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Optimal timing of migratory geese breeding in a warming Arctic

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CHAPTER 3

Potential for an Arctic-breeding migratory bird to adjust spring migration phenology to Arctic amplification

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ABSTRACT

Arctic amplification, the accelerated climate warming in the polar regions, is causing a more rapid advancement of the onset of spring in the Arctic than in temperate regions. Consequently, the arrival of many migratory birds in the Arctic is thought to become increasingly mismatched with the onset of local spring, consequently reducing individual fitness and potentially even population levels. We used a dynamic state variable model to study whether Arctic long-distance migrants can advance their migratory schedules under climate warming scenarios which include Arctic amplification, and whether such an advancement is constrained by fuel accumulation or the ability to anticipate climatic changes. Our model predicts that barnacle geese *Branta leucopsis* suffer from considerably reduced reproductive success with increasing Arctic amplification through mistimed arrival, when they cannot anticipate a more rapid progress of Arctic spring from their wintering grounds. When geese are able to anticipate a more rapid progress of Arctic spring, they are predicted to advance their spring arrival under Arctic amplification up to 44 days without any reproductive costs in terms of optimal condition or timing of breeding. Negative effects of mistimed arrival on reproduction are predicted to be somewhat mitigated by increasing summer length under warming in the Arctic, as late arriving geese can still breed successfully. We conclude that adaptation to Arctic amplification may rather be constrained by the (un)predictability of changes in the Arctic spring than by the time available for fuel accumulation. Social migrants like geese tend to have a high behavioural plasticity regarding stopover site choice and migration schedule, giving them the potential to adapt to future climate changes on their flyway.

Introduction

During the period 1880–2012, global average temperatures have risen with 0.2°C per decade and are projected to continue to rise (Parry et al. 2007; Stocker et al. 2013). In the Arctic region, temperatures are increasing more rapidly (Cohen et al. 2014) and are predicted to be 2.2 to 2.4 times higher than the global average by the end of the 21st century through accelerated temperature rise, a process called Arctic amplification (Serreze et al. 2009; Stocker et al. 2013). As a consequence, the spring phenology in the Arctic has advanced and the growing season lengthened, and concurrently, the optimal time window to reproduce for many animals is advancing considerably (Tulp & Schekkerman 2008; Post et al. 2009). Winters in the Arctic are inhospitable, and many animals are therefore migrants that visit the Arctic only in summer. Migrants such as birds need time to prepare for their migration, and they have to time their journey based on cues at their departure site, that may be far away from the Arctic (Bauer et al. 2011). The asynchronous advance of spring phenology between temperate wintering areas and Arctic breeding grounds could severely impair their ability to advance their spring arrival (Klaassen et al. 2012; Kölzsch et al. 2015). As reproductive success is largely determined by the timing of spring arrival (Sedinger & Flint 1991; Møller 1994), changes in spring arrival may have considerable effects on individual fitness and eventually on population dynamics (Møller et al. 2008; Both et al. 2009; Saino et al. 2011).

For Arctic-breeding long-distance migratory birds, spring arrival is probably a trade-off between the benefits of early arrival and those of accumulating body stores during migration (Prop et al. 2003). In order to time the hatching of chicks with the short peak of local food abundance, birds need to arrive early enough to start breeding before the onset of local spring (Sedinger & Raveling 1986; Lepage et al. 1998). To initiate egg-laying shortly after arrival and survive the fasting period of incubation (Eichhorn et al. 2010), larger birds such as geese take part of the necessary body stores with them from distant wintering and staging sites (Drent et al. 2006). These birds build up their reserves during the early stages of migration, and like other migratory animals follow a ‘green wave’ of successive peaks in food availability (spring growth of forage plants) along their migratory route (Bischof et al. 2012, van der Graaf et al. 2006; Shariatinajafabadi et al. 2014; Thorup et al. 2017). By eventually overtaking this green wave, they can arrive and start breeding at their Arctic breeding site before the peak in local food abundance, from which the goslings can then benefit after hatching (Kölzsch et al. 2015; Si et al. 2015a). Arctic amplification may shift the current trade-off between early arrival and accumulation of body stores, as it is predicted to shorten the time between peaks in food availability in temperate and Arctic sites and thus, the time available for geese to accumulate fuel and reach the Arctic destination to start breeding before the local onset of spring (Lameris et al. 2017b). In addition, Arctic amplification could potentially break the correlation between

the onset of spring in the Arctic and the cues that birds use to time departure from the wintering grounds. This could pose a further constraint for their capacity to advance spring migration (Kölzsch et al. 2015). Taken together, Arctic-breeding migrants may be forced to make larger compromises on their reproductive needs, by arriving later and/or in poorer body condition (Béty et al. 2003). On the other hand, Arctic amplification is expected to increase the length of the summer season, the period during which geese can stay and forage at the breeding grounds, which may ameliorate conditions for survival of the young (Meltofte et al. 2007) and thus mitigate negative effects of mistimed arrival.

In this study, we investigated the effects of Arctic amplification on timing of migration, body condition and ultimately, reproductive success in a long-distance, Arctic breeding migrant, the barnacle goose (*Branta leucopsis*). Specifically, we asked whether geese can adjust migration phenology to an asynchronous advancement of spring at multiple sites, and to what extent this depends on their ability to anticipate these advancements. To this end, we simulated the optimal spring migration of barnacle goose under sets of climate warming scenarios with synchronous or asynchronous changes between sites, and different lengths of the summer season, using a dynamic state variable model (DSVM; Houston et al. 1988). We hypothesised that geese will be constrained in terms of energy or time, and thus, unable to adapt to an accelerated advancement of spring in the Arctic, even more so when they cannot anticipate this. As a result, we expected geese to either arrive at the breeding grounds on time but with reduced body condition or survival, or fail to arrive on time, and suffer from reduced reproductive success. We expected that the negative effect of mistimed arrival on reproductive success can to some extent be mitigated by the lengthening of the summer season.

Materials and Methods

Study system

We use barnacle geese of the Barents Sea population as our study system, and specifically individuals breeding on the edge of the Kolokolkova bay, northern Russia (68°35'N, 52°20'E). The colony size fluctuates between 500-1500 breeding pairs (van der Jeugd et al. 2003; van der Jeugd et al. 2009, T.K. Lameris unpublished data, 2015). In early spring, barnacle geese of this population reside in the coastal region of the Dutch and German Wadden Sea and depart on spring migration in the beginning of May (Eichhorn et al. 2009). During spring migration, barnacle geese make on average a one-week stopover in the Baltic Sea region, and a one-week stopover in the (sub-)Arctic region (White Sea coast and Kanin peninsula) (de Boer et al. 2014). Foraging habitats consist of agricultural pastures in the temperate region and salt marshes in temperate and (sub-)Arctic region (van der Graaf et al., 2006). Barnacle geese arrive on their breeding grounds in late May, and initiate nests within a few days after arrival (Drent et al. 2007). The migration timing

of geese is very much linked to climate, as the onset of spring and the phenology of food plants determines food intake rates at wintering and staging sites (Prop & Black 1998; Prop et al. 1998) and influences departure decisions during migration (van der Graaf et al. 2006; Duriez et al. 2009, van Wijk et al. 2012; Shariati Najafabadi et al. 2015; Shariati-Najafabadi et al. 2016).

