Rewarding round-trips or tiresome travels?
Comparing migratory and non-migratory lifestyles in barnacle geese
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CHAPTER 7

Synthesis

Michiel P. Boom
Chapter 7

SYNTHESIS

Migration is a well-represented life history strategy among birds, with about 20% of all bird species migrating between distant areas for breeding and survival (Kirby et al., 2008). Covering these distances inevitably involves costs, but these costs are expected to be offset by the benefits of exploiting suitable conditions in different areas throughout the year. Understanding these costs and benefits can provide insight into why some birds migrate, while others are residents. In this thesis, I applied an intra-specific comparative approach to gain insight into the costs and benefits of a migratory life history strategy (hereafter migratory strategy) in the barnacle goose (Branta leucopsis). By comparing migratory and resident barnacle geese, I tried to understand why barnacle geese migrate to the Arctic and how they are able to do so.

In the first part of this thesis, I studied differences between migratory and resident geese during the breeding and wing moulting period to understand the costs and benefits of migrating to the Arctic. In seasonal environments like the Arctic, the decision to breed is expected to depend on local environmental conditions such as the availability of nest sites and food, which depend on spring phenology. In Chapter 2, we used tracking data of female barnacle geese to derive breeding attempts, and investigated differences in breeding propensity and hatching probability in relation to latitude and spring phenology. In the Arctic, breeding propensity and hatching success decreased when onset of spring was late, while both reproductive parameters appeared generally high and independent of spring phenology at temperate latitudes. The Arctic breeding grounds are expected to provide good conditions for raising goslings, which we examined in Chapter 3 by comparing gosling growth among three populations (North Sea, Baltic and Barents Sea). We found that the faster growth in the Arctic could largely be explained by longer day lengths, which lengthens the available feeding time for the goslings. This fast growth is also necessary, since the short Arctic summer places a time constraint on geese breeding at high latitudes. In Chapter 4, we investigated this time constraint by comparing the timing of breeding and moult in the North Sea, Baltic and Barents Sea populations. We found a shorter time interval between breeding and moult in the Arctic compared to the temperate breeding populations, indicating a stronger time constraint at high latitudes. Furthermore, females appeared to require a period of recovery after incubation before they start with their wing moult. Migratory geese are likely facilitated in coping with this time constraint by the increased foraging time they experience, as day length increases while migrating north. In the second part of this thesis I investigated this by studying differences in circadian rhythms and activity patterns between migratory and resident geese. In Chapter 5, we used implanted body temperature loggers to examine the circadian rhythm during spring and autumn migration, and we found that geese were able to rapidly adjust their circadian rhythm to changing daylight conditions. In Chapter 6, we analysed year-round tracking and
accelerometer data to compare (foraging) activity of migratory and non-migratory geese over the full annual cycle. We found that migratory geese are more active throughout the year, especially prior to spring and autumn migration. This increased foraging activity was only partly explained by the longer day lengths experienced at high latitudes.

We have thus discovered differences in breeding propensity, growth rate, foraging activity and timing of breeding and moult between geese of migratory and resident populations. However, we cannot relate these differences to differences in migratory strategy alone. Populations that differ in their migratory strategy are inevitably bound to differ in other respects as well. Migratory and resident birds of the same species necessarily differ in at least their wintering or breeding area, which implies they experience different environmental conditions during part of their annual cycle. This is especially important for populations that differ in breeding area, because the environmental conditions on the breeding grounds play an important role in shaping fitness related traits such as clutch size and growth rate (Lack, 1968). Furthermore, the conditions experienced during the part of the annual cycle when migratory and resident geese are separated, might also affect differences observed on the common wintering grounds through carry-over effects (Inger et al., 2010; Hoye et al., 2012), which further complicates the application of a comparative approach. Species in which migrants and residents share the same breeding grounds, but where migrants winter elsewhere, might therefore appear more suitable to investigate the costs and benefits of migration (Newton, 2008; Brown et al., 2021). However, by studying such species we focus on migrations that are more likely to provide benefits during the winter period, ignoring migrations that primarily have evolved to enhance breeding success. Such an approach is thus not representative for Arctic-breeding species, because almost all Arctic-breeding birds are migratory and the costs and benefits of migration are therefore inseparable from the effects of breeding area. This does not mean we cannot learn anything from comparing migratory and resident barnacle geese. The breeding range expansion observed in the barnacle goose provides the opportunity to look into the requirements for barnacle geese to breed successfully, and study the adaptation to a new breeding environment. Although this is a slightly different perspective, the knowledge gained on the costs and benefits of a migratory and resident strategy in the barnacle goose does allow us to evaluate this.

