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Outflying climate change

Optimal timing of migratory geese breeding in a warming Arctic

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CHAPTER 9

Synthesis:
Optimal timing of migratory geese breeding in a warming Arctic

Climate warming and spring phenology along the flyway of barnacle geese

The onset of spring from a goose perspective

The onset of spring is a key event in the annual cycle of animals living in seasonal environments. While the winter is a strongly stringent period, when short time for foraging and low food quality puts pressure on animals to acquire enough resources for daily upkeep (Owen et al. 1992), these limitations are lifted during spring. With more daylight hours the time for foraging increases, and as temperatures start to increase, thermoregulation costs start to drop and food availability gradually increases, as insects start to appear and forage plants start to grow. Graminoids, which are the main forage plants for geese, peak in protein concentrations shortly after the onset of spring (van der Graaf et al. 2006). These beneficial conditions for foraging allow geese to start accumulate body stores to prepare for migration or reproduction. During migration, geese and other bird species are considered to time their migration in phase with a "green wave" of the delayed onset of spring, benefiting from maximum food quality (van der Graaf et al. 2006; Shariatinajafabadi et al. 2014; Thorup et al. 2017). Approaching the breeding grounds, geese then overtake this green wave to arrive in front of peak food quality (Kölzsch et al. 2015; Si et al. 2015a) which they then match with the moment of largest energetic requirements for their goslings. In this way the onset of spring forms a crucial factor in spring phenology of Arctic geese, which in temperate wintering and staging sites determines the phenology of their food plants (van Eerden et al. 2005; van der Graaf & Stahl 2006; van der Graaf et al. 2006), and later in the season provides an important cue for departing on migration (Bauer et al. 2008a; Duriez et al. 2009; van Wijk et al. 2012). Which exact environmental predictors geese use to perceive the onset of spring is not entirely clear, but several studies have investigated measures in temperature or vegetation greenness as proxies for the onset of spring. As a result, migration timing of geese has been found to correlate with accumulated temperature, in plant phenology known as growing degree days (GGD) (Bauer et al. 2008a; Duriez et al. 2009), with a derivative of GDD (third derivative, known as the "GDD-jerk") (van Wijk et al. 2012; Kölzsch et al. 2015), or with vegetation greenness as measured by satellite imagery (Shariatinajafabadi et al. 2014; Si et al. 2015a). When geese approach Arctic regions on their spring migration, snow cover may be used for timing of migration, as it limits feeding opportunities on Arctic staging sites as well as accessibility of nesting sites (Madsen et al. 2007; Jensen et al. 2008; Si et al. 2015b). Also we see that the date of snowmelt can be used as a prediction for peak food quality in the Arctic (Chapter 7). Which cues geese use to time their migration may also importantly change during their migratory journey, with fine-tuning to local phenology becoming more important as geese approach their Arctic breeding grounds (Bauer et al. 2008a; Shariati-Najafabadi et al. 2016). While recently it has become apparent that also

other factors, such as predation danger and food availability, can influence migration timing (Eichhorn et al. 2009; Jonker et al. 2010), climatic factors determining the onset of spring have strong regulating effects on the migration timing of geese.

An advancing onset of spring under Arctic climate warming

The Arctic is the earth's region which is predicted to be most subjected to climate warming (Stocker et al. 2013), but evidence is building up that rapid climate warming in the Arctic is already taking place (Stroeve et al. 2007; Serreze et al. 2009; Serreze & Barry 2011). To investigate whether climate warming has led to an advanced onset of spring in the Arctic, I combined temperature and snow cover data along the migratory flyway of barnacle geese breeding in the Russian Arctic. I used a combination of different measures for the onset of spring, with accumulated temperature in temperate staging sites and date of snowmelt in (sub) Arctic staging and breeding grounds (see Box 9.1 for methods). Although we can observe no clear temperature trends during the past 30 years in temperate and sub-Arctic sites, a warming trend becomes evident in Arctic staging sites and much more strongly in the breeding grounds during the past ten years (Figure 9.1a), clearly showing the effects of 'Arctic amplification'. The onset of spring has advanced with 8.2 days over 30 years in the last Arctic staging site, Kanin peninsula (light red), and 33.4 days over 15 years in the Arctic breeding site at Kolokolkova Bay (red lines), while no such change has occurred in temperate staging grounds. In contrast, the onset of spring in the Baltic Sea (yellow) has become more delayed over the past 30 years. The strong differences in rates of climate warming along the migratory flyway of barnacle geese also become clear from temperature anomalies in May, the month most important for goose migration, in 2015 (Figure 9.1b) and 2016 (Figure 9.1c). While 2016 was the warmest year since modern recordkeeping began in 1880 (Blunden & Arndt 2017), it can be expected that these records are only to be broken in the near future, with temperatures as in 2016 becoming the norm rather than the exception (Stocker et al. 2013). If the Arctic keeps warming at a faster rate than temperate regions (Serreze & Francis 2006b), this will result in unequal advancement in the onset of spring along the flyway of Arctic migratory geese. This is problematic, as geese should advance their timing of reproduction on the breeding grounds under rapid climate warming, but may not be able to advance their migration timing from temperate regions where climate warming is occurring at a slower rate. An unequal advancement in the onset of spring can impact the migration timing of geese by 1) changing the timing of food availability, and 2) change the cues which geese currently use to optimally time their migration. I will discuss these two issues separately in the paragraphs below.
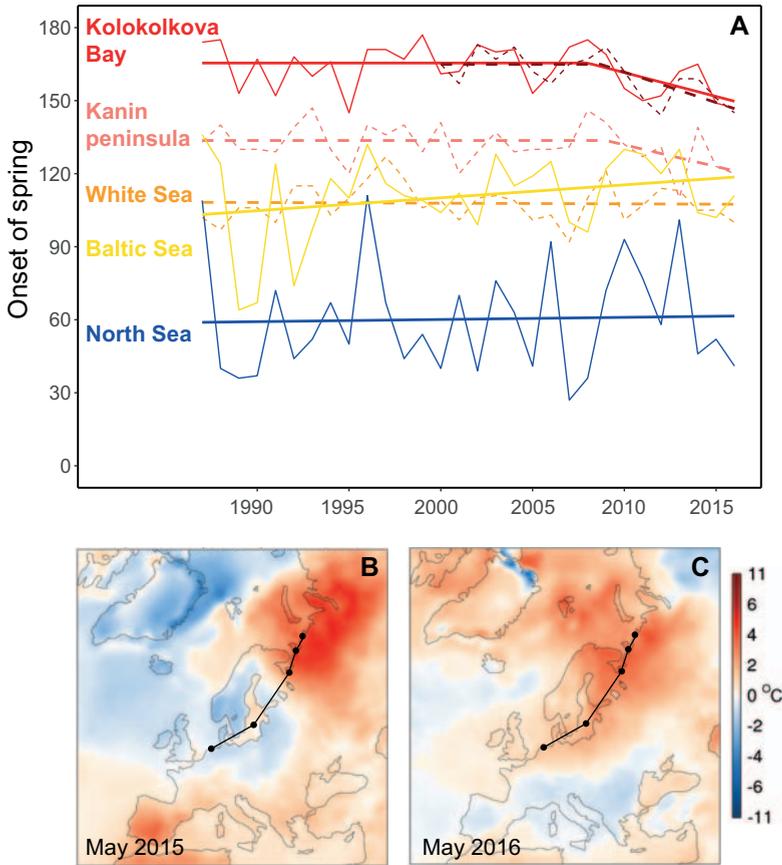
Figure 9.1: (A) The onset of spring has strongly advanced in the past decade in the Arctic, but not in temperate and sub-Arctic sites. Solid lines show onset of spring as measured by GDD, dashed lines show the onset of spring as measured by date of 50% snowmelt. (B – C) Temperature anomalies during May 2015 and 2016 (relative to mean temperature 1981 - 2010) along the migratory flyway of barnacle geese (black dots and lines) show conditions in the Arctic which are warmer than average, while conditions in temperate regions are around or below average. Data and maps were provided by ECMWF Copernicus Climate Change Service.

