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

Boom, M.P.

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CHAPTER 1

General introduction

Michiel P. Boom
GENERAL INTRODUCTION

One of nature’s most striking phenomena is the annual movement of billions of animals known as migration. Throughout evolutionary history, migration appeared in a wide variety of taxa, including mammals, insects, fish and amphibians, but it is best known for its occurrence in birds. There is large variation in both the species performing migration as well as the journeys they undertake. Insects are among the smallest migrants (Fijen, 2021), while the 24-27 m long blue whale is the largest migrant roaming the planet (Hoare, 2009). Consequently, migration distances show considerable variation, with the longest round-trip recorded being over 80,000 km for the Arctic tern (Sterna paradisaea, Alerstam et al., 2019)). Besides body size and migration distance, migration strategies differ among species and individuals. For example, animals can be obligate or facultative migrants (either migrating every year, or only under certain environmental conditions), can vary in their migratory route while heading towards the same destination, or have different travel schedules (using non-stop travel or frequent stops), with the longest known non-stop flight performed by bar-tailed godwits (Limosa lapponica) flying over 8000 km across the Pacific Ocean in 9 days (Gill et al., 2009).

The wide occurrence of migration, inspired a scientific interest to understand the evolution of migration. Early theories concerned the “northern ancestral home” hypothesis, which assumes that glaciation forced northern breeding birds to migrate south during the winter months, and the “southern ancestral home” hypothesis, where glacial retreat actually provided new breeding areas in the northern region for birds originally living further south (Lincoln 1939). Over the years, the knowledge on migration expanded and currently the evolution of migration is considered in a cost-benefit framework, where migration is a life history strategy to maximize fitness.

The benefits of migration

Lack (1954, 1968) was one of the first to acknowledge that migration was a product of natural selection and thus had to be considered adaptive. In order for a migratory life history strategy to be adaptive, the fitness benefits must outweigh the costs. These benefits can act on an organism’s reproduction, survival or growth (Shaw, 2016). Heape (1931) proposed to categorize migratory movements based on three main motives: 1) avoid unfavourable conditions, 2) reproduce, 3) increase access to food. Depending on the species, a combination of these factors can be involved in shaping migration. For example, movement to the breeding grounds can be driven by increased access to food, while movement to non-breeding areas is necessary to escape unfavourable conditions to increase winter survival.

Migratory movements to avoid unfavourable conditions are widespread among migratory birds. Many species that reproduce in Arctic areas migrate south to avoid the
inhospitable climate of the Arctic winter (Newton, 2008; Alerstam & Bäckman, 2018), and many species in mountainous regions migrate to lower altitudes to escape the risks of alpine winter (Boyle et al., 2010). However, unfavourable conditions are not necessarily climatic. Predation is considered unfavourable, and a relief from predation pressure has been demonstrated to be a potential driver of migration (Fryxell & Sinclair, 1988; Alerstam et al., 2003). For example, waders that migrate to the Arctic were found to experience lower nest predation rates compared to wader species breeding at temperate latitudes (McKinnon et al., 2010), and tropical birds that migrate to higher altitudes to breed experienced lower nest predation further uphill (Boyle, 2008). Birds can also reduce exposure to pathogens and parasites by migrating between areas where parasite or pathogen prevalence is low (Alerstam et al., 2003; Altizer et al., 2011), as has been proposed for waders that migrate between Arctic breeding areas and coastal habitats (Piersma, 1997). Furthermore, migration can be used to avoid or reduce competition. Migrating between areas that are suitable for survival or breeding only, allows migrants to utilize areas which are not suitable for a resident life history strategy, thereby omitting competition with residents (Alerstam et al., 2003; Somveille et al., 2015).

When specific conditions are needed for the offspring, migration can occur out of need for a suitable rearing environment (Shaw, 2016). This is common in amphibians in which the aquatic larval phase of the offspring requires the terrestrial adults to migrate to aquatic areas specifically to reproduce (Russell et al., 2005). However, migrations to reproduce are also known to occur in birds. The high insect abundance on the Arctic tundra in summer is considered a driver of migration for waders, because their offspring is dependent on insects during growth, before they can switch to marine invertebrates (Schekkerman et al., 2003; Tulp, 2007). The generality of this potential driver of migration is confirmed by Fokkema et al. (2020), who show that both growth and survival of offspring benefit from the specific conditions at the breeding grounds in species from different taxonomic groups, ranging from dark-bellied brent (Branta b. bernicla) to humpback whale (Megaptera novaeangliae) and Pink salmon (Oncorhynchus gorbuscha).