Where to breed? – A goose perspective

Barnacle geese have long been considered specialists of the high Arctic, breeding on rocky cliffs on the islands of Novaya Zemlya and Svalbard. However, the recent range expansion of the barnacle goose forces us to reconsider this assumption, and poses the question why geese did not breed in the temperate zone (their wintering grounds) before. By outlining the requirements for reproduction in the barnacle goose, we can deduce why the Arctic offers suitable conditions for breeding, which in turn can provide insight in the changes that have
enabled barnacle geese to start breeding at lower latitudes. The three main requirements for successful reproduction in the barnacle goose relate to resource availability and a safe breeding environment, which also benefit the adults during moult: 1) Adult geese need to be able to acquire enough resources for egg production and incubation (breeding condition); 2) Goslings need to be able to acquire enough resources for growth; 3) predation pressure needs to be low to limit predation of eggs and goslings (figure 7.1), while also providing a safe environment to moult for the adults. Below I will discuss how barnacle geese meet these requirements by migrating to the Arctic to breed, and the consequences that come with migration to the Arctic. Subsequently I will address the changes that have allowed barnacle geese to start breeding in their wintering grounds and adopt a resident strategy.

**Migrating to the Arctic to breed**

The resources needed for egg production, incubation and gosling growth present the geese with a challenge. Barnacle geese are small herbivores that lack the adaptations to a plant-based diet found in large herbivores and ruminants, who have a long gut structure and long food retention time for efficient digestion of plant material (van Soest, 1994). Geese have to make do with a short digestive track and a low retention time, which makes them dependent on high quality food and enough time available for foraging (Prop & Vulink, 1992; Prop et al., 2005). The nutritious quality of vegetation peaks shortly after the onset of vegetation growth, when the protein content is high but plant maturation has not yet caused digestibility to decrease (Sedinger & Raveling, 1986; Prop et al., 2005; Lameris et al., 2017b). For geese, it is therefore important to time their presence with the local onset of vegetation growth to ensure access to high-quality food for themselves and their goslings (van der Graaf et al., 2006). However, adult barnacle geese and their goslings depend on the same food resource. This means that when adult geese need to use the food quality peak to acquire resources for egg production and incubation in their breeding area, the same food quality peak is unavailable for their goslings. The goslings would then hatch too late, when food quality has already declined (Doiron et al., 2015). By migrating to the Arctic to breed, barnacle geese have been able to solve this problem by using sequential peaks in food quality that occur due to the latitudinal delay in onset of vegetation growth, the so called “green wave” (van der Graaf et al., 2006; Shariatinajafabadi et al., 2014). The successive onset of vegetation growth while moving northwards, allows the geese to use food quality peaks at stop-over sites to acquire resources for egg production and incubation (Nolet, 2006; Drent et al., 2007). During the last leg of migration, the geese then overtake this green wave, which enables them to arrive ahead of the food quality peak on their breeding grounds (Kölzsch et al., 2015; Si et al., 2015). This means that migrating barnacle geese are highly dependent on the timing of this food quality peak, which is mainly determined by the onset of spring.
We investigated the importance of the timing of onset of spring on the decision to breed in Chapter 2, and found that in the Arctic, breeding propensity (i.e., probability of breeding) was high in years with early springs and decreased when spring was late. In years with late springs, the geese have to postpone breeding because nest sites might be unavailable upon arrival, or to ensure the hatching of the goslings is matched with the food quality peak. When breeding is postponed, body stores collected for egg production and incubation have to be used for maintenance (MacInnes, 1978; Ankney, 1984) and therefore, a lower proportion of the population might be in breeding condition when it is time to start nesting (Chapter 2). When the geese start breeding in time, the goslings hatch around the time of the food quality peak, which then provides ideal feeding conditions for the growing goslings as well as moult ing adults. The importance of timing of breeding also becomes apparent from our study on gosling growth, where we show that in the Arctic, late hatching goslings grew slower (Chapter 3), which is generally attributed to a mismatch with the food quality peak (Doiron et al., 2015). Regardless of timing of hatching, in the Arctic the goslings experience unlimited foraging time provided by the 24h day lengths, which allows for fast growth (Chapter 3). Growing quickly is advantageous, because it reduces the period during which the goslings are exposed to high predation risks (Samelius & Alisauskas, 1999; Dmitriew, 2011). Predation pressure itself is generally lower at Arctic latitudes compared to temperate latitudes (McKinnon et al., 2010; Léandri-Breton & Béty, 2020), presumably because the number of predators as well as the diversity of predator species is lower (Díaz et al., 2013). This lower predation pressure improves the chances on successful breeding because fewer eggs are being predated during nesting and fewer goslings will be predated during the period of growth when they are small and vulnerable. Furthermore, the adults themselves profit from this relative safety during the period of wing-moult, when they are temporarily flightless and therefore vulnerable as well. Migration to the Arctic thus allows barnacle geese to accumulate the necessary body stores to start nesting in time, while also providing a nutritious and safe environment for gosling growth and moult.