1. Food availability

In the first place, differing rates of climate warming along the flyway may change the current pattern of the green wave which barnacle geese track. If peak food availability falls before or after the current arrival of geese, this will affect their revenues for accumulating body stores during migration. Already now, under varying onset of spring in the Arctic, there may be strong yearly variations in how well geese can track a green wave, and to what extent they can use a green wave to supply their body stores. Preliminary results show that in years with strong climate warming in the Arctic, the green wave itself becomes shorter, as the onset of spring in the Arctic relative to temperate stop-over sites falls relatively

early (Figure S1). In these years, geese may reach Arctic staging sites relatively late and stage here for a shorter period, as they are more concerned with reaching their breeding on time than staging on these sites. Given the rapid migration schedules which we find in years with early snowmelt in the Arctic, with some geese migrating from their wintering to their breeding site in 5 days, it is questionable whether geese will continue to surf on a green wave under future climate warming.

Secondly, an increase in temperature may differently affect food availability in temperate and Arctic sites. In Chapter 2 I use an experimental approach to show that a temperature increase of 1.5 °C does not affect the timing of the forage plant quality peak at temperate staging sites, but has an advancing effect at Arctic sites. While climate warming may not affect the timing of the green wave at temperate staging sites, forage plants will peak in quality much earlier in the Arctic, especially given the strong advance in the onset of spring on the Arctic breeding site in the last decade (Figure 9.1a). If geese are indeed relying on a green wave to arrive with ample body stores on the breeding grounds, a lack of advancement in food peak phenology along the flyway may cause geese to delay their arrival, as they have to wait for optimal food quality before migrating, or to arrive with a lower body condition, as they continue on migration without benefitting from optimal foraging food quality on stopover sites. In addition, the experiment in Chapter 2 shows that climate warming will lead to a faster decrease in food quality in the Arctic, as has been previously observed in the Canadian Arctic (Doiron et al. 2014). High quality food in the form of grass tillers containing high concentration of proteins has been shown to be essential for gosling growth and survival (Lepage et al. 1998; Doiron et al. 2015) and a faster decline in food quality is likely to have strong fitness consequences (Reneerkens et al. 2016).

2. Cues

An advancing onset of spring by itself may not be the main problem for migratory birds, but rather the change in climatic connectivity, the correlation of climatic variables between wintering and breeding grounds (Saino & Ambrosini 2008). Although certain periods of the year show high climatic connectivity between sub-Saharan wintering grounds and temperate breeding grounds of passerines (Saino & Ambrosini 2008), allowing birds to predict the moment of optimal arrival, this is not the case for the flyway of barnacle geese (Kölzsch et al. 2015). The temperate wintering and staging sites in the North Sea and Baltic Sea share a similar climate, but show little climatic connectivity with the stop-over sites and breeding sites in the Arctic. Due to low climatic connectivity, local climatic cues in temperate sites do not give correct predictions of optimal arrival in the Arctic in a given year. This suggests that even without climate warming, local environmental conditions may not provide useful cues for migrants. A stable cue not related to the local environment, such as photoperiod or a calendar cue (Åkesson et al. 2017) can be used as a

safeguard for birds to make sure not to depart too late under a relatively late onset of spring in the wintering grounds (Bauer et al. 2008a). Still, geese appear to use local temperature and vegetation greenness to time their departure from temperate staging grounds (Bauer et al. 2008a; Duriez et al. 2009; Shariatinajafabadi et al. 2014; Kölzsch et al. 2015; Si et al. 2015a). However, due to the low climatic connectivity, this results in a migration timing which is hardly plastic under advancing phenology in their northern breeding grounds, as witnessed by a stable date of migration departure for barnacle geese in the Svalbard population (Tombre et al. 2008) and the Barents Sea population (Eichhorn et al. 2009).

Limiting factors for advancing migration and reproduction phenology

The unequal advancement in the onset of spring between temperate staging and Arctic breeding grounds will affect both food availability and cues which geese can use to time their migration. This can in turn constrain an advancement in the timing of migration, by 1) changing the timing of food quality and availability at a faster rate in the Arctic then in temperate regions, there constraining the time available for accumulating body stores before and during migration (constraint hypothesis), and 2) a rapid advancement of Arctic spring without a change in the local cues at staging sites, making it more difficult for geese to correctly time their departure for migration (cue hypothesis; Visser et al. 2012). The pivotal question is which of these mechanisms forms a more important limiting factor for adapting phenology of migration and reproduction to climate warming.

Timing of fuelling for migration

While the migration period is often viewed as the time during which animals move from their wintering grounds to their breeding grounds, the time needed for energy deposition prior to departure is just as crucial in animal migration (Alerstam & Lindström 1990). Preparation for the migratory period may already start in mid-winter, when animals can feed on locally abundant resources to make the journey to a next stopover site (Bayly et al. 2012; Thorup et al. 2017). Some birds which travel large distances between wintering and breeding grounds, such as Arctic Terns travelling over 80.000 km between Antarctica and the Arctic (Egevang et al. 2010), may in fact be in a migratory state for the larger part of the year, continuously preparing for a next migratory flight. An advancement in reproduction phenology may not only require migrants to advance their timing of active migration, but also in the preparation of migration. Energy deposition or ' fuelling', is only possible when energy intake exceeds energy expenditure (Lindström 2003), and an advancement in fuelling may be limited by the revenues for foraging early in the season. For barnacle geese fuelling in North-Western Europe during early spring, short day length permitting only little time for grazing during the day and low quality of forage plants can importantly limit the daily energy intake of geese (Owen et al. 1992), while

cold conditions can keep energy expenditure at high levels. Although an advancement in fuelling may be constrained, geese may currently not be driven to initiate fuelling at the earliest possible day, suggested by an increase of body mass occurring only in late spring (Ebbinge & Spaans 1995). This creates a challenge when investigating whether a time constraint potentially limits the advancement of fuelling for migration. I strived to answer this question using a theoretical approach, a dynamic migration model in which we advanced optimal conditions for reproducing in the Arctic (Chapter 3), and a natural experiment, where we compared time budgets of migratory geese during spring fuelling with those of resident geese, which breed 2 months earlier and appear to be under a stronger time constraint (Chapter 6).

Our dynamic programming model (Chapter 3) calculates the optimal migration strategy in terms of location, day and body condition on a migratory flyway with discrete staging sites. Food becomes available at given times on different staging sites, and availability varies with the season (Figure 3.1a). Individual animals start at a wintering site, and at each time step they may choose to stay and increase body stores by foraging at the current site, or spend energy by migrating to a subsequent staging site. Timing of arrival and body condition together determine the expected reproductive success. We first ran this model for a baseline scenario, in which timing of food availability and optimal reproduction timing reflected conditions encountered by barnacle geese in 2009. When observing the body mass trajectories obtained from the model in the baseline scenario (Figure 9.2b), we can see that the onset of fuelling in mid-March is comparable with onset of fuelling as modelled from time-budgets of geese tracked in 2015 (fig 9.2a; see Box 9.1 for methods). We then compared the baseline scenario with climate warming scenarios, in which we advanced the timing of food availability and optimal reproduction timing, with a relatively larger advancement in Arctic sites compared to temperate sites. Under climate warming, geese were able to advance the onset of fuelling by roughly 52 days when they needed to advance arrival on the breeding grounds by 59 days. As geese in the model initially lost body mass during winter, a response to increase manoeuvrability for escaping predators incorporated in the model, they were able to make a strong advancement in the onset of fuelling by shortening the period of body mass loss (Figure 9.2b, c). Body mass loss during winter months is indeed observed in geese, but it is questioned whether this is an adaptive response of birds, or whether it is driven by a negative energy budget in the stringent winter period (Owen et al. 1992). Nevertheless, the duration of the period of body mass loss in the dynamic programming model seems comparable to results from the time-budget based body mass trajectories (Figure 9.2a). The dynamic programming model thus shows that under the need to advance departure for migration under climate warming, the time available for foraging and food quality early in the season does not limit an advancement in fuelling. On the other hand, when we ran scenarios in which geese were unable to predict, from the wintering grounds, an strongly advancing onset