The model

We employed a dynamic programming approach developed for spring migration (Weber et al. 1998), and earlier applied to geese (Bauer et al. 2006, Klaassen et al. 2006; Bauer et al. 2008b). Given the elaborate descriptions of the model in these earlier papers, we only provide a brief outline in the following paragraph, an appended description in the supporting materials (supplementary materials), and a section on the terminal reward function which was modified to model a changing climate. Furthermore we describe calculations on energy intake and expenditure, including the empirical data on which this was based, in the supplementary materials.

The model calculates the optimal migration strategy in terms of location (i), time (t) and body condition (x) for individual geese in spring. Migration starts at the wintering site along the Wadden Sea coast. During their journey towards their breeding grounds at the Kolokolkova bay, geese can stop on several locations to feed: the Baltic Sea region, the White Sea coast and Kanin Peninsula (Figure 3.1a). The model unit of time is one day. At $t = 0$, i.e. January 1, all individuals reside at the wintering site. At each time step (t_1, t_2, \dots, T), an individual may stay and forage at its current location, where it will gain energy taking in food and lose energy for maintenance, of which both rates are site and time specific. Alternatively an individual can move to a subsequent site, which incurs flight costs. Consequently, its body condition and/or location may change. The time of arrival on the breeding grounds and the body condition at arrival jointly determine the expected reproductive success which is described in the terminal reward function (see below). Using a linear programming (backward) approach, the model identifies the optimal – fitness maximizing – decisions for all combinations of fuel load x , time t and location i , for which it uses the terminal reward function as a starting point. These optimal decisions are then used to generate (forward) individual migration itineraries and predict timing of migration, staging site choice, staging duration, survival and reproductive success for a given scenario of environmental variables. The simulation for an individual is terminated when it reaches the breeding site, when it dies (when its body condition is reduced to 0), or when the endpoint of the time series, T (day 181, June 30), is reached.

Terminal reward function

The expected reproductive success of an individual depends on its time of arrival on the breeding grounds and its body condition at arrival. Both determine when and in which

condition the individual will start breeding. The time reward (K) is determined by the timing of breeding (t_b) relative to the start of the breeding window (t_o). The state reward (R) is determined by its body condition at the start of breeding (x_b).

The time reward K indicates the probability that an individual reproduces successfully. Geese can only breed successfully when they start breeding within a short period after the onset of spring (the 'breeding window'). As weather conditions vary between years, the start (t_o) of this breeding window is also variable. The geese cannot predict this moment exactly, but can make an estimation based on the general climatic conditions along their flyway (Kölzsch *et al.*, 2015). In a given year, t_o can occur with a certain probability (depending on a probability density function, Figure 3.1c, supplementary materials) at a given time point t , between an earliest possible date $t_{o,min}$ to a latest possible date $t_{o,max}$. Between $t_{o,min}$ and the day after $t_{o,max}$, the time rewards decreases from one to zero, reflecting the general decline of reproductive success with the advancing season and in late years (MacInnes *et al.* 1974; Davies & Cooke 1983). The maximum time reward for a given year is reached at t_o . The eventual time reward of an individual depends on the date at which it starts breeding, t_b , relative to the start of the breeding window t_o .

$$K(t_b, t_o) = 1 + \frac{t_{o,min} - t_b}{(t_{o,max} + 1) - t_{o,min}} \quad (3.1)$$

When arriving before the start of the breeding window t_o (i.e. $t_a < t_o$, so before spring has started), a goose has to wait until t_o to start breeding, so $t_b = t_o$. When a goose arrives after the start of the breeding window (i.e. $t_a \geq t_o$, when spring has already begun), it can start breeding immediately, so $t_b = t_a$.

If an individual arrives in time, the state reward R is a measure of its reproductive output, i.e. the number of eggs it can lay, which depends on the body condition at the start of breeding (x_b). As we assume that food availability on the breeding grounds before the onset of spring is very low, a goose that arrives before the start of the breeding window t_o will deplete its body reserves while awaiting the earliest possibility for nest initiation:

$$x_b = x_a - (t_o - t_a) * e \quad (3.2)$$

where x_a is body condition at arrival and e is the daily maintenance energy. When a goose arrived after the start of the breeding window ($t_a \geq t_o$), x_b equals x_a . Subsequently, the state reward is:

$$R(x_b) = \frac{x_b - x_c}{r} \quad (3.3)$$

with x_c the minimum amount of reserves needed to start breeding and complete incubation (thus, if $x_b < x_c$, $R(x_b) = 0$) and r the reserves required to produce one egg. As

barnacle geese usually lay clutches of three to six eggs (van der Jeugd et al. 2003; Eichhorn 2008), the maximum state reward is six.

Thus, the expected reproductive success for an individual that reaches the breeding site N at time t in condition x is:

$$F(x, t, N) = \sum_{t=t_{o,min}}^{t_{o,max}} (p(t_o = t) * K(t_b, t_o) * R(x_b)) + B \quad (3.4)$$

with $p(t_o = t)$ the probability that t is the start of the breeding window t_o (based on probability density functions, Fig. 1c), $K(t_b, t_o)$ the time reward, $R(x_b)$ the state reward and B the future reproductive success.

Calibration and scenarios

The basic model was calibrated against spring migration trajectories of eleven barnacle geese tracked in 2009 and nest initiation data and survival data of barnacle geese recorded in our study site at the Kolokolkova Bay (see supplementary material). We then ran several sets of scenarios with the basic model (as described above) that were based on (1) increased temperatures in all sites with or without amplified temperature rise in the Arctic; (2) assumptions on the geese' ability to anticipate amplified temperature rise at the Arctic sites; and (3) changes in the length of the breeding window. All combinations of these scenarios simulations were run with 100 individuals and repeated 20 times.

1. Temperature rise

The IPCC (Stocker et al. 2013) predicts that annual mean surface air temperature could maximally rise between 2.6 and 4.8°C, and that temperatures in the Arctic will rise to reach 2.2 to 2.4 times higher than the global average in the period of 2081-2100, compared to the period 1986-2005. Based on this, we used temperature rises in the temperate zone (i.e. the Wadden Sea, the Baltic Sea and White Sea coast) of between +0 to +5 °C, while temperature in the Arctic (the Kanin and Kolokolkova bay locations) was set at 1, 1.5, 2 or 2.5 times higher than in the temperate zone (Arctic amplification; Table 3.1). For all sites we gathered daily temperature data from the period 1959 to 2014, and added the described temperature values to attain temperature data for every scenario. Growing degree days (GDD) are a cumulative temperature sum which characterises the phenology of vegetation growth (van Wijk et al. 2012). These were calculated from the scenario temperature data, from which we then calculated a daily GDD value for an average year between 1959 and 2014. Based on correlations from the literature between GDD and food quality and quantity (supplementary materials), we calculated the daily energy intake of a goose as a function of GDD, for every site and Julian day for all scenarios (Figure 3.1b). Simultaneously we recalculated the probability density function of t_o as a function of GDD

(supplementary materials) to advance the optimal breeding window under increasing temperatures at the breeding site. These probability densities not only advanced but also broadened with increasing temperatures (see Lengthening breeding window below). We therefore advanced the distribution of the original probability density function for a scenario of +0 °C, proportional to the maximum probability of the calculated probability density, to keep the width of the breeding window constant (Figure 3.1c).