The consequences of migration to the Arctic

The comparison of resident and migratory geese also reveals the consequences of a migratory life. The energy required for migration appears to come at the expense of clutch size and body mass at the start of incubation, because migratory geese lay a smaller clutch than residents (-1 egg), and start incubation with a lower body mass (Eichhorn et al., 2010). The potential to compensate the energy expended due to migration is limited, because the geese need to start breeding shortly upon arrival. Migratory geese need to start breeding in time, because their reproductive strategy is closely linked with the timing of peaks in food quality. Although these peaks are generally higher at high latitudes they are also much more narrow, and consequently, migratory geese are on a tight schedule (Drent et al., 2003). The geese have to depart in time to use food peaks along their migratory route and need to start...
breeding in time in order to let hatching coincide with availability of high-quality food at the Arctic breeding grounds. Furthermore, the goslings need to be fully grown and adults need to have moulted in time to be able to prepare for the autumn migration and fly south before winter conditions set in. A migratory strategy thus comes with time constraints on the annual cycle, specifically on the stages of migration, breeding and moult. In Chapter 4, we show that the interval between breeding and moult is shortest for geese breeding in the Arctic, which is illustrative of this constraint. Overlap between breeding and moult appears impossible, especially for females who need to recover from incubation before they can start moulting (Chapter 4). After moult, migratory geese also need time to prepare for autumn migration and when spring is late, the breeding season might therefore be too short. This is also supported by our findings in Chapter 2, where we show that breeding propensity decreases with later springs in the Arctic, especially at high latitudes where the breeding window is generally shortest. Because migration, breeding and moult follow each other in quick succession, migratory geese have to meet the energy requirements of these stages in a short period of time. The geese are facilitated in dealing with this time constraint by the improved feeding conditions (food availability, food quality and foraging time) that coincide with migrating north. In Chapter 5 we show that during migration, barnacle geese are capable of quickly adjusting their circadian rhythm, which allows them to fully exploit the longer day lengths experienced when flying north. The long days also ensure rapid growth of the goslings (Chapter 3), which reduces the time required for successful reproduction. Despite experiencing longer days than resident geese during the summer half year, we find that migratory barnacle geese extend foraging activity beyond the daylight period prior to spring and autumn migration (Chapter 6), which illustrates the need to rapidly accumulate body stores. This increased foraging activity and associated increase in food processing and metabolic turnover also requires a larger metabolic machinery, and correspondingly Resting Metabolic Rate (RMR) of migratory geese was found to be higher during summer than in resident geese (Eichhorn et al., 2019). This increase in RMR is likely a plastic response to the increased foraging activity of migratory geese during moult. Over the full annual cycle, migratory barnacle geese spent more time foraging than resident geese, especially in the periods prior to migration. We therefore conclude that, beyond the evident costs of the migratory journey, a migratory life comes with additional energetic expenses in geese, which requires increased foraging activity (Chapter 6).