of spring in the breeding grounds, they were unable to arrive in time on the breeding grounds. Our dynamic migration model thus predicts that cues, not constraints, are the most important limiting factor for advancing migration timing.
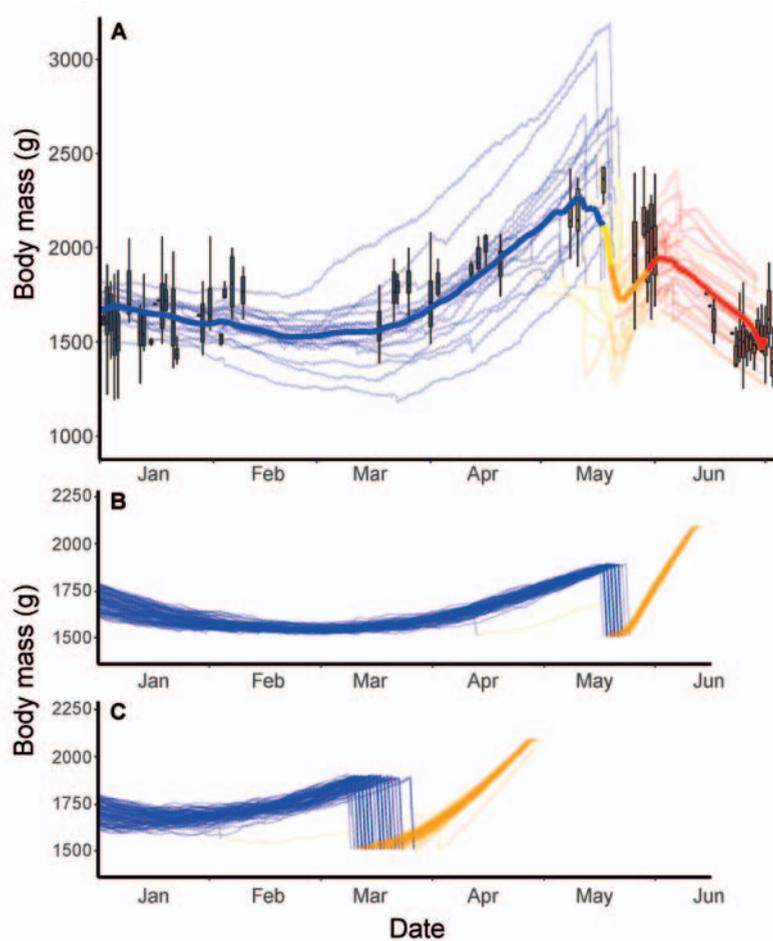

Figure 9.2: (A) Body mass trajectories for individually tracked barnacle geese in the spring of 2015, as modelled from accelerometer derived time-budgets and environmental data, with thin lines showing individual geese and the thick line showing average body mass. Boxplots show body mass measurements taken at the same day numbers between 1980 – 2017. Colours show locations (blue = Wadden Sea region, yellow = Baltic Sea region, orange = Barents Sea stop-overs, red = Kolokolkova Bay). (B-C) Modelled body mass trajectories of geese from the dynamic migration model described in Chapter 3, under environmental conditions as in the callibration scenario of 2009, and the extreme scenario of +5 °C warming and an amplification factor of 2.5.

An important difference between the output from the dynamic programming model and the body mass trajectories obtained from time-budgets is the relatively rapid fuelling rate shown in the body mass trajectories, which is confirmed by body mass measurement taken in the field (Figure 9.2a; Eichhorn 2008). While we have used fuelling rates based on foraging in natural salt marsh habitats in the dynamic programming model, barnacle geese currently make more use of agricultural habitats for fuelling where intake rates are higher (Box C). While it has been suggested that by fuelling only in these habitats they might miss important protein sources necessary for successful reproduction (Prop & Black 1998), there appears to be no difference in amino acids acquired by geese in both habitats (Eichhorn et al. 2012), and we find that also geese which only use agricultural habitats for fuelling can successfully reproduce (Box C). Moreover, faster fuelling rates in agricultural habitats would even increase the potential for advanced fuelling under climate warming.

In recent decades barnacle geese have expanded their breeding range from the Arctic to temperate latitudes, where they have taken up a resident lifestyle (van der Jeugd et al. 2009). As resident and migratory geese mix during winter, they still show genetic exchange between populations (Jonker et al. 2013). Although resident barnacle geese have advanced their laying dates by 2 months in comparison to their Arctic counterparts, they apparently breed too late, as most individuals initiate nesting while the prospects for survival of their offspring are already declining (van der Jeugd et al. 2009). This is supported by the fact that another species of goose breeding in temperate Europe, the greylag goose *Anser anser,* is able to nest already in early March, with their chicks hatching in time to profit from high food quality (Kamp & Preuss 2005). It is hypothesized that resident barnacle geese are limited in time to acquire enough body stores for earlier breeding. As it can thus be expected that resident barnacle geese start to deposit energy to fuel body stores at their earliest possibility, this creates a unique opportunity to test whether migratory barnacle geese, which may not initiate fuelling at the earliest possibility, still have leeway to advance the onset of fuelling. In Chapter 6 we study the onset of fuelling with GPS-loggers including accelerometers, deployed on a migratory and resident population of barnacle geese. Accelerometers can be used to distinguish different types of animal behaviour (Shamoun-Baranes et al. 2012). I compared accelerometer-based time budgets, and found that despite differences in time spent grazing in early winter, both resident and migratory populations of barnacle geese started to increase grazing in mid-February (Figure 6.3a and b). This increase resulted from a constantly increasing grazing time with increasing day length, supplemented with grazing during moonlit nights to keep a stable grazing time per day until mid-February. Energetic costs still remained high until mid to end February (Figure 6.2 c and d), potentially limiting fuelling. To find out when geese were able to deposit energy and thus increase in body mass, we combined time-budgets with data on potential energy intake and calculations of energy expenditure (basal metabolic

costs and thermoregulation costs) to model body mass trajectories over the season (Figure 6.3). These show that both populations started to increase in body mass around mid-March, matching body mass measurements of migratory geese (Figure 9.2a). Despite the lack of an advancement in fuelling for resident geese, we still find evidence that geese may be able to advance the moment of fuelling. Geese appear able to compensate for limited grazing during short days by grazing during moonlit nights (Ebbinge et al. 1975), but also increased day time grazing as a response to higher energy expenditure or lower metabolisable energy intake, suggesting that geese are not necessarily limited in daytime hours to increase grazing. The similar onset of fuelling in both populations however indicates that geese initiate fuelling as a response to increasing day length. The onset of fuelling has indeed been shown to be endogenously determined in passerines, suggesting that this is rather inflexible (Maggini & Bairlein 2010; Bairlein et al. 2013; Maggini et al. 2017). While there may be time to advance fuelling, geese seem constrained by inflexible cues to advance under climate warming, which again supports the cue hypothesis.

Timing of migration departure

Although animals may be busy preparing for migration for months in advance, active migration starts only when animals begin their journey towards their breeding grounds. Migration departure may have a range of different drivers, depending on the migratory strategy of a species or individual (Schmaljohann & Eikenaar 2017). Some animals migrate northwards by 'hopping' or 'skipping' (Piersma 1987), making several shorter migratory flights to reach their destination, meanwhile making use of multiple stopover sites. This strategy is used by for example greater white-fronted geese *Anser albifrons* (Kölzsch et al. 2016a), which can in this way make optimal use of a green wave of peak food quality on staging sites (van Wijk et al. 2012). Departure for migration in such a strategy may be importantly determined by increasing revenues for foraging on subsequent staging sites later in the season, making it more beneficial to continue migration to following staging sites. On the other side of the spectrum are species which make a migratory ´jump´, reaching their northward destination in one or two long migratory flights (Piersma 1987). Typical examples include mostly high Arctic species, such as bar-tailed godwits *Limosa lapponica* (Battley et al. 2012) and brent geese *Branta bernicla* (Green et al. 2002). These migrants use only few stopover sites and may stage for long period on their wintering grounds (Ebbinge & Spaans 1995). Their departure for migration may then be more importantly driven by either their internal state, such as the amount of accumulated body stores (Schmaljohann & Eikenaar 2017), and environmental factors, including cues which can predict the optimal timing of arrival on the breeding grounds (Bauer et al. 2011) or favourable wind conditions for migration (Piersma & Jukema 1990). As discussed above, different rates of climate warming in temperate wintering grounds and Arctic breeding grounds may have strong impact on environmental factors, including