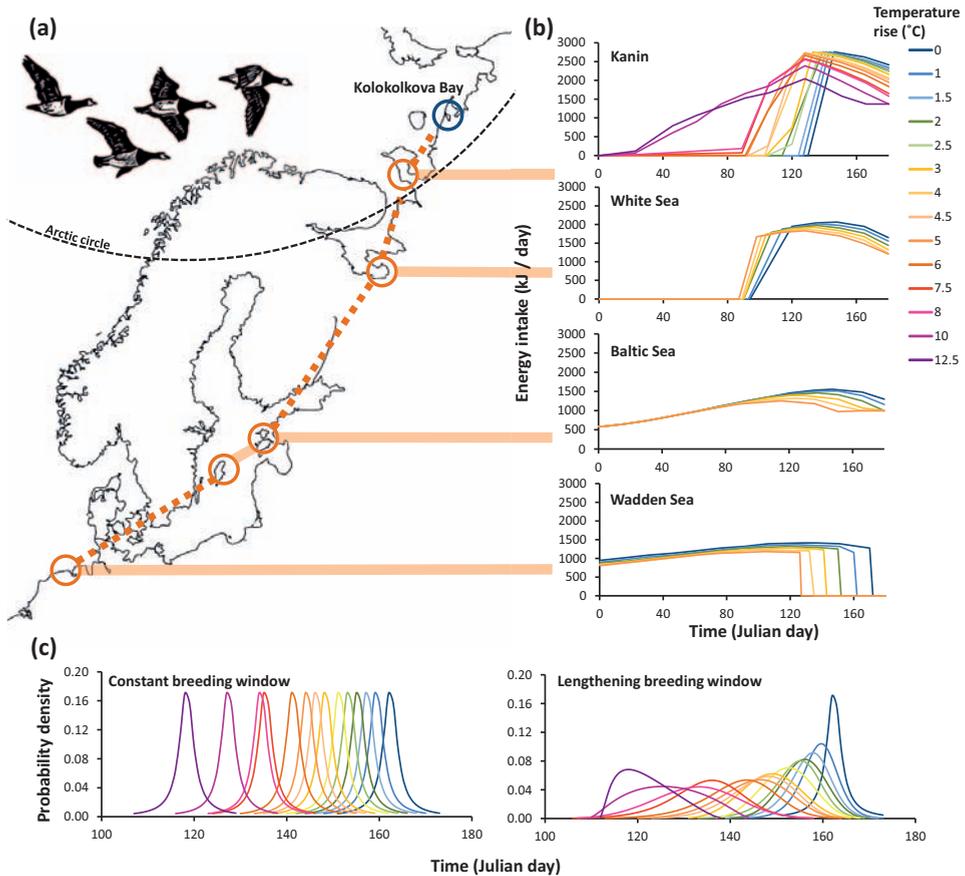


Figure 3.1: Spring flyway of barnacle geese of the Barents Sea population (a), and, for all temperature scenarios, intake rates on the model sites (b) and breeding window probability density curves (c). Barnacle geese started from their wintering site at the Wadden Sea and bred at the Kolokolkova bay along the Barents Sea coast (blue circle). During migration, geese could stop at several stopover locations (orange circles): the Baltic Sea, the White Sea coast and Kanin. On each site, food availability changes characteristically over time (b), which may be altered by climate change and depend on specific scenarios of temperature increase (from 0 to 12.5 as indicated with line colours). At the breeding site, the breeding window (c) advances with increasing temperatures, while in other scenarios, it can also lengthen.

2. Anticipation of Arctic amplification

In contrast to the above, we also ran scenarios in which geese were ignorant of the amplified changes in the Arctic. To this end we used an alternative model in which the optimal decision matrix was calculated for synchronous temperature rise over the entire flyway, while the geese experienced Arctic amplification in the forward iteration. The geese expected and thus based their migration decisions on temperature rise in the Arctic sites to be of the same magnitude as in temperate sites, also when they actually differed.

3. Lengthening breeding window

Rising temperatures may not only advance phenology but also incur changes in the length of seasons. In longer summer seasons, a late onset of breeding might be less penalized as goslings have a longer period to grow, resulting in a broader optimal breeding window. In addition to the temperature rise scenarios above, in which the optimal breeding window only advances with rising temperatures, we ran scenarios with broadening breeding window by taking the original probability density distributions of t_0 calculated according to GDD (Figure 3.1c). Distributions at the highest temperature scenarios (+7.5, +8, +10, +12.5 °C) were steeper and narrower than expected, as we did not allow the optimal breeding window to start before January 1 (t_0 in the model).

Results

1. Temperature rise

Before reaching the breeding grounds, almost all geese in our model flew non-stop from the Wadden Sea to the Kanin site, skipping the Baltic Sea and White Sea sites, and the departure from the Wadden Sea was thus synchronous with arrival at the Kanin stopover site. Geese arrived at the Kanin stopover site as soon as potential intake rates in Kanin exceeded those in the Wadden Sea in all temperature scenarios, except for the most extreme warming and amplification scenarios (+5°C & 2.0 – 2.5x amplification), when they departed 10 – 12 days later (Figure 3.2). The geese thus departed from the Wadden Sea before food conditions peaked and extended their stay at the Kanin stopover sites (Figure 3.2).

Our model predicted that geese were able to advance their arrival at the breeding grounds according to the advancing optimal breeding window under all temperature rise scenarios, provided that they could anticipate Arctic amplification (Figure 3.3a). In the most extreme warming and amplification scenario (+5°C & 2.5x amplification) geese arrived up to 44 days earlier than in a scenario with no temperature rise (arrival on day 117.73 ± 2.17 compared to day 161.96 ± 0.90 ; mean \pm SD). Despite an increasingly earlier arrival, average arrival condition remained high in all temperature rise scenarios (ranging between 19.72 ± 1.53 and 19.90 ± 0.45 MJ) and reproductive success was unaffected (Figure

3.4a). Survival did not differ between temperature rise scenarios and was generally high (ranging between 0.90 ± 0.03 and 0.92 ± 0.03).

Table 3.1. Overview of temperature rise scenarios. Colours denote the temperature range as used in the figures.