Breeding at temperate latitudes – seizing the opportunity
Barnacle geese breeding at temperate latitudes need to meet the same requirements for successful reproduction as geese breeding in the Arctic (figure 7.1). In fact, for geese to become residents, all these requirements need to be fulfilled in the same area. Presumably, changes in resource availability and predation pressure needed to take place to make this possible. Agricultural intensification and the coinciding nitrogen deposition have greatly
improved feeding conditions for the barnacle goose in the Netherlands since the 1970s (van Eerden et al., 2005). By applying fertilizer to grasslands, modern mowing schemes and grazing regimes, the natural food quality peak in the Netherlands was replaced by almost continuous availability of high-quality food for the geese (van der Graaf, 2006; Feige et al., 2008). This continuous availability of high-quality food enables adult geese to acquire the resources needed for egg production and incubation (Eichhorn et al., 2012), while the same area still offers food of sufficient quality for the growing goslings (figure 7.1). Breeding propensity and hatching success at temperate latitudes was generally high, and independent from spring phenology (Chapter 2), likely because spring phenology no longer determines the availability of high-quality food (van der Graaf, 2006). In Chapter 3, we found that goslings grow slower in temperate regions compared to the Arctic, but demonstrate that this difference can largely be explained by the differences in day length between the Arctic and temperate breeding areas, which indicates that it is mostly foraging time that is limiting growth of temperate goslings rather than food quality. Additionally, our analysis in Chapter 3 showed that while late hatching goslings in the Arctic grow slower, there was no such effect in the temperate resident population. Timing of hatching thus appears to have little effect on the food conditions encountered by the temperate goslings because food quality remains high throughout the season, resulting in comparable growth of early and late hatching goslings. This releases the resident geese from the time constraint imposed by the need to match reproduction with the peak in food quality.

The artificially created high food quality on the temperate breeding grounds has enabled barnacle geese to meet the first two requirements for breeding: facilitating the acquisition of body stores in adults while also providing food for the goslings. In addition, humans also provided a safe breeding area through a profound impact on predation pressure in the temperate region. We can distinguish between direct effects of humans on predation of barnacle geese through goose hunting and indirect effects through human impact on natural predator populations. Evidence of the effects of hunting on breeding stem from settlements in the Russian Arctic, where barnacle geese were intensively hunted and large numbers of eggs were collected. After abandonment of these settlements following the collapse of the Soviet Union, the numbers of breeding barnacle geese rapidly increased in these areas (Filchagov & Leonovich, 1992). Barnacle geese were traditionally hunted on their temperate wintering grounds as well, but hunting was banned in the Netherlands in 1950 onwards to protect the population of only 10,000 birds at that time (Madsen et al., 1999). The ban on hunting on the wintering grounds might have facilitated the establishment of temperate breeding colonies. Humans also have an indirect impact on predation pressure. Temperate regions generally housed a wide diversity of predators including white-tailed eagles (Haliaeetus albicilla), red foxes (Vulpes vulpes) and polecats (Mustela putorius), which are capable of predating geese and their eggs. Persecution of mammalian predators and birds of prey by humans during the 19th century resulted in strong reductions and
Figure 7.1: Requirements for successful reproduction (black ovals), and the strategies to meet these requirements in migratory and resident barnacle geese. Factors related to food availability are depicted in green, factors related to predation in orange. Black arrows show the importance of the factors in meeting the breeding requirements. Square boxes indicate the areas associated with meeting the requirements, where solid borders indicate year-round use, and dashed borders indicate temporary use. Foraging time is shown from spring (bottom) to the end of summer (top). The red arrow indicates the changes that made breeding on the wintering grounds possible: improved feeding conditions (grassland fertilization), reduction of predators (hunting and pesticides).
even local extinction of predator populations in north-west Europe (Bijleveld, 1974; Breitenmoser, 1998). Furthermore, the wide application of insecticides like DDT during the mid-20th century had detrimental effects on avian predator populations (Bijleveld, 1974), thereby reducing the natural predation pressure on geese. By banning hunting activities and reducing natural predator populations, humans have created a relatively safe breeding environment for barnacle geese. In combination with the improved feeding conditions, this has likely enabled barnacle geese to start breeding at temperate latitudes and adopt a resident life history strategy.