the timing of food availability on staging sites, but also the value of local cues to correctly predict the timing of optimal conditions in the breeding grounds. This can strongly affect the timing of departure for migrants, but in what way depends on their migration strategy. For barnacle geese, multiple studies have shown how they make use of a green wave during migration (van der Graaf et al. 2006; Shariatinajafabadi et al. 2014; Si et al. 2015a) which would suggest a 'hopping' strategy (Hübner et al. 2010). On the other hand, the low predictability between stop-over sites (Kölzsch et al. 2015) might allow for such a strategy within temperate or Arctic segments of their flyway, but not between segments. The long staging time in the wintering grounds during which barnacle geese accumulate a large energy deposit (Figure 9.3a) is more reminiscent for birds which use a 'jump' strategy (Lindström & Piersma 1993; Piersma 2002). It may be difficult to name a single strategy for barnacle geese, but the essential question in the scope of climate warming is what determines the decisions for migration timing in barnacle geese.
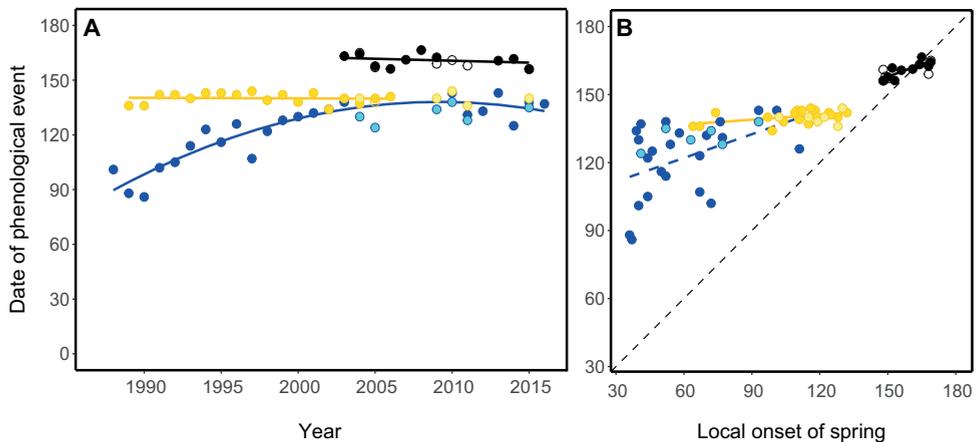

Figure 9.3: (A) Departure from the Wadden Sea (blue), Baltic Sea (yellow), and nest initiation dates (black) of barnacle geese between 1987 and 2016. Dark-blue and yellow dots show counts of mass migration, black dots show average nest initiation dates in the Kolokolkova Bay. Light-blue, light-yellow and white dots show data from individually tracked birds (Chapter 7). Lines show linear regression of the migration count data and average laying dates. (B) Migration and reproduction timing as affected by the date of local onset of spring, which is measured by GDD for the Wadden Sea and Baltic Sea (see above) and by date of 50% snowmelt in the Kolokolkova Bay. The dotted line shows y = x, on which dates would fall if birds would match departure / laying dates with the local onset of spring. Data from mass migration counts from the Wadden Sea were provided by Kees Koffijberg, data from Baltic Sea by Götz Eichhorn (Eichhorn et al. 2009).

Within the temperate segment of their migration, barnacle geese have shown a strong shift in migration timing, as shown by Eichhorn and colleagues (Eichhorn et al. 2009). During past decades, barnacle geese have delayed their departure for migration from their

wintering grounds in the North Sea region, thereby decreasing staging time on stopover sites in the Baltic Sea (Figure 9.3a; see Box 9.1 for methods). This appears not so much a response to a change in local climatic conditions (Figure 9.3b), but more likely has evolved in reaction to increased competition for food at the Baltic staging sites, where a local breeding population of barnacle geese has increased in recent decades (van der Jeugd et al. 2009). Alternatively, perceived predation risk increased due to increasing numbers of local white-tailed eagles *Haliaeetus albicilla* (Jonker et al. 2010). Potential metabolisable energy intake derived from food and dropping samples and dropping rates, show that energy intake is currently much lower in the Baltic region compared to the North Sea region (Figure B.5). Additionally, from time budgets derived from accelerometer data of migrating barnacle geese, I show that barnacle geese which make a stopover in the Baltic Sea region spend relatively little time grazing (Figure B.4), instead displaying more inactive behaviour. This is a likely indication that geese have reacted to low food quality by shortening their stay in the Baltic, and using the Baltic stopover mostly for resting. However, by using acceleration data I probably lump resting and vigilant behaviours together in inactive behaviours, and the increased amount of time inactive may thus indicate that geese cannot forage as they have to remain vigilant for marauding white-tailed eagles. Currently, variation in departure from the North Sea region mostly results from differences between individual migration strategies rather than differences between years.

While timing of departure from the North Sea differs between individual barnacle geese, departure from the Baltic Sea is very much synchronized, with all geese departing within a few days (Box B, Chapter 3). The date of departure also shows little variation between years (Figure 9.3a), and although there is adjustment of departure dates to local onset of spring, the reaction norm to earlier onset of spring is very slight (0.07 days earlier departure per earlier day onset of spring, Figure 9.3b). Local climate in the Baltic region is supposedly not a reliable cue for predicting climatic conditions in the Arctic (Kölzsch et al. 2015), and as I show in Chapter 7, the departure timing of geese is not adjusted to optimal timing of arrival in the Arctic breeding grounds. A rigid timing of migration departure may result from the use of local climate-related cues, which have not shown change over time, or from static photoperiodic cues (day length) (Gwinner 1996; Duriez et al. 2009; Conklin et al. 2013). Alternatively, migration departure could be constrained by the time needed to fuel up before departure, especially when birds need body stores not only to fuel their migration, but also their reproduction (Drent et al. 2007; Kölzsch et al. 2016a). As shown above, an advance in the timing of fuelling may also be constrained the use of cues which do not give information on optimal timing of migration under climate warming. Although a rigid departure timing may result in an arrival timing which is on average optimal under yearly variations in the current Arctic climate, lack of plasticity may become problematic under ongoing advancement of the onset of Arctic spring.

Timing of arrival and reproduction

Despite a rigid departure timing from the Baltic, I show in Chapter 7 that barnacle geese are very flexible in adjusting their arrival to local climatic conditions on their Arctic breeding grounds. Geese advanced their arrival in years with an earlier onset of spring (measured as the date of snowmelt) in the Arctic, thus appearing to be capable of adjusting migrating timing under conditions of climate warming. Geese can make such an adjustment in arrival timing by flexible duration of stopover time along the Barents Sea, essentially increasing their migration speed by reducing time on stopovers (Schmaljohann & Both 2017). While approaching the breeding grounds, local climatic conditions become better correlated with those on the breeding grounds (Kölzsch et al. 2015). This allows birds to assess the progress of spring conditions on the breeding site from staging sites, and to decide to continue on migration if they run the risk of arriving too late. Rather than staging on stop-over sites along the Barents Sea, geese seem to skip part of the green wave and continue to their breeding grounds when spring comes early. Advanced arrival on the breeding site may be beneficial due to the priority of certain resources, such as high quality territories (Kokko 1999), but its main benefit in the light of climate change is the possibility for advanced timing of reproduction (Both & Visser 2001). However, in Chapter 7 we show that despite a strong advancement in arrival timing under an early onset of spring, barnacle geese advanced their laying dates much less. As this resulted in a phenological mismatch with strong fitness consequences, we argue that under earlier springs geese lay at suboptimal dates as they are unable to lay earlier. While arriving much earlier, geese seem to need the 'pre-breeding' time after arrival to fuel up to an ample body condition necessary for laying and incubating eggs (see next paragraph). We show that they use this pre-breeding time mostly for grazing, and use more locally acquired body stores for egg production when spending more time pre-breeding, but also in years with an earlier onset of spring. Combined with the fact that geese do not lay much larger clutches in years with an early onset of spring, which shows that the acquired resources during the pre-breeding period are not used to produce more eggs, this suggests that an increased pre-breeding period after advanced arrival results from the necessity for refuelling.

