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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.

KEYWORDS
Branta leucopsis, climate change, dynamic state variable model, global warming, mistimed arrival

1 | 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, Canziani, Palutikof, van der Linden, & Hanson, 2007; Stocker et al., 2013). In the Arctic region, temperatures are increasing more rapidly (Cohen et al., 2014) and are predicted to be 2.2–2.4 times higher than the global average by the end of the 21st century through accelerated temperature rise, a process called Arctic amplification (Serreze, Barrett, Stroeve, Kindig, & Holland, 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 (Post et al., 2009; Tulp & Schekkerman, 2008). 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, Hoye, Nolet, & Buttemer, 2012; Kölzsch et al., 2015). As reproductive success is largely determined by the timing of spring arrival (Møller, 1994; Sedinger & Flint, 1991), changes in spring arrival may have considerable effects on individual fitness and eventually on population dynamics (Both et al., 2009; Møller, Rubolini, & Lehikoinen, 2008; 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, Black, & Shimmings, 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 (Lepage, Gauthier, & Reed, 1998; Sedinger & Raveling, 1986). To initiate egg-laying shortly after arrival and survive the fasting period of incubation (Eichhorn, van der Jeugd, Meijer, & Drent, 2010), larger birds such as geese take part of the necessary body stores with them from distant wintering and staging sites (Drent, Fox, & Stahl, 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; Shariatinajafabadi et al., 2014; Thorup et al., 2017; van der Graaf, Stahl, Klimkowska, Bakker, & Drent, 2006). 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., 2015). 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., 2017). 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 (Bety, Gauthier, & Giroux, 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, Clark, McNamara, & Mangel, 1988). We hypothesized 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.

2 | MATERIALS AND METHODS

2.1 | 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 and 1,500 breeding pairs (T.K. Lameris unpublished data, 2015; van der Jeugd et al., 2003, 2009). 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, Drent, Stahl, Leito, & Alerstam, 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 determine food intake rates at wintering and staging sites (Prop & Black, 1998; Prop, Black, Shimmings, & Owen, 1998) and influence departure decisions during migration (Duriez et al., 2009; Shariati-Najafabadi et al., 2016; van der Graaf et al., 2006; van Wijk et al., 2012).

2.2 | The model

We employed a dynamic programming approach developed for spring migration (Weber, Ens, & Houston, 1998) and earlier applied to geese (Bauer, Madsen, & Klaassen, 2006; Bauer, Van Dinther,

Høgda, Klaassen, & Madsen, 2008; Klaassen, Bauer, Madsen, & Tombre, 2006). 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 (Appendix S1), 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 Appendix S1.