**Barnacle geese in a changing world**

As discussed above, the past changes in land use and predation pressure facilitated the southward range expansion of the barnacle goose and has allowed the geese to adopt a resident life history strategy. However, the environment in which the geese live remains dynamic and the current situation is subject to changes as well, which might have consequences for migratory and resident barnacle geese. One of the most apparent changes is climate warming, which results in rising temperatures and an advancing onset of spring (Badeck et al., 2004; Pachauri et al., 2014). The climate is warming faster in the Arctic than in temperate regions, and as a consequence spring is advancing faster at high latitudes as well (Høye et al., 2007). This is especially challenging for migratory geese that depend on spring phenology at different latitudes for successful reproduction. To cope with these changes, migratory geese need to arrive earlier on the breeding grounds and thus have to advance the timing of migration. In response to earlier springs, barnacle geese arrived earlier on the breeding grounds by accelerating migration, but did not advance egg laying enough to match the advancement of spring, and needed to use local resources to refuel before being able to start breeding (Lameris et al., 2018a). As a consequence, hatching was mismatched with the food quality peak resulting in reduced gosling survival. These negative consequences of climate warming for Arctic migratory geese might be offset by positive effects on other reproductive parameters (Nolet et al., 2020), such as the higher breeding propensity in early springs (Chapter 2). However, when spring continues to advance and the increasing mismatch with the food peak reduces gosling survival further, the overall effect of earlier springs at the current Arctic breeding grounds might become negative. Migratory geese might respond to this by shifting their breeding areas to the north-east, where the effects of warming allow breeding in areas where snowmelt previously occurred too late (Huntley et al., 2007; Jensen et al., 2008).

The resident population is less likely to experience such negative consequences of climate warming, since warming is less pronounced at temperate latitudes (Stocker et al., 2014) and resident geese appear less dependent on spring phenology for successful reproduction (Chapter 2, Chapter 3). Nonetheless, climate warming is found to cause more frequent heat waves on the resident breeding grounds (Meehl & Tebaldi, 2004), which
potentially results in heat stress for the geese. We did not observe a response in body temperature during the warmest period of the day (14:00-18:00 local time), in 7 resident geese with implanted body temperature loggers, to increased ambient temperatures during heat waves that occurred 15-27 July and 29 July - 07 August 2018 (figure 7.2). Future analyses of activity during heat waves might give insight of the behavioural adaptations geese use to cool down. Nonetheless, this suggests that at least adult geese are able to cope with the current heat waves. However, the impact on goslings remains unclear, and when goslings are found to be more vulnerable to heat stress, this might affect the reproductive success of the resident population.

Figure 7.2: Mean body temperature (between 14:00 and 18:00 local time) of resident barnacle geese during July-September 2018. The grey line shows the mean ambient temperature, the shaded band the minimum and maximum ambient temperature as measured by the weather station in Wilhelminadorp, close to the breeding grounds of the resident population (retrieved from ECAD dataset, (Klein Tank et al., 2002)). Orange bars above the x-axis indicate the periods of two heatwaves (KNMI, 2022).

Climate warming can also result in shifts in the distribution of predators, which might lead to increased predation pressures. The numbers of white-tailed eagles have increased at the Arctic study site, resulting in increased predation of goslings and adults (OBP, TKL, MPB pers. obs.). Furthermore, in 2018, we observed a female brown bear (*Ursus arctos*) with two young close to the study site, while a male brown bear was observed predating over 300 goose and gull nests in 2019 (MPB, pers. obs.). Similar extreme predation events are observed on Spitsbergen and in the Canadian Arctic, where the occurrence of polar bears (*Ursus maritimus*) has increased in response to decreased hunting opportunities on sea ice (Gormezano *et al.*, 2017; Hamilton *et al.*, 2017). On Spitsbergen, polar bear predation was found to have a large impact on reproductive success of birds, with over 90% of the nests of barnacle goose, common eider (*Somateria mollissima*) and glaucous gull (*Larus hyperboreus*)
being predated (Prop et al., 2015), and similar reports exist for the Canadian Arctic (Rockwell et al., 2011). For resident geese, predation pressure is more likely to be affected by human interference. The increasing numbers of wintering and breeding geese along the North Sea coast have resulted in conflicts with agriculture, as goose grazing results in damage to crops (Fox et al., 2017). In response, derogation shooting has been applied as a management tool in the Netherlands, especially in the Delta area, in an attempt to limit the numbers of the local breeding population to reduce the damage. The increased hunting pressure has been found to reduce the annual survival of geese from the resident population (van der Jeugd & Kwak, 2015), and derogation shooting might thus lead to a population decrease. Furthermore, natural predation is expected to increase, because the ban on DDT allowed fox numbers to increase and have led, in combination with measures to improve water quality, to the return of the white-tailed eagle to the Netherlands as a breeding bird (Zeiler, 2019). The population increase of white-tailed eagles in the Baltic area has been associated with the decline of the breeding population on Gotland (Larsson unpubl.), and the increasing number of eagles during summer in the Netherlands might eventually have similar effects.