This implies that regardless of a flexible timing of migration and the possibility to advance arrival on the breeding grounds under climate warming, the timing of reproduction for geese is more importantly determined by the time necessary to acquire body stores for breeding. In most species of waterfowl the female incubates the eggs alone, and as this leaves little time for foraging during the incubation period, she needs to have energy reserves in store to finance both egg laying, but also a period of fasting while incubating the eggs (Spaans et al. 2007; Eichhorn et al. 2010). This makes the energy reserves necessary for reproduction relatively large, and geese can only start laying when having acquired a minimum threshold of resources (Rowe et al. 1994). Being a partial

capital breeder (Drent et al. 2006; Nolet 2006), barnacle geese are able to bring part of the required body stores with them from temperate staging sites, but also rely on body stores which are acquired locally (Hahn et al. 2011) or on proximate staging sites (Klaassen et al. 2006). As geese appear to be unable to predict conditions in the Arctic from temperate staging sites, not only their departure timing, but also the amount of body stores upon departure may show little variation between years. After departure they lose part of these body stores by migration itself and thus need time to replenish these stores, either on Arctic stopover sites or on the breeding grounds itself. This is nicely visible in the body mass trajectories of individually tracked birds in 2015 (Figure 9.3a), where geese bring more body stores on migration to the Arctic than necessary for migration only, but replenish body stores after arrival, on stop-over sites or during pre-breeding, to gain a body condition high enough to fuel reproduction. The time needed to refuel after departure from the Baltic Sea therefore forms the main limitation for an advancement in timing of reproduction, rather than an advancement in the timing of arrival. Changes in arrival time may more importantly reflect a choice in where resources for breeding are acquired.

Waterfowl are known to be flexible in the extent to which they rely on capital breeding stores (Klaassen et al. 2006; Williams et al. 2017). In Chapter 7, I show that the extent to which barnacle geese use local or capital stores reflects their timing of migration, and geese use more local resources for reproduction when arriving at the breeding grounds early. Under climate warming, when early snowmelt causes advanced forage plant growth on the breeding sites, geese may opt to spend less time on Arctic stopover sites and arrive earlier on the breeding site to fuel there, which makes them shift more towards an income-breeding strategy. Regardless of such a shift, the time needed to acquire the amount of necessary body stores may not change much, shown only by a small advancement in laying dates under climate warming (Figure 7.1b). This suggests that advancement of reproduction timing is mainly limited by a time-constraint. This time-constraint may come about by a lack of advancement in migration departure, which seems to result from the use of cues which no longer match the advancing onset of spring in the Arctic. In conclusion, the main limiting factor for advancing migration and reproduction phenology, are cues at wintering and staging sites, due to which geese initiate fuelling and migration too late. A time-constraint exists in combination with a too late departure for migration.

Breeding strategy may be a keystone factor determining the ability of migratory birds to advance migration timing under climate warming. While capital breeders may show a strong acceleration of migration speed as we have seen in Chapter 7, the migration speed of smaller birds which are not capital breeders appears much more rigid (Schmaljohann & Both 2017). The duration and speed of migration is mostly determined by the time spent fuelling on stopover sites (Alerstam & Hedenström 1998; Alerstam 2003). For income breeders, which gather the energy stores needed for reproduction locally on the

breeding site, the accumulation of body stores on stopover sites serves primarily to fuel migration itself. As this generates short stopover times, it can be expected that without increased fuelling rates on stopover sites (Hedenström et al. 2007) there is little room for income breeders to shorten their stopover duration and thus accelerate their migration (Schmaljohann & Both 2017) but see (Ahola et al. 2004; Marra et al. 2005). Arctic shorebirds, which breed at similar sites as Arctic-nesting geese but are income breeders (Klaassen et al. 2001), form a useful analogy to waterfowl as capital breeders. Arctic shorebirds seem to show little flexibility in migration arrival under changing climatic conditions (Meltofte et al. 2007). Laying dates of 8 species of Arctic shorebirds in Barrow, Alaska, have in the past 14 years advanced at a slower rate than the date of snowmelt, on average 0.36 day earlier laying date per earlier day of snowmelt (Saalfeld & Lanctot 2017), where we find a similar value for barnacle geese (0.35, Chapter 7). This timing of reproduction may become similarly mismatched with the peak in food availability, which comes in the form of arthropod abundance for shorebirds, and also appears to be regulated by the onset of spring and possibly the date of snowmelt (Tulp & Schekkerman 2008; Reneerkens et al. 2016). Income and capital breeders, although differing in their ability to adjust migration arrival, both will need to advance migration departure, in order to advance their laying dates under Arctic climate warming.

Fitness consequences of a warming Arctic

Despite the observed advancement in laying dates for barnacle geese when facing an earlier onset of spring (Chapter 8), as found in many other species (Crick et al. 1997; Saalfeld & Lanctot 2017), we have seen that this advancement may not be enough as goslings suffer from a phenological mismatch with peak food availability in earlier springs (Chapter 7). There is increasing evidence that many species are facing phenological mismatches under climate warming, also in the Arctic (Stenseth & Mysterud 2002; Visser & Both 2005; Donnelly et al. 2011; Saino et al. 2011; Gilg et al. 2012; Thackeray et al. 2016). These mismatches can have strong effects on offspring growth (Doiron et al. 2015; van Gils et al. 2016) and may incur fitness costs (Post et al. 2008; Clausen & Clausen 2013; Zimova et al. 2016). Although a lack of advancement in breeding phenology has been connected to population declines in many trans-Saharan migrants (Both et al. 2006; Møller et al. 2008; Saino et al. 2011), it is still under debate to what extent mismatches affect demography (Miller-Rushing et al. 2010; Reed et al. 2013a; Dunn & Møller 2014; Franks et al. 2017). In contrast to the emergence of phenological mismatches under climate warming, an earlier onset of spring has also been associated with ameliorated conditions for reproduction for animals breeding in the Arctic. Earlier springs provide an advanced food availability (Chapter 2), from which birds can profit on arrival, in turn allowing more birds to nest (Jensen et al. 2014; Van Oudenhove et al. 2014) and to accumulate more body stores which they can use to lay a larger clutch (Rowe et al. 1994; Van Oudenhove et al. 2014). Higher

nest survival and in earlier and warmer springs has been found for species of waterfowl and waders (Meltofte et al. 2007; Dickey et al. 2008; Van Oudenhove et al. 2014; Wood et al. 2016). This indicates that climate warming in the Arctic may differentially affect early and late stages of reproductive success (Dickey et al. 2008; Van Oudenhove et al. 2014), with earlier food availability providing benefits in terms of body condition and survival for adults but not for their offspring, which hatch too late to profit.

In Chapter 8 I collaborated with colleagues who collect data on in high Arctic colonies in Svalbard, to investigate whether barnacle geese benefit from earlier springs by increasing reproductive output up to gosling hatch. We show that when the onset of spring fell earlier barnacle geese are not only able to advance laying dates but also lay slightly larger clutches. A lower synchrony in laying dates in earlier years suggested geese were less time-constrained to initiate laying, potentially allowing more individuals to nest than in late years. Nevertheless, the number of hatching goslings did not show a strong trend with the onset of spring. Larger clutch size in years with an early onset of spring was apparently counteracted by an increase of partial nest predation or decrease of egg fecundity. Hatching success was not affected by the onset of spring in our study site in low Arctic Russia, but was much higher in years with an early onset of spring in one of the high Arctic sites in Svalbard. Early nesting geese are able to 'escape' from predation by polar bears (*Ursus maritimus*), which arrive in barnacle goose colonies in June are the main nest predators in these colonies. In years when geese nest relatively late, polar bears are able to reduce nesting success down to zero (Prop et al. 2015). When looking at the total reproductive success measured up to hatching, an earlier onset of spring has no beneficial effects on reproductive success, at least not in the lower Arctic.