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 1a). The model unit of time is 1 day. At *t* = 0, that is January 1, all individuals reside at the wintering site. At each time step (*t*₁, *t*₂, . . . , *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
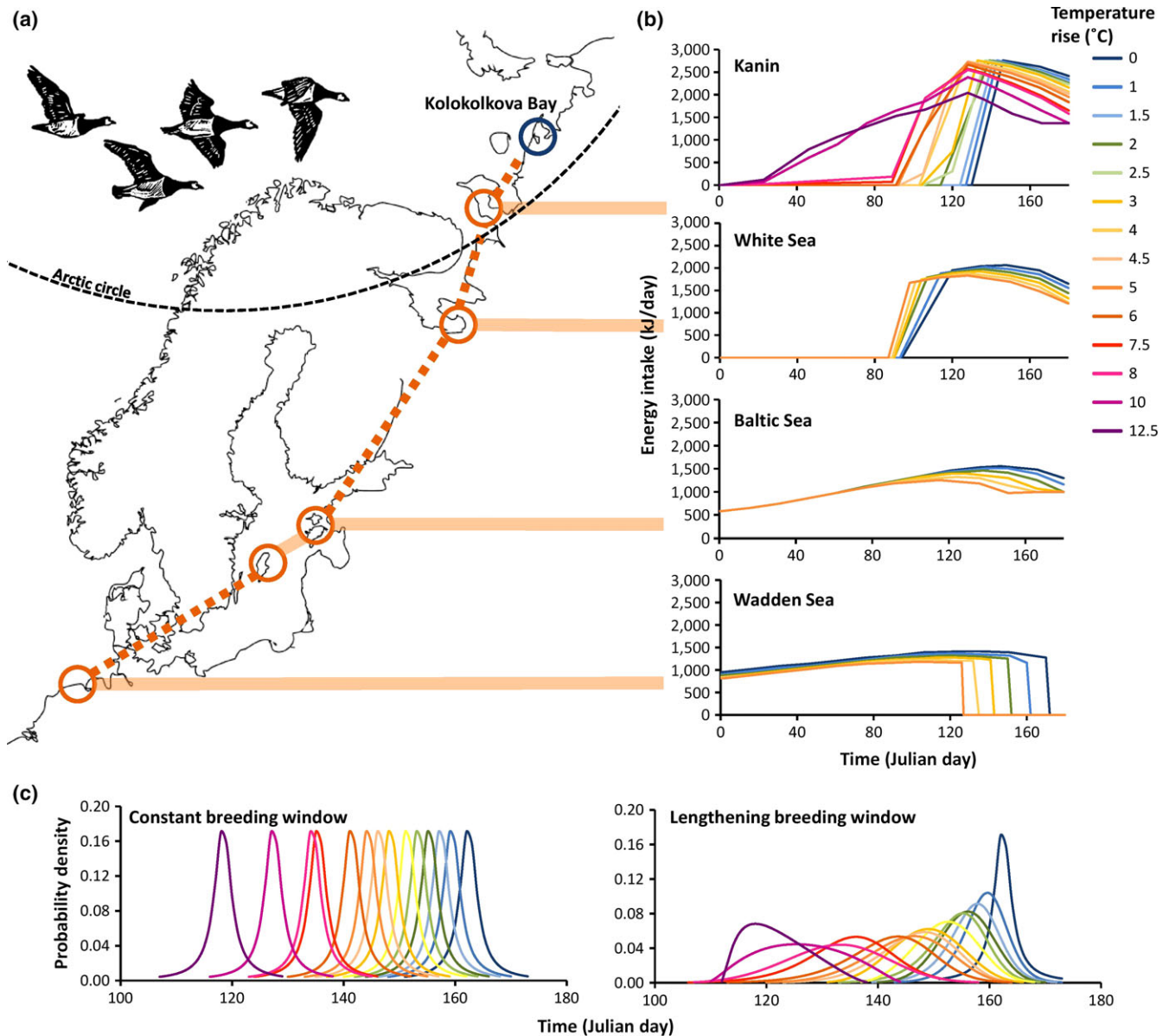
FIGURE 1 Spring flyway of barnacle geese of the Barents Sea population (a), and, for all temperature scenarios, intake rates on the model sites (b) and breeding window probability density curves (c). Barnacle geese started from their wintering site at the Wadden Sea and bred at the Kolokolkova bay along 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

at arrival jointly determine the expected reproductive success which is described in the terminal reward function. 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.

2.3 | 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_0). 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_0) 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_0 can occur with a certain probability (depending on a probability density function, Figure 1c, Appendix S1) at a given time point t, between an earliest possible date $t_{0,min}$ and a latest possible date $t_{0,max}$. Between $t_{0,min}$ and the day after $t_{0,max}$, the time rewards decrease from one to zero, reflecting the general decline in reproductive success with the advancing season and in late years (Davies & Cooke, 1983; MacInnes, Davis, Jones, Lieff, & Pakulak, 1974). The maximum time reward for a given year is reached at t_0. 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_0.

$$K(t_b, t_0) = 1 + \frac{t_{0,min} - t_b}{(t_{0,max} + 1) - t_{0,min}} \qquad (1)$$