Towards understanding flexibility in the barnacle goose
The ongoing changes in environmental conditions require barnacle geese continuously to adapt, and over the past decades, they have shown a remarkable ability to do so. In response to changing environmental conditions barnacle geese have successfully colonized new breeding habitats (Feige et al., 2008; Chapter 2), have shown flexibility in gosling growth (Chapter 3), and were able to shift the timing of breeding and moult (Chapter 4). Furthermore, barnacle geese have been found to change their stopover routines in response to increased competition (Eichhorn et al., 2009; Tombre et al., 2019) and predation pressure (Jonker et al., 2010) within a short period of time. Such changes are likely facilitated by the social (migratory) behaviour of geese, where naïve individuals can “learn” to use other areas from individuals with experience (Oudman et al., 2020). This can also play a role in the rapid colonization of new breeding areas, after these are discovered by dispersing individuals. Several marked barnacle geese are found to have dispersed along the flyway (Chapter 4; van der Jeugd & Litvin, 2006; van Der Jeugd, 2013). The most extreme known case of dispersal concerns a marked barnacle goose born in the resident population in 2019, which was observed in eastern China in January 2021 (Moonen, 2021). In Chapter 4, we show that dispersing individuals were able to adjust the timing of breeding and moult to their new breeding environments, which is important for dispersal to be successful. Furthermore, this dispersal of geese with a resident origin to migratory populations indicates that resident barnacle geese can become migrants again.

The remarkable flexibility we observe in the barnacle goose raises questions on whether the successful colonization of new breeding areas has mainly been possible due to individual plasticity, or whether genetic differences are involved as well. Jonker et al. (2013) show
genetic differences exist between the migratory and resident population, but also note that genetic exchange occurred. New techniques, such as Genotyping-by-Sequencing, can now be used to investigate if genetic differentiation is taking place and assess the potential for speciation (Gómez-Bahamón et al., 2020). This might occur when the populations become reproductively isolated, for example due to differences in timing of breeding (Tobias et al., 2020). It is especially intriguing that, while experiencing the same environmental cues (photoperiod and temperature) in April on the shared wintering grounds, migratory geese continue to prepare for migration while resident geese start breeding. The genetic and environmental basis of the observed differences in timing of breeding can only be disentangled by an experimental approach. To this end, eggs of the resident and migratory population need to hatch in the same environment and subsequently, the timing of these individuals needs to be compared. Such a “common garden” approach is suitable to test for a genetic basis without the confounding effects of the environment (De Villemereuil et al., 2016). This can be taken one step further, by performing a “reciprocal transplant experiment”, in which eggs are exchanged between the populations to hatch. In addition to disentangling the genetic basis from the environmental effects, this allows for the assessment of local adaptation by comparing the performance (e.g. reproduction, survival) of individuals hatched from translocated eggs with native individuals (De Villemereuil et al., 2016). The shifts in behaviour and life history traits, which are required for initial establishment in a new breeding environment, could well be the facilitated by phenotypic plasticity (Atwell et al., 2014). Therefore, it would be interesting to assess the role of the environment in the observed differences in timing of annual cycle stages between resident and migratory geese. By bringing adults of both populations into a common environment (“common environment experiment”), the role of the environment in the observed differences can be tested. In Box 7.1, I present preliminary results of a pilot experiment of such a common environment experiment.

The barnacle goose as a model species
The barnacle goose has been able to expand its breeding range southward and thereby adopt new life history strategies, which allowed us to study questions on the costs and benefits of migration within the same species. In contrast, many other Arctic-breeding species appear restricted in their breeding range, and generally show a poleward shift in breeding distribution (Parmesan & Yohe, 2003; Parmesan, 2006). This provokes questions on how representative the barnacle goose is as a model species, and why we do not observe such range expansions in other species such as Arctic-breeding waders.