Temperature rise in temperate region (°C)	Temperature rise in Arctic (°C)				
	No temperature rise	Temperature rise, no Arctic amplification		Temperature rise & Arctic amplification	
		Null scenario	x 1	x 1,5	x 2
0	0	-	-	-	-
1	-	1	1.5	2	2.5
2	-	2	3	4	5
3	-	3	4.5	6	7.5
4	-	4	6	8	10
5	-	5	7.5	10	12.5

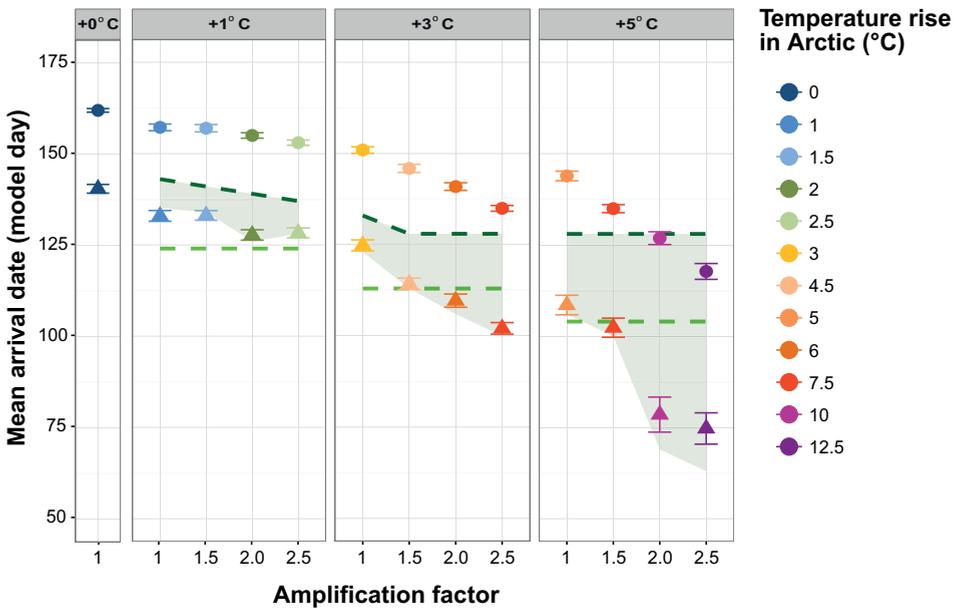


Figure 3.2: Mean arrival date at the Kanin stopover site (triangles) and at the breeding area (circles) under different temperature scenarios. The colour scale indicates temperature rise at the Arctic sites, error bars represent standard deviation. The dotted lines show the moment of peak food availability at the wintering site in the Wadden Sea (light green) and the Kanin stopover site (dark green). The green shaded area shows the period during which food availability in Kanin exceeds the Wadden Sea, prior to the peak food availability at Kanin. In the scenarios shown, geese could anticipate Arctic amplification and the breeding window was constant.

2. Anticipation of Arctic amplification

When geese were unable to anticipate Arctic amplification, our model predicted that arrival date at the breeding grounds only varied with temperature rises at the temperate sites but not with those in the Arctic. Therefore, arrival was increasingly mismatched with the optimal breeding window (Figure 3.3b). Although arrival condition did not differ from other scenarios (ranging between 19.35 ± 1.07 and 19.88 ± 0.66 MJ), the mismatched arrival resulted in considerably reduced reproductive success under the most extreme temperature rise scenarios (Figure 3.4b). Average survival did not differ from other scenarios (Figure 3.4b). Average survival did not differ from other scenarios and varied little (ranging between 0.89 ± 0.03 and 0.92 ± 0.02).

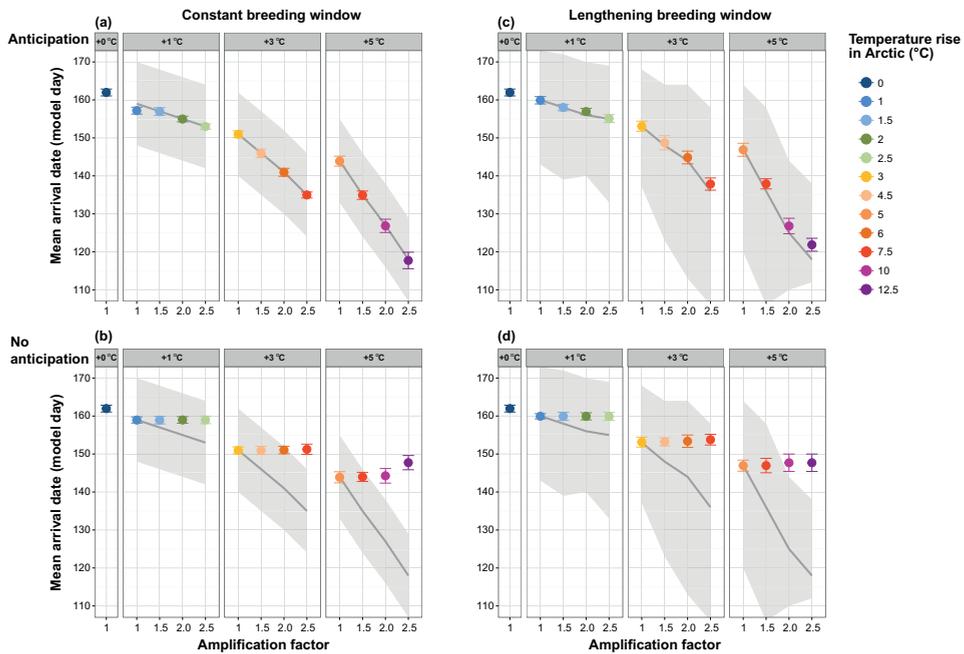


Figure 3.3: Mean arrival date under different temperature rise scenarios, with the panels showing temperature rise at temperate sites (Wadden Sea, Baltic Sea, White Sea) of +0, +1, +3 and +5°C, and on the x-axis, the amplification factor for temperature rise at the Arctic sites (Kanin, Kolokolkova bay). Colour scale indicates temperature rise at the Arctic sites, error bars represent standard deviation. The lower and upper boundaries of the grey areas indicate the start (to,min) and the end (to,max) of the optimal breeding window, with the dark grey line indicating the date at which the probability for to to occur is highest. Different figures show different scenarios and model versions: (a) basic model, (b) geese cannot anticipate amplified arctic warming, (c) increasing summer length under anticipation and (d) increasing summer length, and geese cannot anticipate amplified arctic warming.

3. Lengthening breeding window

A lengthening of the breeding window affected reproductive success. When geese could anticipate Arctic amplification and thus advanced their arrival date accordingly, reproductive success was generally slightly lowered when the breeding window lengthened (Figure 3.4a,c). Under a broadening optimal breeding window, the time reward for starting to breed even at the best possible moment, namely the onset of spring (t_0), was lower than under scenarios with constant breeding window length (equation 3.1, Figure 3.1c). When geese could not anticipate Arctic amplification, reproductive success was generally higher with broader breeding windows as compared to scenarios with a constant breeding window (Figure 3.4b, d), as the geese still arrived within the breeding window (Figure 3.3d).