When arriving before the start of the breeding window t_0 (i.e., $t_a < t_0$, so before spring has started), a goose has to wait until t_0 to start breeding, so $t_b = t_0$. When a goose arrives after the start of the breeding window (i.e., $t_a \geq t_0$, 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, that is 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_0 will deplete its body reserves while awaiting the earliest possibility for nest initiation:

$$x_b = x_a - (t_0 - t_a) * e \qquad (2)$$

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 ($t_a \geq t_0$), x_b equals x_a. Subsequently, the state reward is as follows:

$$R(x_b) = \frac{x_b - x_c}{r} \qquad (3)$$

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 (Eichhorn, 2008; van der Jeugd et al., 2003), 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 as follows:

$$F(x, t, N) = \sum_{t=t_{0,min}}^{t_{0,max}} (p(t_0 = t) * K(t_b, t_0) * R(x_b)) + B \qquad (4)$$

with $p(t_0 = t)$ the probability that t is the start of the breeding window t_0 (based on probability density functions, Figure 1c), $K(t_b, t_0)$ the time reward, $R(x_b)$ the state reward and B the future reproductive success.

2.4 | 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 Appendix S1). We then ran several sets of scenarios with the basic model (as described above) that were based on (i) increased temperatures in all sites with or without amplified temperature rise in the Arctic; (ii) assumptions on the geese's ability to anticipate amplified temperature rise at the Arctic sites; and (iii) changes in the length of the breeding window. All combinations of these scenarios simulations were run with 100 individuals and repeated 20 times.

2.4.1 | 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 2.2–2.4 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 and +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 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 characterizes 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

TABLE 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	×1	×1.5	×2	×2.5
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

correlations from the literature between GDD and food quality and quantity (Appendix S1), we calculated the daily energy intake of a goose as a function of GDD, for every site and Julian day for all scenarios (Figure 1b). Simultaneously, we recalculated the probability density function of t_0 as a function of GDD (Appendix S1) 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 1c).

2.4.2 | No 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.

2.4.3 | 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 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).

3 | RESULTS

3.1 | Temperature rise

Before reaching the breeding grounds, almost all geese in our model flew nonstop 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 & 2.0–2.5× amplification), when they departed 10–12 days later (Figure 2). The geese thus departed from the Wadden Sea before food conditions peaked and extended their stay at the Kanin stopover sites (Figure 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 3a). In the most extreme warming and amplification scenario (+5°C & 2.5× 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 ± 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 4a). Survival did not differ between temperature rise scenarios and was generally high (ranging between 0.90 ± 0.03 and 0.92 ± 0.03).

3.2 | No 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 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 4b). Average survival did not differ from other scenarios and varied little (ranging between 0.89 ± 0.03 and 0.92 ± 0.02).

3.3 | 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 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 1, Figure 1c). When geese could not anticipate Arctic amplification, reproductive success was generally higher with broader breeding windows as compared to

