the time required for fueling, rather than the arrival time,



Figure 2. Timing of Snowmelt, Peak Food Quality, Migration, and Reproduction

(A) The date of peak nitrogen concentration in sprouts of the forage plant *Carex subspathacea* in the Kolokolkova Bay advances with an earlier date of snowmelt (solid green line) and falls approximately 1 month after the date of snowmelt (white-green transition). Circles represent measured (green) and modeled (white; see STAR Methods and [5]) peaks in nitrogen concentration in different years.

(B) The date of snowmelt in the Arctic breeding sites of barnacle geese in Kolokolkova Bay (solid line) and Kolguev Island (dashed line) varies between years but has advanced by almost 1 day per year between 2003 and 2015 (green solid line).

(C) In years with earlier snowmelt at the Arctic breeding sites, 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 lay dates. Circles (geese breeding at Kolguev Island) and triangles (geese breeding at Kolokolkova Bay), averages ±SD, represent data from different years, closed symbols represent average lay dates of tracked birds, and open triangles represent average lay dates for the entire Kolokolkova Bay colony (years 2003, 2006–2009, and 2013–2014).

(D) Boxplots of "migration speed" (see STAR Methods) show how geese speed up their migration in years with earlier snowmelt. Note that migration speed was calculated only over part of the total migration route, i.e., between departure from Baltic stopover and arrival at the breeding grounds, and does not include time for body store deposition prior to departure from the Baltic.

See also Figure S1 and Table S1.

constrains Arctic-breeding barnacle geese to advance lay dates. Such a time constraint is analogous to the situation in recently established temperate-breeding populations of barnacle geese, which experience a phenological mismatch as they are unable to accumulate enough body stores early in the season [15].

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. Adjustment in migration speed may be feasible for geese, but not for smaller migrants [11], because geese have greater flexibility in using either capital or income resources for reproduction [12, 20], allowing them to adjust the extent of stop-over site use. Despite a substantial advance in arrival (which may be beneficial for the acquisition of territories [23]), geese do not advance their lay dates sufficiently to fully avoid a mismatch in years with early snowmelt, and they therefore suffer from reduced reproductive success.

For capital breeders, the main limitation in advancing lay dates may not be spring arrival [24], but the time required for the acquisition of nutrient reserves to fuel and initiate reproduction. Female geese require an adequate level of body stores for egg production and to sustain incubation [13, 25]. Also, besides other factors, a certain threshold of body stores is necessary to initiate rapid follicular growth (RFG) from which follicles take 12 days to fully develop [26]. Normally, after having left the Baltic, barnacle geese use Arctic staging sites (especially along the White Sea coast, 400--800 km away from the colony) for approximately 3 weeks [27]. From there, they can much better judge climatic conditions on the breeding site, accumulate sufficient body stores and initiate RFG. Under conditions of early snow melt in the Arctic, the geese move very quickly through or skip altogether Arctic staging sites in a rush to occupy breeding territories. Thus, time required for re-fueling and follicle development together most likely prevent the geese from laying quickly upon arrival at colony in a year with early snow melt.





Figure 3. Reproductive Output

(A) When date of snowmelt is earlier in the Kolokolkova Bay (white circles and black line), barnacle geese experience a larger mismatch between lay date and snowmelt (green squares and 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 larger.

All data points represent averages ± SD. See also Figure S2 and Table S2.

Traveling into the Arctic with more body stores accumulated upstream could reduce the pre-laying period in the colony. Due to an increased flyway population and limited staging capacities in the Baltic, most barnacle geese, however, skip this temperate staging site nowadays, despite energetic costs of carrying higher fuel loads [28]. Such strategy has been facilitated by a transition to include foraging on improved agricultural grassland during pre-migratory fueling in the wintering area [29]. With high departure fuel loads, geese can skip staging sites both in the Baltic and Arctic, i.e., perform more or less a non-stop migration, but, as we suggest, they need to replenish their body stores at breeding grounds before they can start laying eggs.

Although acceleration of migration provides flexibility to make small advancements in lay dates, stronger shifts in lay dates require an advancement of the moment of fuel deposition. This advancement goes hand in hand with an advancement in migration departure, but also the onset of pre-migratory fuel deposition at the wintering grounds. Geese are most likely not limited by food resources at temperate wintering grounds to advance fuel deposition and migration departure [30, 31], but there is no indication that they have advanced fuel deposition in the past decades [32]. At the same time, barnacle geese do not seem to adjust their migration phenology at temperate sites to the timing of snowmelt on the breeding grounds. Spring phenology on

Figure 4. Resource Acquisition for Egg Production

(A) Time budgets in the Arctic between departure from the Baltic Sea and lay 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 and red show time spent grazing, black shows flying, and gray shows short stopovers. Individuals were sorted by the day of arrival at the breeding site.