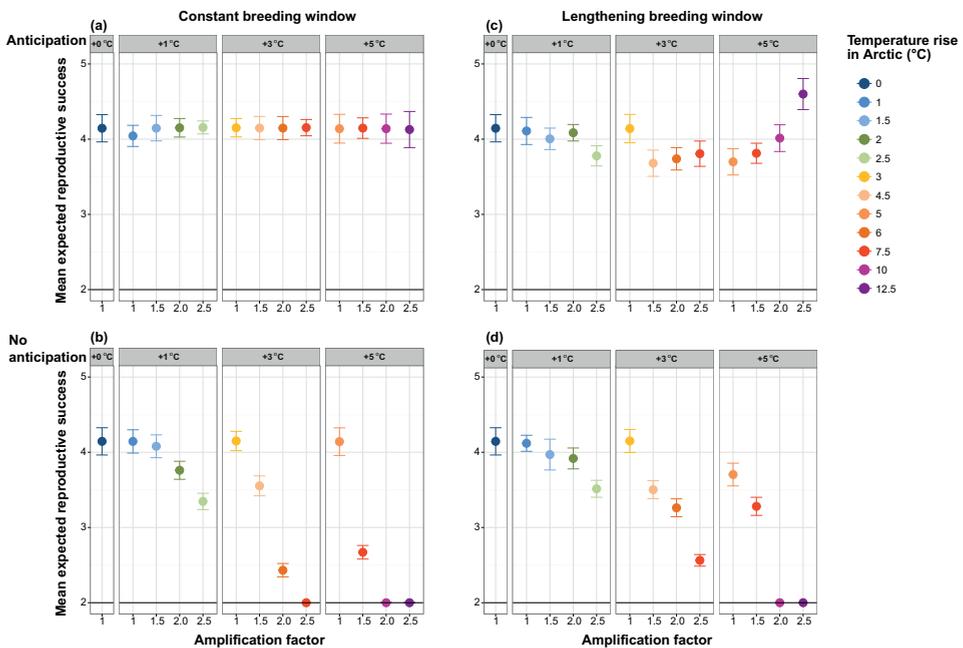


Figure 3.4: Mean expected reproductive success under different temperature rise scenarios, with the panels showing temperature rise at temperate sites (Wadden Sea, Baltic Sea, White Sea) of +0, +1, +3 and +5°C, and on the x-axis, the amplification factor for temperature rise at the Arctic sites (Kanin, Kolokolkova bay). Colour scale indicates temperature rise at the Arctic sites; error bars represent standard deviation. The horizontal line at $y = 2$ marks the portion of future reproductive success that every individual receives regardless its time or state reward, all values above the line indicate current reproductive success. Different figures show different scenarios and model versions: (a) basic model, (b) geese cannot anticipate amplified arctic warming, (c) increasing summer length under anticipation and (d) increasing summer length, and geese cannot anticipate amplified arctic warming.

Discussion

In contrast to our expectations, our model predicted that barnacle geese were potentially able to arrive at the breeding area on time in all scenarios, without compromising arrival condition or survival. However, this largely depended on their ability to anticipate warming along their migration route: When geese were not anticipating Arctic amplification, they increasingly mistimed arrival and reproduction with rising Arctic amplification factor. The negative effect of mistimed arrival on reproductive output was to some extent mitigated by increasing summer lengths under temperature rise in the Arctic. According to our simulations for geese that did not anticipate, reproductive success can be reduced by 50 - 90% under temperature rise of 1-3°C in the temperate and 2-6°C in Arctic regions, which are conditions predicted by the IPCC for the period of 2046-2065 (Stocker et al. 2013). This suggests that the potential for migrants to advance the timing of migration in response to Arctic amplification is critically constrained by their ability to anticipate on advancing spring phenology, rather than by the time to accumulate body reserves prior to migration.

In order to adapt to Arctic amplification, geese advanced their migratory schedule and departed from wintering and stopover sites before food availability peaked. As they advanced departure from the wintering site, they extended their staging time at Arctic stopover sites, which have earlier been suggested to enable geese to arrive with ample body stores to start breeding on arrival (Hübner 2006). In the Netherlands, the daily energy intake rate is apparently sufficient already prior to its peak value for the geese to accumulate energy stores for migration to the Arctic, suggesting that geese have enough leeway to advance fuelling for migration. This is also shown by barnacle geese that have adopted new breeding areas in the Baltic and the South West of the Netherlands since the 1980s, and which can acquire sufficient body reserves early in the season to advance the timing of reproduction by roughly two months relative to the Arctic breeding populations (van der Jeugd et al. 2009). Not all migratory animals might be able to advance fuelling in preparation for migration. For example, the departure dates of smaller long distance migratory passerines from the wintering areas seems to be currently constrained by low fuelling rates in years with lower productivity (Jonzen et al. 2006; Tøttrup et al. 2012). Migratory species with more complex dietary requirements seem indeed to be more constrained in advancing their spring phenology (Végvári et al. 2009), while geese might be able to overcome such a constraint by making use of more stable resources in fertilized grasslands (van Eerden et al. 2005, Dokter et al. unpublished), which are less susceptible to climatic variation between years.

Many migratory animals time their migration using proximate cues based on both internal and external, environmental information to time their migration (Duriez et al. 2009; Bauer et al. 2011; Mysterud 2013). These cues have evolved under past climatic conditions (Visser et al. 2004) and might thus lose their predictive value when

(asynchronous) global warming in the future changes the correlation between climatic conditions and the optimal moment of migration (Kölzsch et al. 2015; Mysterud 2013). The inability to correctly predict an advancing spring can have a major effect on reproductive success via belated arrival and thus mistimed reproduction (Clausen & Clausen 2013, Doiron et al. 2015; Lane et al., 2012), as we also find in our model (under no anticipation). Currently, barnacle geese seem unable to anticipate year-to-year variations in climatic conditions on the breeding grounds (Kölzsch et al. 2015) and during spring migration do not adapt their departure date from the Baltic Sea to climatic variations between years (Eichhorn et al. 2009). Although we show in our model that longer summers may slightly mitigate negative effects on reproductive success, migratory animals will need to adopt new migration strategies by changing the cues or behavioural rules they use to time migration, to anticipate the future phenology at the breeding site (Visser et al. 2004; Visser 2008; McNamara et al. 2011). Such an adaptation might be constrained by the rate of change through genetic variation (Anderson et al. 2013; Robinson et al. 2009). In long-lived species, including geese, strategies often spread through the population by social learning, i.e. juveniles adopt the migration strategy of their parents or other older, more experienced individuals (Sutherland 1998; Mueller et al. 2013; Teitelbaum et al. 2016). This cultural transmission allows relatively fast adaptation compared to genetic change (Sutherland 1998; Visser 2008). As learning seems to play an important role in optimizing individual migratory performance (Madsen 2001), newly adopted, successful migration strategies need to be passed on to other individuals in order for the population to adapt. Several goose species already show high potential of changing their migration strategy at short term in response to varying or novel environmental conditions, like changes in spring temperature (Bauer et al. 2008b; Dickey et al. 2008), introduction of a novel disturbance regime (e.g. Béchet et al. 2003; Klaassen et al. 2008a) and feeding conditions altered by overexploitation (e.g. Cooch et al. 1993; Madsen 2001). Such a high behavioural plasticity through learning may enable geese to depart earlier in response to climate warming, and thus adapt to Arctic amplification. Our study suggests that the relevant question to ask is whether the rates of adaptation match those of climate warming in the Arctic. Furthermore, if climatic conditions between different stages of the migratory route become completely uncoupled and therefore unpredictable for migrants, any adaptation would be insufficient, increasing the chance of mistimed arrival. Such a mistimed arrival on the breeding grounds can have strong negative impacts on reproductive success, and in the long run also impact population sizes (Clausen & Clausen 2013; Doiron et al. 2015; Knudsen et al. 2011).