In general, Arctic-breeding waders are expected to have similar requirements for successful reproduction as the barnacle goose, since they also need to acquire resources for egg production (breeding condition) and need a safe environment with sufficient food to raise offspring (figure 7.1). However, there are ecological differences between barnacle
geese and waders, which likely affect the availability of suitable breeding environments and therefore the potential for changes in breeding range. Both adult barnacle geese and their goslings are dependent on high quality food plants, a resource that has become widely available due to the agricultural interest to produce grass with high protein content for livestock (van Eerden et al., 2005; Eichhorn et al., 2012). Species with similar resource requirements like the greater-white fronted goose, have also been found to start breeding in the Netherlands (Voslamber et al., 2007). In contrast, adult Arctic waders mainly depend on marine invertebrates, while their offspring is entirely dependent on insects during the period of growth (Schekkerman et al., 2003; Tjørve et al., 2007). Schekkerman et al. (2003) report comparable insect abundance between an Arctic and a temperate breeding site for waders, but also point out that insect availability might be lower at the temperate site due to more difficult detection and capture in the taller grass compared to a tundra habitat. Furthermore, the past decades insect populations have generally declined in temperate regions as a result of land use change and use of pesticides (Goulson, 2019), which has been associated with declines in insectivorous birds (Newton, 2004; Hallmann et al., 2014). The Arctic, with its high insect abundance, therefore likely remains the most suitable breeding environment for many waders. The wide availability of agricultural grasslands also results in many suitable stopover sites for geese, which can facilitate changes in migration routes (Heldbjerg et al., 2019) and might make it possible to reach new breeding areas. Waders are dependent on intertidal areas as stopover sites, which are less widespread and under threat from land use changes (Lindström & Agrell, 1999; Piersma et al., 2017), and this might hamper Arctic waders in finding new migration routes and breeding areas. In short, while the availability of areas that provide environmental conditions required for successful reproduction in the barnacle goose (availability of high-quality forage and low predation pressure) has increased, this has not been the case for waders.

This example illustrates the importance of the ecological characteristics of a species in order to understand the observed pattern. Generalizing findings from a model species across multiple species thus requires appreciation of the ecological differences and similarities. Making comparisons between model species that differ in ecology (e.g. waterfowl, waders and seabirds) can greatly improve our knowledge on these ecological differences and similarities, which is crucial in understanding the variation in species responses to environmental change.

**The future of migration**

Human activity now affects ecosystems all over the world. The human impact is so widespread that we have entered a new era: the Anthropocene. Human-induced environmental change includes direct effects such as changes in land use, as well as indirect effects like climate warming. These changes alter the environments in which animals live, but the type of changes as well as the rate of change depends on the geographical
location. Migratory birds rely on spatially distant areas for breeding and survival, and are therefore likely to encounter variable changes throughout their range (Wilcove & Wikelski, 2008). In order for migratory species to persist, they must be able to cope with these changes. Studies on the costs and benefits of migration provide insight into why birds migrate in the first place, which is an important step to understand the potential impact of environmental change on migratory bird populations, and on the viability of a migratory life history strategy. Land use change can destroy habitat for wintering, stopover or breeding, and in species that are unable to find another suitable area the cost-benefit balance of migration might change as such that migration is no longer adaptive. Climate warming presents different challenges, related to the shifts in phenology of food peaks. Migratory species that rely on seasonally occurring food peaks at different latitudes generally struggle to adapt, because the shift in food peak phenology varies with latitude as well (Menzel et al., 2006). This results in a mismatch between the arrival of migratory birds and the occurrence of the food peak, affecting the benefits of migration (Møller et al., 2008). For some species, humans will provide new suitable habitat, which can serve as wintering, stopover or breeding areas. This is the case for species whose habitat requirements match with human goals for the environment, such as geese profiting from current grasslands. Other species benefit as well from increased food availability due to human presence. Corvids (Corvus spp.) and gulls profit from human garbage as a food source (Hobson et al., 2015), and garden birds such as blackcaps profit from garden feeding (Bonnet-Lebrun et al., 2020; van Doren et al., 2021). Humans generally live at the same location year-round, thereby providing food that is independent of seasonality. Areas inhabited by humans can thus support both breeding and survival, thereby facilitating a resident life history strategy. In short, human-induced environmental change can alter the cost-benefit balance of migration, and might reduce the occurrence of a migratory life history strategy. In the future, environmental changes might alter the cost-benefit balance of migration again, possibly favouring a migratory strategy over a resident strategy. To understand the ability of birds to switch between a resident and migratory life history strategy, experimental approaches to disentangle the genetic and environmental basis for the observed differences between migrants and residents are essential. It is clear that current environmental changes affect migratory bird populations, migration routes and even migration as a life history strategy. I believe migration itself should be regarded as a part of biodiversity, which is worth conserving. Humans mainly cause the current changes in the environment, and this inevitably makes us responsible for all life affected by these changes. Therefore, it is our obligation to protect migration as a phenomenon.
Box 7.1 Migratory and resident barnacle geese in a common environment: First insights of an experimental approach

A common environment experiment can be used to investigate the role of the environment on the observed differences between migratory and resident barnacle geese. To this end, we needed to bring geese of a migratory and a resident population into captivity and keep them under the same environmental conditions. During the period in captivity, we can monitor body mass to see if differences in body mass dynamics between migrants and resident geese persist when geese from both populations experience the same environmental conditions. Furthermore, we can gain insight in flexibility of the timing of annual cycle stages such as moult, by comparing the timing of these stages, for example by measuring the growth of the ninth primary feather after primaries are shed. Here I describe the results of a pilot common environment experiment on the differences between migratory and resident barnacle geese.