(B) In 2015, geese which spent longer than 8 days pre-breeding used a larger fraction of local resources for egg production. Shown are averages ± SD.

(C) Boxplots showing that 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).

See also Figure S3 and Table S3.

temperate and Arctic sites along the flyway are not correlated [8, 33], and, like many other long-distance migrants, geese presumably lack reliable cues to correctly adjust migration phenology at temperate sites to conditions on the breeding grounds [34]. Little change in departure dates is observed for many Arctic long-distance migrants [7, 28, 35], which may be due to small changes in local phenology [28] or a strict use of photoperiod cues [36]. Such an inflexible timing of migration departure may be optimal on average under yearly fluctuations in Arctic climatic conditions. When spring starts late, geese would want to avoid arriving too early under adverse conditions [37], which may impact reproductive success or even their own survival. Given these large yearly fluctuations, our current observations on how geese adjust their migration may not reflect their full potential to adjust to long term trends in climate change. As geese are social migrants, a successful shift in departure dates performed by some individuals may rapidly spread through the population via social learning [38, 39]. However, if a change in departure timing requires a change in cue sensitivity [40], it can form an important constraint for further advancement of arrival and lay date under rapid climate change in the Arctic.

We show for the first time that capital-breeding migratory geese are able to accelerate spring migration and advance arrival time under climate warming by reducing time spent on stopovers. Despite this advanced arrival, birds are unable to advance their timing of reproduction, as birds need time to refuel on the breeding grounds after accelerated migration. The resulting phenological mismatch has severe fitness consequences. As geese do not depart earlier from their temperate staging sites in response to earlier Arctic springs, they run into a time-constraint in the Arctic and cannot advance reproduction sufficiently. Under a warming climate, effects on fitness due to such constraints may be exacerbated in the near future by limiting the possibilities for successful reproduction in migratory Arctic species, potentially impacting population viability. Whether these migrants can adapt their cue sensitivity and match their migration timing to changing climatic conditions will be a pivotal question in a rapidly warming Arctic [37].

STAR***METHODS**

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information includes three figures and three tables and can be found with this article online at https://doi.org/10.1016/j.cub.2018.05.077.

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AUTHOR CONTRIBUTIONS

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR*METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Modis snow cover data MOD10a2	[41]	https://nsidc.org/data/mod10a2
Geolocator position data 2004–2005	[25]	https://www.movebank.org/movebank/#page=studies,path=study2231619
PTT position data 2009–2011	[42]	http://s1.sovon.nl/onderzoek/esa/esa_meeuwen_en_ganzennw.asp
Raw and analyzed data	This paper;	http://doi.org/10.17632/wkv96vcvnj.1
	Mendeley Data	
Software and Algorithms		
R language	[43]	https://www.r-project.org/
SIAR r package	[44]	https://cran.r-project.org/web/packages/siar/siar.pdf
Lme4 r package	[45]	https://cran.r-project.org/web/packages/lme4/lme4.pdf

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Thomas K. Lameris (thomaslameris@gmail.com).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We used published tracking data of barnacle geese [27, 42, 46], and added data from 40 female barnacle geese that were caught on their nests and equipped with UvA-BiTS GPS-loggers (19 g [47]) with Teflon backpack harnesses [48] in the summer of 2014. Accelerometers were calibrated on 8 barnacle geese kept in captivity at our research facilities in Wageningen, the Netherlands. Collection of these data was in agreement with institutional guidelines, as approved by the animal experimentation committee of the Royal Netherlands Academy of Arts and Sciences (protocol NIOO 14.01 and 14.07).

Food quality data

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 [6]. We used nitrogen concentration as proxy for food plant quality, because it relates directly to protein content and correlates well with digestibility [49]. 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 [50], 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 $+1.5^{\circ}$ C warming, and from these data we constructed a model to calculate the day of peak nitrogen concentration for the years 2004 – 2009 and 2013.

Snow cover data

We estimated snow cover during spring for the years 2003 – 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 [51], 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. [52]). We estimated snow cover using satellite images of the MODIS snow cover product (MOD10a2 [41]). 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 (500 m 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%.

Migration tracking data

We determined timing of migration and lay dates from spring migration tracks and observations in the field. We collected spring migration tracks from barnacle geese 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 [27] for details). In addition, in 2004, 16 female barnacle geese were caught during moult and implanted with PTT satellite transmitters (30 g [46]), 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 [47]) with Teflon backpack harnesses [48]. In the summer of 2015 we remotely downloaded data from these loggers which resulted in 24 spring migration tracks. In the winter of 2008 and 2009, 15 female barnacle geese were captured using canon nets on their wintering grounds in the northwestern 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 [42]; 4 of them migrated to breeding grounds on the island of Kolguev between 2009 – 2011 [53], which resulted in a total of 9 migration tracks included in this analysis. 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 [54].