Responses of migratory animals to climate warming can extend beyond changes in migratory timing, especially when climate warming affects the spatial distribution of habitats and resources (Robinson et al. 2009; Teitelbaum et al. 2015; Wauchope et al. 2016). Suitable breeding and staging habitats are likely to shift northward with the temperature

rise (ACIA, 2004; Hughes, 2004; Kaplan & New, 2006). In response, species may follow the northward shift of the climate envelope and use wintering and breeding sites further north of the current sites (Huntley et al., 2006; Visser et al., 2009; Pavón-Jordán et al., 2015), increase the distances they travel between wintering and breeding sites (Teitelbaum et al., 2015) or possibly even shift their migratory routes (Wauchope et al., 2016). When animals can shorten the distance between the wintering and breeding area, this may in some environments enable them to predict spring phenology on the breeding sites more accurately and thus may be an adaptation to keep up with earlier springs (Visser et al., 2009).

Our model predictions suggest that the potential of Arctic-breeding long-distance migrants to adapt to Arctic amplification is predominantly determined by the ability to anticipate the timing of Arctic spring. Especially generalist long-lived, social migrants have high potential to adapt their migratory behaviour fast enough to keep up with advancing Arctic springs when they are not constrained by fuelling rates early in the season, as our results here suggest. In order to validate and complement model predictions, it is important to monitor migratory behaviour of populations that experience asynchronous climate warming along their migratory flyways, and to gain further insight in the ability of migratory birds to adopt new cues to time their migratory journeys.

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Supplementary material

1. Terminal reward function

1.1 Probability density function t_0

Nest initiation dates of the Barnacle Goose breeding colony at the Kolokolkova Bay (Tobseda: 2003-2006, 2008, 2009 and 2014; data provided by K.E Litvin) were correlated with temperature data from weather station Konstantinovsky, Russia (Carbon Dioxide Information Analysis Center, USA). Three different aspects of mean daily temperature were correlated with the nest initiation dates: the accumulative sum of temperatures, or Growing Degree Days (GDD), the change in temperature per day (GDD") and the acceleration of temperature (GDD_{jerk}). These were determined according to the methods in van Wijk et al. 2012, using a threshold temperature for plant growth at all locations of 0°C. A high correlation ($R^2 > 0.7$) between the nest initiation dates and the GDD of 30 to 100 of the same year was found. Although the GDD of 30 had the weakest correlation of these ($R^2 = 0.761$), GDD 30 was used as predictor of onset dates of the breeding season (t_0) as the GDD 30 most often preceded the mean nest initiation dates, which is expected when geese would base their timing on GDD 30 (Fig. S1). The t_0 for 49 years during the period 1959 to 2014 was then predicted using $t_0 = 0.29 * GDD + 114.98$. The probability density function of t_0 was determined accordingly. In order to smooth out year effects, various distributions were fitted to the probability density function with the help of EasyFit (version 5.6). The most significant distribution was selected.

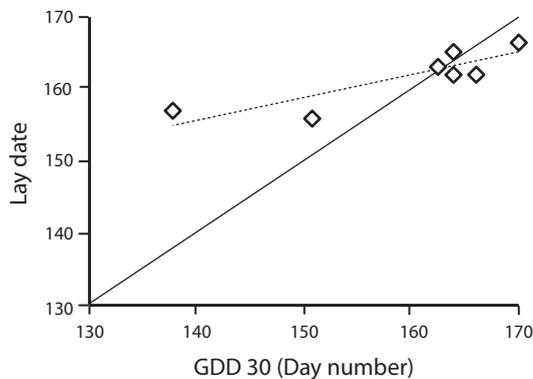


Figure S3.1. Relation between the date when Growing Degree-Days reaches 30 (GDD30) and average lay dates (LD) of barnacle geese in the breeding colony at the Kolokolkova Bay for the years 2003-2006, 2008, 2009 and 2014. Linear (dashed) regression line shows the relation $LD = 0.29 * GDD_{30} + 114.98$, the solid line shows $x=y$.

1.2 Calculations for state reward

The fuel load of an individual goose is described in the model as x , for which $1x = 0.232$ MJ (Table 3.1). The necessary fuel load which a goose needs to have upon arrival in order to breed depends on the costs of incubation. During incubation a barnacle goose loses on average 300 grams of fat, or 11790 kJ, i.e. $50.8x$. The average residual fuel load consists of 70 grams of fat, i.e. $11.9x$. Accordingly, the amount of energy needed for incubation and thus the critical amount of reserves upon arrival (x_c) is $62.7x$ or 14616 kJ (Drent *et al.*, 2007). The state reward then depends on the extra fuel load which a goose has left for laying eggs. To produce an average brood of 4.5 eggs, a barnacle goose needs 100 grams of fat, i.e. 3930 kJ (Drent *et al.*, 2007). Consequently, the amount of reserves needed to produce one egg accounts to 873 kJ, i.e. $3.8x$.

2. Backward iteration

Using the terminal reward function as a starting point, the backward iteration identifies the optimal (i.e. fitness maximizing) decisions for all combinations of fuel load x , time t and location i . An individual can either decide to remain at its present site and forage (H_f) or depart to a location further along the migration route (H_d):

$$F(x,t,i) = \max[H_f(x,t,i), H_d(x,t,i)] \quad (\text{S3.1})$$

2.1 Foraging

The amount of energy the goose could add to its body stores in the case that it stayed at its present location is determined by the maximum daily energy gain (g , in x/day), foraging intensity (u) and daily energy expenditure (e , in x/day). Maximum daily energy intake rates varied through time and per site, and had a predefined level of stochasticity of $1x$. The fraction of a day spent feeding is given by the feeding intensity u , i.e. with constant eating ($u=1$) or not eating at all ($u=0$). The fuel load at the next time step was calculated as follows:

$$x_{t+1} = x_t + u * g(i,t) - e \quad (\text{S3.2})$$

Feeding intensity and fuel load incur a predation risk:

$$\beta(x,u) = m_o(i) + m_\beta(i) \frac{(x + u * g(i,t) - e)^{a+1} - x^{a+1}}{(a+1) * (u * g(i,t) - e)} \quad (\text{S3.3})$$

where $m_o(i)$ is a background mortality risk and $m_\beta(i)$ the constant attack rate, which were set to 10^{-8} and 10^{-3} respectively on all locations. a is an indicator of the mass-dependent escape performance and was set to 2.

The optimal foraging intensity u^* is determined as:

$$H_f(x, t, i) = \max_u [(1 - \beta(x, u)) * F(x + ug(i, t) - e, t + 1, i)] \quad (S3.4)$$

Maximum fuel load was 800 gram, assuming a lean body mass of 1500 g and a maximum body mass of 2300 g (Eichhorn 2008). One gram of body mass contained 29 kJ (Madsen & Klaassen 2006) and thus, maximum energy load was 23.2 MJ. When an individual's fuel load was reduced to 0, it died.

2.2 Departure

During migratory flights, body reserves are depleted depending on distance D , so

$$x_a = \left(\frac{c^2}{(c - c(1 - (1 + \frac{x}{x_{max}})^{-0.5} - D))^2} \right) * x_{max} \quad (S3.5)$$

where the constant c is a flight range parameter described by:

$$c = \frac{D_{max}}{1 - (1 + \frac{x_f}{x_{max}})^{-0.5}} \quad (S3.6)$$

x_f is the amount of reserves used for flight, which in case of the Barnacle Goose equals x_{max} . The maximum flight distance D_{max} is described by:

$$D_{max} = \frac{x_{max}}{f} \quad (S3.7)$$

where f is the average flight cost in kJ/km.