FIGURE 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
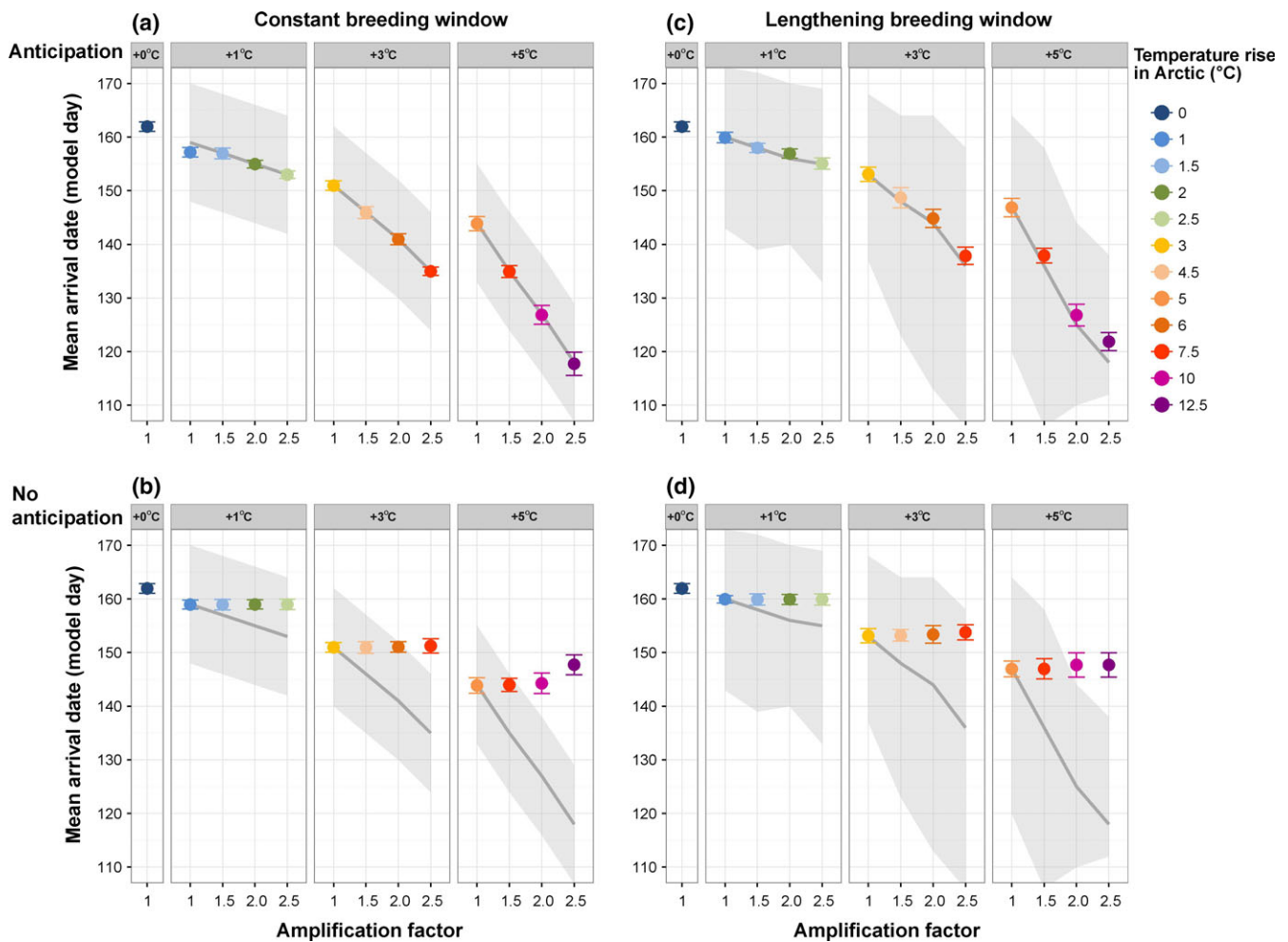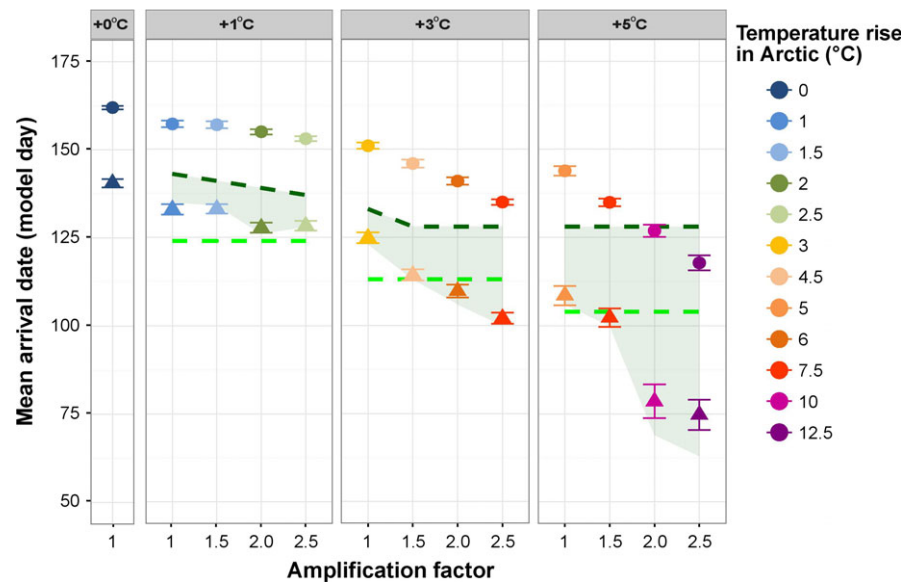