In Chapter 7 we show that the peak in food quality falls roughly 25 days after the date of 50% snowmelt, and hence in order to match the moment of gosling hatch with this peak, barnacle geese have to initiate laying around this date of snowmelt. When they initiate nesting after the date of snowmelt, their goslings suffer from a reduction in daily survival rate. Survival rate decreases with an earlier date of snowmelt and a larger 'mismatch', measured as the difference between laying dates and date of snowmelt. When goslings hatch relatively late, food quality of forage plants may already be strongly reduced, as shown in Chapter 2 and by Doiron and colleagues (Doiron et al. 2014). Such a reduction in food quality and availability has been shown to strongly affect growth rate (Lepage et al. 1998; Brook et al. 2015; Doiron et al. 2015; Richman et al. 2015), but also survival, as goslings cannot survive on diets too poor in proteins (Lindholm et al. 1994; Richman et al. 2015). Also, smaller goslings are probably more susceptible to predation, diseases and exposure to cold, thereby suffering from lower survival (Lindholm et al. 1994). This is confirmed by our own observations at the study site in the Russian Arctic, where we often observed the smaller goslings to be taken by avian predators, glaucous gulls *Larus hyperboreus* and white-tailed eagles.

If not all components of reproductive success are affected in the same way by climate warming, it becomes relevant to take these components together to study the total effects of climatic variation on demography. Such analysis is typically conducted by studying the number of recruits in a population under years varying in weather conditions (Van Oudenhove et al. 2014). When combined with the birthdate of these recruits, this also allows studying the selection pressure on earlier laying under climate warming (van Noordwijk et al. 1995; Both & Visser 2001). Although the effect of hatching date on survival to the wintering grounds has been calculated for our colony in Arctic Russia by combining results from multiple years (van der Jeugd et al. 2009), the low proportion of marked individuals and difficulty of identifying individuals during incubation does not allow a similar comparison among-years. However, by combining multiple components on reproduction and survival in a matrix model as developed by Crets-Fokkema and colleagues (Crets-Fokkema et al. 2017) we can get a first grip on the effect of climatic variation on recruitment up to the 1st year in barnacle geese. I combined our data from the study site in Arctic Russia on the number of hatchlings, nest survival, gosling survival until fledging, fledgling survival to the wintering grounds and survival during winter months and spring migration, which was complete for the years 2003 – 2007 (see Box 9.1 for methods). From this analysis it appears that recruitment is strongly affected by date of snowmelt, with lower recruitment when snowmelt comes earlier (Figure 9.4a)., This is mainly caused by low gosling survival up to fledgling in years with early snowmelt. The average number of offspring that reaches the wintering grounds comes close to the average percentage of juvenile barnacle geese observed in the Netherlands during winter (9.7 % calculated vs. 11.7 % observed, data from (Hornman et al. 2016)). The pattern over years in observed percentage of juvenile birds does not match these results (Figure 9.4c), likely as the wintering population of barnacle geese in the Netherlands consists of birds breeding in the Arctic, the Baltic Sea region and in the North Sea region, which may strongly differ in reproductive success (van der Jeugd et al. 2009). Current reproductive success in temperate colonies may be more importantly driven by density-dependent effects rather than climatic variation (Madsen et al. 1999).

Although I show that the effects of a phenological mismatch on reproduction can potentially be strong, it is still questionable to what extent this will affect populations. Low reproductive success in years with mismatches may be compensated for by increased survival during winter months as competition for resources becomes smaller (Reed et al. 2013a, 2013b) or as food availability in wintering grounds is not a limiting factor, as is likely the case for barnacle geese which can feed on agricultural grasslands (van Eerden et al. 2005). In case mismatches are dependent on yearly climatic variations and do not take place in every year, the lower recruitment after a mismatch may be compensated by years without mismatches (Figure 9.4b). Despite current strong climatic variations (Figure 9.1a), many species which experience mismatches may not yet be affected in their

demography. The current population of barnacle geese wintering in NW-Europe is still showing an increase (Hornman et al. 2016), but it is not entirely clear whether this reflects an increase in both temperate and Arctic populations. Especially given the fact that there is still exchange between populations (van der Jeugd & Litvin 2006; van der Jeugd 2013; Jonker et al. 2013), the effects of climate change are unlikely to show at population level for barnacle geese. This may however quickly turn around when climate warming will follow the route predicted by the IPCC (Stocker et al. 2013), and years with an early onset of spring in the Arctic will become the norm rather than the exception.
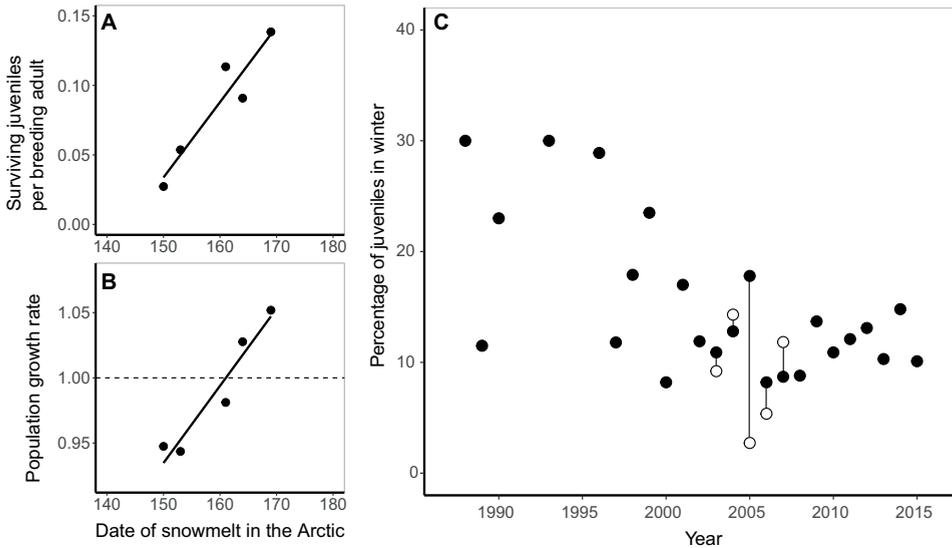

Figure 9.4: (A) The number of recruits (juveniles which survive up to the following summer) per breeding adult bird, given for 5 years (2003 – 2007) differing in date of snowmelt on the Arctic breeding site. (B) The population growth rate (lambda), calculated from adult survival and the number of recruits (see Box 9.1 for methods). (C) Percentage of juvenile birds observed in flocks of barnacle geese in the Netherlands between 1988 and 2015 (data from SOVON (Hornman et al. 2016)). White points show the predicted percentage of juveniles from the matrix model, vertical lines connect these to observed percentages in these same years.

How can geese adjust timing of migration to a rapidly warming Arctic?

If a current mistiming of reproduction in years with early snowmelt has such strong consequences on fitness of Arctic migrants, then what is their scope for advancing their reproduction and their migration timing under persistent climate warming in the Arctic? As we have seen, the time needed to acquire enough body stores for breeding after departure from temperate staging sites seems the main limitation to advance timing of reproduction. As a consequence, geese may only be able to advance reproduction under climate warming if they can adjust both departure for migration and the body stores they

bring with them, as predicted by our dynamic migration model as the optimal strategy (Chapter 3). While geese may not be time-constrained to advance departure, we show that the potential of geese to advance migration departure is very much dependent on their ability to predict, from their temperate wintering and staging grounds, the rapid climate warming on their breeding grounds. Indeed, we have seen that barnacle geese do not adjust timing of departure from the North Sea and the Baltic Sea to climatic conditions in the Arctic (Chapter 7), and timing of departure from the Baltic Sea seems to be only partially driven by local climatic conditions, and is likely the result from static cues such as photoperiod (Rees 1982). Alternatively, migration departure could be limited by the moment at which geese have acquired ample body condition for migration. While in theory geese appear able to advance the onset of fuelling (Chapter 3 and 6), the onset of fuelling may also be driven by day length as a static cue. With the optimal moment of reproduction in their Arctic breeding grounds being far apart from the onset of fuelling in the wintering grounds, in both time and space, it cannot be expected that geese can adjust their timing to yearly variations in the optimal timing of breeding.