Female geese from the resident breeding population were captured with clap nets on the nest on the breeding grounds in the SW of the Netherlands in May 2018 (N=3), and in October 2019 using canon nets (N=8). Female geese from the migratory population were caught on the wintering grounds in the Netherlands close to Eemdiijk using whoosh-nets (N=5) in January 2020. After capture, the geese were brought to the waterfowl facility at NIOO, where they were allowed to forage on grass, could also feed on artificial waterfowl food. Birds of both populations were kept in the same outside aviary where they were exposed to natural photoperiods and temperatures. Geese were weighed bi-weekly (every 2 weeks), and during the moult period, the moult status was checked and the ninth primary was measured when primaries were shed. Body mass was corrected for size using the “scaled mass index” following Peig & Green (2009), using the same parameters as in Chapter 6. Body mass was compared over a 2-year period (November 2019 – September 2021). Moult (ninth primary growth) was compared in 2020. Onset of moult was calculated as described in Chapter 4, using the first measurement of the growing ninth primary for each individual and back calculating based on a primary growth rate of 6.98 mm/day.

Comparing body mass dynamics in a common environment

Body mass dynamics of migratory and resident geese showed a similar overall pattern, with increases in body mass during spring followed by a decrease in body mass during the moult period (figure B7.1). However, in spring, body mass of migratory geese seemed to increase faster, and migratory geese thus seemed to become heavier than
resident geese. This indicates that the migratory geese still accumulated body stores, presumably for migration (and subsequent egg laying and incubation). This increase in body mass was observed in both years. Body mass of migratory geese did decrease around the same time as in resident geese, so no prolonged increase in body mass was observed as occurred in migratory geese in the wild (Chapter 6). Furthermore, during August-October 2020 body mass of migratory geese appeared to increase again, matching the pre-migratory period in autumn in the wild. During the same period, body mass of resident geese remained more stable. During winter, body mass of geese from both populations seemed similar.

Comparing timing of moult
Resident geese showed more variation in timing of moult than migratory geese (figure B7.2), corresponding with observations in geese of both populations in the wild (van der Jeugd et al., 2009, Chapter 4). Resident geese seemed to moult 9 days earlier than migratory geese with the onset of moult dated on July 17 ± 8.50 (mean ± SD), compared to July 26 ± 6.88 for the migratory geese. The resident geese in the experiment moulted later than resident geese in wild, while the migratory geese in the experiment moulted around the same time as wild migratory geese (Chapter 4). None of the geese in the experiment laid eggs, so all can be considered non-breeders. The difference observed between migratory and resident geese in the experiment is
somewhat smaller than the 13-day difference observed between non-breeders of the Arctic migratory and temperate resident population in the wild (Chapter 4).

**Figure B7.2:** Ninth primary length of resident and migratory barnacle geese during the period of moult while kept in a common environment. Blue points indicate the primary measurements on resident geese, blue lines connecting measurements on the same individual. Dark red points indicate primary measurements on migratory geese, with the dark red lines connecting measurements on the same individual.

**Discussion**

The data collected on 11 resident and 5 migratory geese kept under the same environmental conditions show a persistence of differences in body mass in spring which can be interpreted as body store accumulation for migration. However, these sample sizes are limited, and for birds that are captured on the wintering grounds, the population to which they belong is not entirely certain. A method to genetically distinguish birds from the resident and migratory populations would be an essential tool for future application of this common environment approach. Despite the limited sample size, we observe that migratory geese no longer extend the period of body mass increase in spring, which indicates that fuelling behaviour is at least partly a plastic response to the environment. Timing of moult in migratory and resident geese was relatively similar, but that was mostly because resident geese in the experiment moulted later than geese in the wild, and not because migratory geese advanced moult. It remains therefore unclear whether the migratory birds were not able to advance moult, or whether the experienced environmental conditions were better suited for a later moult, and therefore resident geese delayed the timing of moult.