FIGURE 3 Mean arrival date under different temperature rise scenarios, with the panels showing temperature rise at temperate sites (Wadden Sea, Baltic Sea, White Sea) of +0, +1, +3 and +5°C, and on the x-axis, the amplification factor for temperature rise at the Arctic sites (Kanin, Kolokolkova bay). 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 ($t_{0,min}$) and the end ($t_{0,max}$) of the optimal breeding window, with the dark grey line indicating the date at which the probability for t_0 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
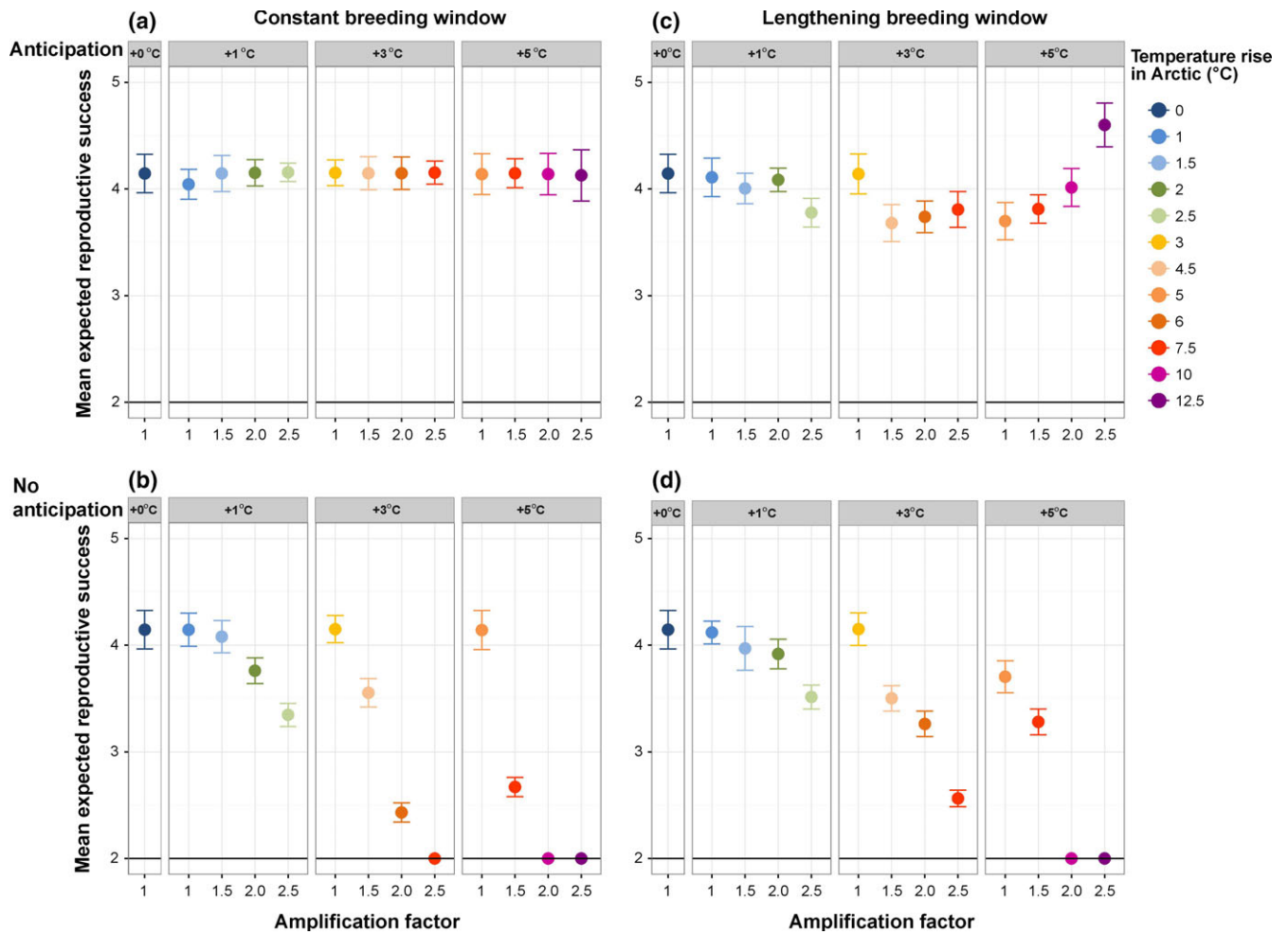
FIGURE 4 Mean expected reproductive success under different temperature rise scenarios, with the panels showing temperature rise at temperate sites (Wadden Sea, Baltic Sea, White Sea) of +0, +1, +3 and +5°C, and on the x-axis, the amplification factor for temperature rise at the Arctic sites (Kanin, 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