To advance the onset of fuelling in the wintering grounds and the departure for migration from staging sites, geese will thus need to adjust their sensitivity to the cues they currently use (Visser 2008; McNamara et al. 2011). As an example, if barnacle geese use a photoperiodic cue and their departure from the Baltic Sea coincides with a day length of 17.4 hours (daynumber 140), they should adjust their date of departure to coincide with a shorter day length, such as 17.0 hours (daynumber 135). While most of the advances in migration timing which are currently observed are ascribed to phenotypic plasticity (Knudsen et al. 2011), changes in cue sensitivity are often considered to be implausible within the limits of phenological plasticity in an individual, as individual birds typically show little variation in migration timing (Van Buskirk et al. 2012; Conklin et al. 2013; Gill et al. 2014). Alternative to phenotypic plasticity, changes in timing may come about by evolutionary responses. Although the general potential of evolutionary response to drive changes in phenology and migration timing has been shown (Pulido 2007; van Asch et al. 2012), the only study to date with the data necessary to link genetic change with advanced migration timing, found that an advance in migration timing occurred due to phenotypic plasticity, as selection for migration timing only occurred on the non-genetic component of this trait (Tarka et al. 2015). Also, the Arctic region harbours many species which live relatively long, and for which evolutionary changes may act too slow to allow an adequate response to rapid climate warming (Gilg et al. 2012).

If Arctic migrants are to adjust their migration timing to climate warming, this will be most likely via phenotypic plasticity. As pointed out before, individual geese may be able to adjust migration timing within temperate and Arctic segments of their migration route. This is shown by the increasing delay in departure from the North Sea in the past decades, likely resulting from individually altered behaviour (Eichhorn et al. 2009), but

also by the advance in arrival on the breeding sites under early snowmelt, which partially results from individuals advancing their migration timing in the Arctic (Chapter 7). Given the rigid timing of departure from the Baltic Sea, it is the question whether a phenotypic response is also possible in adjusting migration timing between temperate and Arctic segments. Given the flexibility in other migration segments, flexibility in migration timing may come about rapidly in barnacle geese, as they are social migrants. In geese and other long-lived bird species, such as cranes, social learning may play an important role in transferring migration and reproduction strategies within a population, as juveniles adopt the strategies of their parents or other adults (Mueller et al. 2013; Teitelbaum et al. 2016). Such a cultural transmission is relatively fast compared to genetic change (Sutherland 1998; Visser 2008). Many of long-lived birds guide their offspring during their first southward migration, and stay together for the large part of winter. Juveniles and adults only become separated during spring (Jonker et al. 2011), after which juveniles make their first northward migration without their parents. Nevertheless, migration in groups together with other individuals allow juveniles to pick-up important knowledge on migration and stopover strategies (Agostini et al. 2017). During their life, individuals may be able to optimize migration strategies by learning from past mistakes (Madsen 2001). If some individuals initiate an early departure from the wintering site, for example the single individual departing from the Baltic Sea 8 days before average departure at 20th of May in 2015 (Figure B.1), this may show rapid spread through the population, given that this advance is beneficial for reproduction. Although social learning may allow for rapid adaptation, its success depends on the question whether the rate of adaptation can equal the rate of Arctic climate warming.

If birds fail to adjust their migration phenology to climate warming, an alternative option to avoid a mismatch between the moment of chick hatching and peak food quality may be to migrate further north (Burger & Both 2011; Burger et al. 2013). Modelling studies show that suitable habitat for Arctic breeding birds will indeed shift northward (Jensen et al. 2008; Wauchope et al. 2017), and there are indeed examples of birds which have made a northward shift in their breeding grounds (Knudsen et al. 2011). For barnacle geese breeding along the Barents Sea, the most likely shift would be to start occupying northern parts of Novaya Zemlya. Given their high site fidelity (Karagicheva et al. 2011), geese may not be prone to make such a northward shift.

Forward look

In this thesis I have studied the limitations of long-distance migrants to adjust migration and reproduction timing to rapid climate warming in the Arctic by zooming into the barnacle goose as a model species. Barnacle geese, and geese in general, appear to have traits which facilitate a large flexibility in migration timing. Their reproduction can be financed by an adjustable mixture of capital body stores brought in from afar or locally

acquired income, which allows for similar flexibility in migration timing. Geese may surf on a green wave to acquire these resources during a 'hopping' migration, but may also deploy a 'jump' migration, where they profit from high food availability in manmade agricultural landscapes to depart relatively late from the wintering grounds, partly skip the green wave, and arrive early at their Arctic breeding sites where they can acquire the rest of the necessary body stores for breeding. Geese have already shown flexibility in adjusting migration timing by individual plasticity and social learning, which may also enable them to adjust their departure on migration timing under persistent early onsets of spring in their Arctic breeding grounds. Nevertheless, I have shown that this flexibility in migration timing cannot lift the current time-constraints to adequately advance reproduction timing under rapid climate warming in the Arctic. The rise of a phenological mismatch between late hatching chicks and food quality which peaks much earlier in the season has strong consequences on fitness components, eventually precipitating to consequences for the population growth rate.

While there may be hope for geese to advance migration departure, and thereby timing of reproduction, through social learning under ongoing climate warming, this may be very different for most other Arctic migrants. Passerines, seabirds and waders breeding in the Arctic, in contrast to geese, do not migrate together with their parents (van de Kam et al. 2004; Péron & Grémillet 2013), which means that they depend largely on internal mechanisms to time their migration (Åkesson et al. 2017). While Arctic shorebirds migrate in flocks, adults and juveniles often travel separately (van de Kam et al. 2004), which also does not enable the passing on of changes in migration timing. Also in contrast to geese, which winter mostly in anthropogenic landscapes where food is abundant (van Eerden et al. 2005), Arctic shorebirds depend on natural wetlands which are under increasing pressure from anthropogenic use (Halpern et al. 2008) through habitat destruction and the harvesting of food sources on which these birds rely (Piersma 2007; Murray et al. 2014). While the increased pressure on these habitats by itself may strongly affect potential fuel deposition rates and survival of shorebirds (Piersma et al. 2016; Studds et al. 2017), this becomes even more of a threat under the need to advance migration timing under Arctic climate warming.

Many species of Arctic geese have gone through rapid population growth in the past decades (Madsen et al. 1999; Koons et al. 2014; Lefebvre et al. 2017), as after coming close to near extinction they benefitted from hunting restrictions (Fox & Madsen 2017) and high food availability in agricultural landscapes (Abraham et al. 2005; Gauthier et al. 2005; van Eerden et al. 2005). Currently, large populations of Arctic geese cause major damage on agricultural fields, and many species of geese have now been termed as being 'overabundant' (Fox & Madsen 2017; Lefebvre et al. 2017). To resolve the conflict between Arctic goose populations and agriculture, management plans are put into place, involving large-scale harvesting of geese down to a population target level (Koons et al. 2014; Madsen

et al. 2017) and the scaring of geese from agricultural fields (Nolet et al. 2016; Simonsen et al. 2017). However, geese seem to have little other options than to use manmade grasslands, as the natural wetlands which are their original wintering habitat – natural wetlands - are simultaneously being destructed (Gibbs 2000; Kennish 2001; Millennium Ecosystem Assessment 2005; Ma et al. 2014). While wintering goose populations are still numerous in Europe and North-America, geese in China show steep declines (Fox et al. 2011), as they do not have access to agricultural fields and are completely reliant on natural wetlands (Yu et al. 2017). With a rapid growth of the local economy, these wetlands are disappearing through human exploitation and destruction (Fang et al. 2006).

The destruction of wintering and staging habitats of many migratory animals is continuing at fast rates on a global level (Millennium Ecosystem Assessment 2005). Together with the need to advance migratory schedules under human-induced climatic warming, this can become a life-threatening mix for migrants (Travis 2003). Paradoxically, Arctic species which breed on our world's edge, furthest away from large civilizations, may be most vulnerable to this combined anthropogenic threat.