According to the distance between the current and potential target site D_z , the flight speed v and expected fuel load upon arrival x_a at site j , the optimal target site can be determined:

$$H_d = \max_j [F(x_a, t + (\sum_{z=i}^{j-1} D_z / v), j)] \quad (S3.8)$$

3. Calibration

We used parameter values based on literature and subsequent calculations (Table S3.1). The model was parameterized for the year 2009 by using the mean daily temperatures of 2009 for the calculation of food availability. Predicted migration pattern and nest initiation dates were subsequently compared to their empirical equivalents from the year 2009. Spring trajectories from 2009 of eleven barnacle geese showed diverse migration strategies, but geese timed the crossing from the Dutch, German and Baltic spring staging sites to the staging sites on the White Sea coast and further north simultaneously (Fig. S3.2; De Boer et al. 2014). In the simulations, geese flew from the Wadden Sea and Baltic Sea staging sites to Kanin, just north of the White Sea. The simulated arrival date at Kanin (140.53 ± 1.19 ; mean \pm SD) corresponded with the observed arrival date at staging sites on the White Sea coast and further north (139.59 ± 4.13). Mean arrival date at the breeding site in the model (162.00 ± 0.51) closely matches the mean nest initiation date for the breeding site at the Kolokolkova bay in 2009 (162.38 ; K.E. Litvin, unpublished data). Finally, mean survival in the model was 0.91 ± 0.02 and corresponded well with the empirical survival of 0.93 for 2002-2008 (Lameris et al., unpublished data). No further calibration was executed.

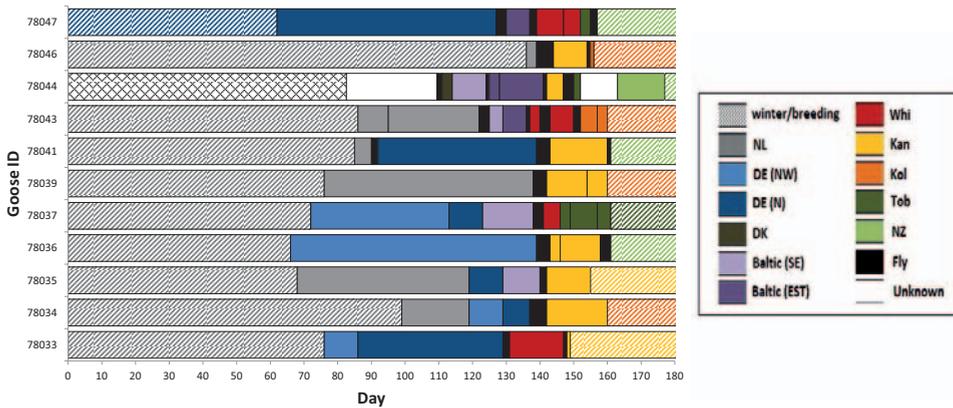


Figure S3.2. Spring migration trajectories for individual barnacle geese of the Barents Sea population in 2009. Black window indicates the crossing (black bars indicate flying (Fly)) around day 140 from temperate staging sites, including sites in the Netherlands (NL), north-west and northern Germany (NW and W DE), Denmark (DK), Sweden (SE), Estonia (EST), to staging sites on the White Sea coast (Whi), Kanin Peninsula (Kan), Kolguev and Tobseda (Tob). NZ stands for Novaya Zemlya, the most northern breeding location. Figure is based on data from de Boer et al. (2015).

Table S3.1. Parameter values used in the model.

Parameter	Value	Reference
Total energy reserves (x_{max})	23.2 MJ	(Eichhorn 2008)
Energy density per x	0.232 MJ	(Madsen & Klaassen 2006)
Initial amount of body reserves (random)	$4640 \text{ kJ} \leq x \leq 11600 \text{ kJ}$	(Eichhorn 2008)
Critical amount of body stores upon arrival (x_c) (x_c)	14616 kJ	(Drent <i>et al.</i> , 2007)
r	3.8	(Drent <i>et al.</i> , 2007)
Flight speed	18m/s	(Green, 2001)
Average flight costs (f)	6.23 kJ/km	(Jonker <i>et al.</i> 2010)
D_{max}	3723.9 km	Follows from x_{max} and f
c	12714.3	Follows from D_{max} and f
Daily energy expenditure (e)	835.2 kJ	(Boudewijn 1984)
Starting time ($t=0$)	January 1	
Endpoint (T ; $t=181$)	June 30	
Future reproductive success (B_0)	2	(Jonker <i>et al.</i> 2010)
Number of stopover sites	4	
Distance Wadden Sea	to Baltic Sea: 1069 km to White Sea: 2246 km to Kanin: 2725 km to Kolokolkova bay: 3055 km	
Distance Baltic Sea	to White Sea: 1177 km to Kanin: 1656 km to Kolokolkova bay: 1986 km	
Distance White Sea	to Kanin: 479 km to Kolokolkova bay: 809 km	
Distance Kanin	to Kolokolkova bay: 330 km	
Mass-dependent escape performance exponent	$a = 2$	(Jonker <i>et al.</i> 2010)
Site-specific constant attack rate	10^{-3}	(Jonker <i>et al.</i> 2010)
Predation risk baseline	10^{-8}	(Jonker <i>et al.</i> 2010)

4. Energy intake and expenditure in temperature rise scenarios

4.1 Daily energy intake

Daily energy intake was related to growing degree days (GDD; see van Wijk *et al.* 2012) based the relationship with biomass and quality measurements of some of the main food plants of Barnacle Geese, specific for wintering and stopover sites (*Festuca spec.* at the Wadden Sea and the Baltic Sea; *Carex spec.* and *Puccinellia spec.* at the White Sea and Kanin (measured at Kolokolkova Bay); van der Graaf *et al.* 2006). As measurements were done on specific locations and in different years, multiple regression analysis was used to

determine the overall relation between growing degree day and grass biomass and quality in order to determine the average daily energy intake for the period of 2004 to 2014 (see Table S3.2 and S3.3). Daily energy intake (kJ/day) was determined by daily food intake (g/day) and metabolizable energy (kJ/g) (Fig. S3.3).

The daily food intake was determined by foraging time (min/day) and instantaneous intake rate (IR; g/min). Daily foraging time depends mainly on the hours of daylight. It is assumed that geese spend 80% of the daytime foraging (Ebbinge et al. 1975; Owen et al. 1992; Prop & Vulink 1992). The IR of barnacle geese is relatively constant across vegetation heights of ≥ 0.9 cm, in which case the mean IR is 0.295 g/min. When vegetation height is below 0.9 cm, IR was calculated according to $0.33 \cdot \text{vegetation height (cm)}$; Durant et al. 2003). Vegetation height was estimated using the biomass measurements. The relation between biomass and vegetation height was based on grass height and biomass measurements of grazed polders in the Netherlands (data provided by Daan Bos). According to these measurements vegetation height is $0.0001 \cdot \text{biomass}^2 - 0.0049 \cdot \text{biomass} + 2.12$ ($F_{2,81} = 176.6$; $P < 0.001$) when biomass consists of ≥ 14.40 g/m². When < 14.40 g/m² the vegetation height is calculated according to $0.14 \cdot \text{biomass}$.