scenarios with a constant breeding window (Figure 4b,d), as the geese still arrived within the breeding window (Figure 3d).

4 | 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 2 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 seem 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, Bókony, Barta, & Kovács, 2010), while geese might be able to overcome such a constraint by making use of more stable resources in fertilized grasslands (A.M. Dokter, W. Fokkema, S. Bekker, W. Bouten, B.S. Ebbinge, H. Olff, H.P. van der Jeugd & B.A. Nolet, unpublished; van Eerden, Drent, Stahl, & Bakker, 2005), which are less susceptible to climatic variation between years.

Many migratory animals use proximate cues based on both internal and external, environmental information to time their migration (Bauer et al., 2011; Duriez et al., 2009; Mysterud, 2013). These cues have evolved under past climatic conditions (Visser, Both, & Lambrechts, 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, Gauthier, & Lévesque, 2015; Lane, Kruuk, Charmantier, Murie, & Dobson, 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 (McNamara, Barta, Klaassen, & Bauer, 2011; Visser, 2008; Visser et al., 2004). Such an adaptation might be constrained by the rate of change through genetic variation (Anderson, Gurarie, Bracis, Burke, & Laidre, 2013; Robinson et al., 2009). In long-lived species, including geese, strategies often spread through the population by social learning, that is juveniles adopt the migration strategy of their parents or other older, more experienced individuals (Mueller, O'Hara, Converse, Urbanek, & Fagan, 2013; Sutherland, 1998; 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., 2008; Dickey, Gauthier, & Cadieux,

2008), introduction of a novel disturbance regime (e.g., Béchet, Giroux, Gauthier, Nichols, & Hines, 2003; Klaassen, Bauer, Madsen, & Possingham, 2008) and feeding conditions altered by overexploitation (e.g., Cooch, Jefferies, Rockwell, & Cooke, 1993; Madsen, 2001). Such a high behavioural plasticity trough 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., 2017). 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 envelop and use wintering and breeding sites further north of the current sites (Huntley et al., 2006; Pavón-Jordán et al., 2015; Visser, Perdeck, van Balen, & Both, 2009), increase the distances they travel between wintering and breeding sites (Teitelbaum et al., 2015) or possibly even shift their migratory routes (Wauchope et al., 2017). 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 into the ability of migratory birds to adopt new cues to time their migratory journeys.

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