Box 9.1 Methods

Climate data

I collected data on the average daily temperature between 1987 and 2015 from weather stations in the North Sea and Baltic Sea region, and calculated an average daily temperature per region. Weather stations along the North Sea included Lauwersoog, The Netherlands (53°24' N, 6°12' E), Wangerland, Germany (53°37' N, 8°01' E), Sankt Peter-Ording, Germany (54°18' N, 8°38' E), List (Silt, Germany) (55°01' N, 8°25' E). Weather stations along the Baltic Sea included Visby, Sweden (57°38' N, 18°17' E), Vilsandi, Estonia (58°22' N, 21°48' E) and Ristna, Estonia (58°55' N, 22°04' E). I collected data on snow cover, measured as the extent of snow around the weather station rated from 0 (no snow) to 10 (full snow cover), from weather stations along the Barents Sea, including Onega, Russia (63°90' N, 38°12' E) and Shoina, Russia (67°88' N, 44°13' E). Additionally, I collected data on daily temperature from Naryan-Mar (67°63' N, 53°03' E), and included snow cover data from our study site at the Kolokolkova Bay (see Chapter 7 for methods). Data from The Netherlands was acquired from the Royal Netherlands Meteorological Institute (www.knmi.nl), data from Germany was acquired from the Deutscher Wetterdienst (www.dwd.de), data from Sweden was acquired from the Swedish Meteorological and Hydrological Institute (www.smhi.nl), data from Estonia was acquired from the Estonian Weather Service (www.ilmateenistus.ee), data from Russia was acquired from the All-Russian Scientific Research Institute of Hydrometeorological Information (www.meteo.ru).

From average daily temperatures I calculated growing degree days (GDD) according to van Wijk et al. (van Wijk et al. 2012), using 0 °C as a threshold temperature for grass growth (Chapter 2). The onset of spring was then determined as the Julian date at which GDD reached 180 (Chapter 3). For snow cover, the onset of spring was determined as the Julian date at which half the snow had melted (a snow cover lower than 6 for data from weather stations, and a snow cover lower than 50% for satellite data).

Body mass trajectories

We used GPS and acceleration data collected from the 18 Barnacle geese equipped with UvA-BiTS GPS-loggers which initiated breeding in 2015, to model their body mass trajectories between January – June 2015. The GPS-loggers stored 48 (wintering grounds) to 288 (breeding grounds) GPS locations per day together with tri-axial accelerometer measurements (0.5 seconds at 20 Hz, i.e. 10 measurements). Energy budgets were calculated from 1) time budgets derived from accelerometer data, 2) metabolisable energy intake from field data and 3) data on thermoregulation and existence energy from weather data and a bio-energetics model. While most information on these components is provided in Chapter 6 and the supplementary methods of this chapter, I here provide details on how these data combined to calculate body mass trajectories, and which assumptions were made.

For one GPS-fix (i) every 30 minutes (locations on wintering grounds) or every 15 minutes (locations beyond wintering grounds), we calculated the bird's body mass (W_i) as a result of

body mass at the previous GPS-fix (i - 1) plus the net intake of metabolised energy (I_i) minus the energy needed for existence (E_i) and thermoregulation (T_i), multiplied by the cost and efficiency of body mass storage or use. We assumed that heat generated during activities can be used for thermoregulation (Paladino & King 1984), and only when $T_i > E_i$ the bird pays additional thermoregulation costs. When energy is metabolised above the energetic needs, birds store the product (P_i) in the form of fat and protein stores with an efficiency of 0.8 (Blaxter 1989). When energetic costs exceed the metabolized energy, body stores are burned to gain energy with an efficiency of 1. Mass change, either for storing or burning body reserves, comes with a cost, for which we use the energy density of deposited tissues as calculated for female pink-footed geese, which equals 29 kJ/g (Madsen & Klaassen 2006).

We collected data on forage plants in the Wadden Sea (Chapter 6), Baltic Sea (Box A) and Barents Sea to calculate metabolisable energy intake (MEI) for staging sites, following the methods as provided in supplementary materials of Chapter 6. I calculated growing degree days for the Baltic Sea from temperature as described above. MEI for staging sites on the Barents Sea was measured by Eichhorn and Prop in 2002 (unpublished), and equalled 2.45 kJ per minute.

As we did not weigh the individual birds during staging at the wintering grounds, we derived a correlation between body size (measured as tarsus length * head length) and body mass from measurements of 29 female geese caught during winter 2008 – 2009 in the province of Friesland, the Netherlands (Ens et al. 2008). Using this correlation (body weight = 0.2186*(tarsus length * head length) + 254.43) I calculated body mass from tarsus length (as taken in summer 2014 at catch) for the 18 barnacle geese.

We validated our model outcomes by comparing body mass (Wi) with body mass taken from 590 adult female geese over the season: 202 geese caught in several places in the Netherlands in January – February 2000 – 2009 (Müskens, unpublished); 29 geese caught in the Lauwersmeer region in January 2008 and 2009 (Ens et al. 2008); 77 geese caught in Schleswig-Holstein in March 1979 and 1989 (Ebbinge et al. unpublished); 67 geese caught in March 2016 and 2017 near Freiburg (Müskens, unpublished); 109 geese caught at Schiermonnikoog in April 2004 (Eichhorn et al. 2012); 29 geese caught in Gotland in May 1982 (Ebbinge et al. unpublished); 68 geese shot by hunters at the Kolokolkova Bay in late May – early June 2003, 2004 and 2015 (Eichhorn, Lameris, unpublished; 3) 76 geese weighed on the nest during incubation in June – early July 2014 and 2015 at the Kolokolkova Bay, including 14 of the GPS-logger geese (following methods (Eichhorn et al. 2010)).

Departure dates

I collected data on departure for mass migration as observed from counting posts at Eemshaven, The Netherlands (53°26' N, 6°53' E) and at Kotka, Finland (60°27' N, 26°56' E). Data from Eemshaven was provided by Kees Koffijbergen (personal communication), and data from Kotka was extracted from Eichhorn et al. (Eichhorn et al. 2009). The date of mass migration

was then determined as the date at which the highest number of barnacle geese were observed to be flying in Eastward direction. I also included average laying date in the study colony at the Kolokolkova Bay, and added data on migration departure from the North Sea and Baltic Sea as collected in Chapter 7. I combined migration and laying dates with the onset of spring as described above for the North Sea region, Baltic Sea region and our study colony at the Kolokolkova Bay.

Population matrix model

I collected data on fecundity and survival to employ a matrix model as described in Crets-Fokkema et al. (Crets-Fokkema et al. 2017). I used this model to calculate per year for our study colony at the Kolokolkova Bay: 1) number of juveniles produced per breeding pair which survived up to the wintering grounds (fecundity divided by juvenile survival up to winter); 2) number of recruits per breeding adult (fecundity divided by juvenile survival up to following summer, divided by two to calculate per adult rather than per breeding attempt) and 3) population growth rate per year (lambda; calculated from the total adult survival chance over one year added to the recruit survival). As fecundity we took the combined measure of total hatching goslings per nest (Chapter 8), as juvenile survival (during growth and development) we took the gosling survival measures (Chapter 7), and as juvenile survival during autumn migration, winter period and spring migration we calculated survival rates with a mark-recapture analysis. We also calculated adult year-round survival in the components autumn migration, winter period and spring migration in a similar fashion.

Barnacle geese were captured and ringed with engraved plastic bands at the study colony at the Kolokolkova Bay between 2002 – 2009 and 2013 – 2015. Geese were observed by a large network of volunteers in the Netherlands (October – April) and by our research team in the breeding colony (late May – August). All observations were collected on www. geese.org. We extracted these observations and ringing data between 2002 and 2016, and separated observations in three periods of three months; autumn (October – December), winter (February – April) and summer (June - August). If a goose was observed once in one of these periods we assumed it was alive. We then ran a mark-recapture analysis with observation probability differing between the three periods, juvenile survival between the summer and autumn period differing between years, and adult survival differing between all three periods and years.

We compared juvenile survival up to the wintering grounds with juvenile percentages observed on the breeding grounds. These were observed by the Dutch Centre for Field Ornithology SOVON and provided by Kees Koffijberg (Hornman et al. 2016). To convert juvenile survival to a percentage of juveniles in the population, we divided juvenile survival by (1 –juvenile survival).