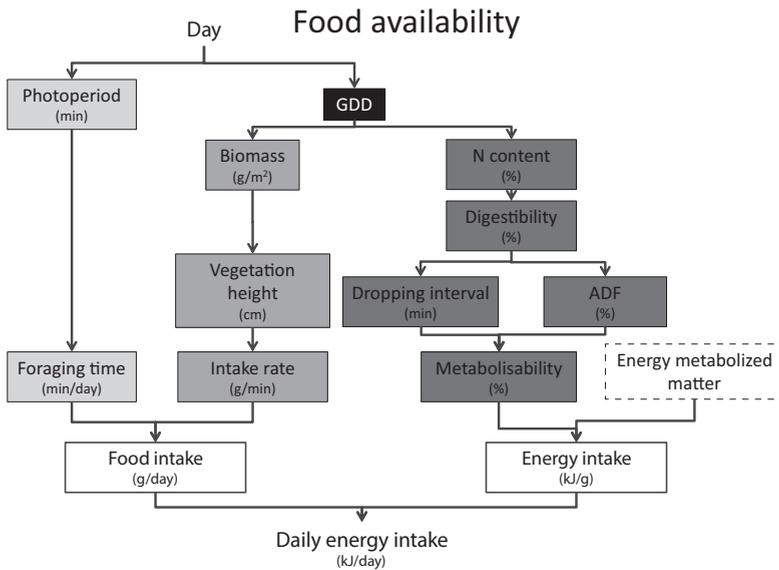


Figure S3.3. Overview of calculation of daily energy intake (kJ/day).

The metabolizable energy was determined by the metabolizability of the food (%) and the energy content of metabolized matter (kJ/g). Metabolizability is strongly related to Acid Detergent Fibre (ADF) content and dropping rate (Prop et al. 2005). Data on the relationship between GDD and these aspects was not available, instead we used the

relationship with food quality measurements described above to predict digestibility (Prop & Vulink 1992). Digestibility was calculated by means of the relation with nitrogen content (Table S3.3) (Prop & Vulink 1992: digestibility = $5.05 \cdot \text{Nitrogen content} + 20.86$; $R^2=0.576$). It is assumed that the relation between nitrogen content and digestibility varies little between different species of grass. We used digestibility to predict ADF content ($-0.2709 \cdot \text{digestibility} + 31.022$) and dropping rate (droppings per minute: $0.153 \cdot \text{digestibility} - 1.0459$), which were used to calculate metabolizability ($-1.81 \cdot \text{ADF} + 3.95 \cdot \text{dropping rate} + 57.68$) (Prop et al. 2005). The total energy intake per grams of food ingested was calculated by multiplying the amount of food metabolized by the energy content of metabolized matter which consists of 18.6 kJ/g (Prop & Black 1998).

4.2 Daily energy expenditure

It is assumed that the daily energy expenditure (kJ/day) of geese consists of activity costs and thermoregulatory costs. Activity costs (C_A) were calculated according to Boudewijn (1984):

$$C_A = 523 \cdot M^{0.74} \quad (\text{S3.9})$$

in which M is the mean body mass of barnacle geese. With a mean body mass of 1.9 kg in spring (lean body mass 1.5 kg (Eichhorn 2008) plus 50% load (maximal load of 400g)), daily activity costs consisted of 841 kJ, or 3.6 x, i.e. 1.7 times the basic metabolic rate (Nolet et al. 1992). Activity costs were held constant through time and across location.

Thermoregulatory costs below a lower critical temperature (LCT) of 7°C amounted to 1.272 kJ/h/°C (Clausen et al. 2012). Daily thermoregulatory costs were calculated using mean daily temperatures of 2004-2014 of six different weather stations: Lauwersoog (The Netherlands), Kalmar and Hoburg (Sweden), Vilsandi (Estonia), Archangelsk and Kanin (Russia). The temperature data for Europe was provided by European Climate Assessment & Dataset (KNMI The Netherlands; Klein Tank et al. 2002) and the data for Russia was provided by Carbon Dioxide Information Analysis Center, USA. Mean daily temperatures of the three weather stations in Sweden and Estonia were averaged to calculate mean daily thermoregulatory costs for geese staging in the Baltic stopover region. Thermoregulatory costs were allowed to vary through the season and per location. No additional thermoregulatory costs were assumed for temperatures above the LCT. When thermoregulatory costs were below the activity costs it was assumed that the heat produced during activity contributed to thermoregulation (Paladino & King 1984). So in this case, no additional energy costs were made to regulate body temperature. According to our calculations thermoregulatory costs never exceeded the activity costs, therefore only activity costs were taken into account in the scenarios.

Table S3.2. Multiple regression analysis of biomass (g/m²) of food plants of barnacle geese on staging sites in relation to Growing Degree Day (GDD). Coefficient estimates are given with \pm 1 SE.

		Biomass		
		Coefficient	t	P
Schiermonnikoog, grazed <i>Festuca</i> (1998)	GDD	0.52 \pm 0.12	4.29	0.005
	GDD ²	-3.1E-04 \pm 7.71E-05	-3.96	0.007
	Constant	-139.87 \pm 43.87	-3.19	0.019
	Model	F2.6 = 13.67		0.006
Gotland, grazed <i>Festuca</i> (2003, 2004)	GDD	0.014 \pm 0.0047	2.88	0.007
	Year	-	1.54	n.s.
	Subarea	-	0.15	n.s.
	Constant	9.46 \pm 2.27	4.17	0.0002
	Model	F1.31 = 8.28		0.007
Tobseda, <i>Carex</i> (2003)	GDD	0.19 \pm 0.02	9.31	1.27E-07
	GDD ²	-8.80E-05 \pm 4.4E-05	-2.02	0.06
	Constant	no intercept*	-	-
	Model	F2.15 = 322		4.78E-13

*it is expected that the growth of *Carex* starts at zero, considering the amounts of snow in winter and early spring in the arctic.

Table S3.3. Multiple regression analysis of nitrogen content (%) of food plants of barnacle geese on staging sites in relation to Growing Degree Day (GDD). Coefficient estimates are given with \pm 1 SE.

		Quality (N%)		
		Coefficient	t	P
Schiermonnikoog, grazed <i>Festuca</i> (1998, 2004)	GDD	-0.0018 \pm 2.9E-04	-6.29	6.28E-06
	Year	-	-1.4	n.s.
	Constant	4.0 \pm 0.20	19.89	1.06E-13
	Model	F1.18 = 39.54		6.28E-06
Gotland, grazed <i>Festuca</i> (2003, 2004)	GDD	-0.0014 \pm 0.00027	-5.11	1.43E-05
	Year	-	0.15	n.s.
	Subarea	-	-0.04	n.s.
	Constant	2.91 \pm 0.13	22.57	<2E-16
	Model	F1.32 = 26.14		1.43E-05
Tobseda, <i>Carex</i> & <i>Puccinellia</i> (2003)	GDD	-0.0037 \pm 0.00083	-4.45	9.82E-05
	Species	-	-0.37	n.s.
	Constant	3.91 \pm 0.24	16.61	<2E-16
	Model	F1.32 = 19.78		9.82E-05