Lay dates and clutch size

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 [15]. 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. Lay dates of birds at Kolguev Island was determined from migration tracks (see below).

Gosling survival data

In the breeding colony at the Kolokolkova Bay in 2003 - 2007 and 2015, we estimated daily gosling survival from series of observations of color-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 color-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.

Accelerometer calibration dataset

For 18 barnacle geese which were fitted with UvA-BiTS GPS-loggers [47] and initiated breeding in 2015, we classified behavior 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 [20]). We calibrated a machine-learning model to classify behaviors from these accelerometer data. We trained and validated the model with a dataset of accelerometer data of filmed behaviors from 8 captive barnacle geese in April 2014. We used this dataset to annotate the behavioral classes inactive, active and grazing. When a goose was sitting or standing still for a period longer than 1 s we annotated inactive behavior. When a goose was walking (head up, not faster than 5 km/h for longer than 1 s) we annotated active behavior. 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 behavior. In all other cases (e.g., other behaviors or transition between behaviors) we did not annotate the data. We annotated the behavioral 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.

Stable isotope data collection

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 lay 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 [19, 29].

We determined the discrimination factor from droppings to down feathers by a comparison of δ 15N and δ 13C 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.

METHOD DETAILS

Timing of migration, lay dates, clutch size

For every spring migration track we determined the day of departure from the North Sea region (first location where longitude >10°; Figure 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 color rings which were conducted for at least 5 hr daily between end of May - mid June (K.E.L., unpublished data). 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 should be calculated over the entire period of migration, from the onset of pre-migratory fuelling to arrival on the breeding grounds [55]. As we lack data on the individual onset of pre-migratory fuelling, we calculate 'migration speed' only for the period between departure from the Baltic Sea region and arrival on the nesting site. 'Migration speed' was calculated in km day⁻¹ 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 (see above) and determined from PTT locations for birds nesting at Kolguev Island. 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 nestina site.

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 hr. We then calculated the total time birds spent on stopover sites between departure from the Baltic and arrival at the breeding site (Figure S1A).

Gosling survival analysis

From gosling observations we calculated overall survival for every family using the 'Mayfield method', i.e., 1 – the total number of goslings lost between observations (functional mortality rate) divided by the number of days between observations (exposure [56]). For every family we determined the mismatch as the difference in days between lay date (hatch date – incubation and laying period of 30 days [15]) 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 (Tables S3 and S4). We modeled the expected number of fledglings (Figure S2) using a fecundity analysis [57], 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 [15], calculated as $S = s^{40}$, where s is daily gosling survival rate [57].

Time budgets

To calibrate the machine learning model we randomly split the dataset of annotated behaviors (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 behaviors (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 onward, when local pre-migratory fuelling rates are close to the peak [29]. We excluded periods of migratory flight (flights of >15 min in NE direction), and only considered stopover sites (see definition above) where a bird remained for at least 6 hr.

Stable isotope analysis

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 analyzed in 6mm diameter metal cups for $\delta 15N$ (%_o difference from the 15N/14N ratio in atmospheric N2) and for $\delta 13C$ (%_o difference from 13C/12C ratio in Vienna PeeDee limestone) in a C:N analyzer (Flash EA 1112 analyzer from Thermo Fisher Scientific, Waltham, USA). The resulting discrimination factor from droppings to down feathers was 0.73 ± 0.49 for $\delta 15N$ and 1.08 ± 0.29 for $\delta 13C$.

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 modeling tool SIAR [44], which takes into account the uncertainties in isotopic composition as well as discrimination factors between different tissues ([58]; see above).

QUANTIFICATION AND STATISTICAL ANALYSIS

We tested the effect of date of snowmelt on peak in nitrogen concentration (as dependent variable) using a linear model. We tested the effect of year on date of snowmelt using a linear model in which we included study area (Kolokolkova Bay or Kolguev Island) as a fixed effect to control for site effects. We tested the effect of date 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 "Ime4" [45] in R 3.0.2 [43], and determined the best model using AIC_c values [59]. We fitted year as a random factor and included fixed factors snowmelt and area, but found that area was never present in the highest ranking model (Table S1). 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 S2). 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 S2). 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 S2). 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 S3). We compared the fraction of local resources between the years 2003 and 2015 using a t test.

DATA AND SOFTWARE AVAILABILITY

All data have been deposited in the Mendeley Data repository at http://doi.org/10.17632/wkv96vcvnj.1:

- 1. Snow cover data; data on food peak timing
- 2. Data on migration and reproduction data
- 3. Data on clutch size
- 4. Data on gosling survival
- 5. Data on stable isotopes in eggs
- 6. GPS-tracks and time budgets spring 2015