Perhaps the most common reason to migrate is increased access to food (Shaw, 2016). Even migrations that primarily take place to avoid unfavourable conditions or reproduce can be linked to access to food. Birds that migrate to avoid harsh winter conditions often do so to increase access to food. The same holds for many migrations to meet offspring requirements, where migration ensures high food availability to raise young. Food is therefore considered the main driver of avian migration (Newton, 2008). This has been illustrated by herbivorous birds that track the successive onset of vegetation growth during migration, ultimately using the increased food availability at the breeding grounds for reproduction (Bauer et al., 2006; van der Graaf, 2006; Shariatinajafabadi et al., 2014). Passerines are also known to track seasonal food peaks when migrating between Europe and Africa (Thorup et al., 2017) and these seasonal food peaks are found to be linked to
survival and reproduction (Visser et al., 2004; Reed et al., 2013). However, access to food is not only determined by the abundance of food itself, but also by the time available for foraging. Diurnal birds are limited by daylight in their foraging activity and therefore profit from longer day lengths. Pokrovsky et al. (2021) illustrated this by showing that by migrating north, birds experience longer day lengths allowing them to prolong their activity period. This potential increase in foraging time might therefore be an additional factor that affects food availability in migratory birds.

The costs of migration

Besides the potential benefits, there are also costs associated with migration. Most obvious are the extra energetic expenses required for the migratory journey itself, which depend on the way of locomotion. Flight and swimming are the most energy efficient ways of locomotion per unit of distance travelled (Tucker, 1970), and unsurprisingly migration is well represented among the avian clade (Alerstam & Bäckman, 2018). Although flight is a relatively efficient way of locomotion, travelling still requires energy, and birds therefore need to increase their energy intake to fuel their migrations (Alerstam et al., 2003; Newton, 2008; Alerstam & Bäckman, 2018). At locations where many individuals flock together at the same time to forage (e.g. stopover sites), birds can experience increased competition (Van Gils et al., 2005; Chudzińska et al., 2015) and depletion of resources (Schneider & Harrington, 1981; Nolet & Drent, 1998), which can affect migration speed and breeding success (Piersma, 1987; Hedenström & Alerstam, 1997).

The period required for migration also puts time constraints on the annual cycle of migratory birds (Jacobs & Wingfield, 2000; Wingfield, 2008). By adding an extra stage in their annual cycle, there is less time available for other stages like breeding or moult. The time allocated to migration includes the time required for fuelling (Hedenström & Alerstam, 1997) as well as the time needed for physiological changes (Ramenofsky & Wingfield, 2007). Shifting one stage would therefore come at the expense of time for the next stage, and although there is some evidence that migratory birds can shift multiple stages (Helm et al., 2019), this might restrain migrants in the flexibility to adjust the timing of annual cycle stages to environmental conditions, which can have negative consequences for their survival (Hemborg & Lundberg, 1998).

The migratory journey itself is also associated with survival risks (Klaassen et al., 2014). Many migratory animals pass ecological barriers where they have limited access to resources, or where they are exposed to adverse environmental conditions. Examples are found in the desert crossings of passerines that migrate between Africa and Europe (Bayly et al., 2012), in Demoiselle cranes (Grus virgo) that fly over the Himalayas, where they experience extremely strong winds (Mi et al., 2022), and in the many species that cross long stretches of ocean (Newton, 2007). Mortality during the crossings of such barriers is found to be higher (Loonstra et al., 2019), and is attributed to starvation, dehydration or
exhaustion (Newton, 2008). Migratory birds might also experience an increased predation risk during their travels, as large numbers of migrants are bound to attract predators (Lindström, 1989). While exhausted or under the pressure to replenish energy for migration, birds can be especially vulnerable to predation (Lehikoinen, 2011; Chudzińska et al., 2015).

The costs and benefits of migration in a changing world

The examples above show the variety of factors that influence the costs and benefits of migration. These factors are not exclusive, and the decision to migrate ultimately depends on the combined effects. Furthermore, these factors are dynamic, as they are influenced by an ever-changing environment. Currently, the world is changing at an unprecedented rate, often as a result of human-induced environmental change. When the environmental conditions change, the costs and benefits of migration might change as well. In response to changes in their environment, birds are found to have adapted their migratory route, as well as wintering and breeding ranges (Sutherland, 1998). Higher winter temperatures have allowed Bewick’s swans (Cygnus colombianus bewickii) to shift their wintering grounds to the north east, thereby shortening their migration distance (Nuijten et al., 2020), blackcaps (Sylvia atricapilla) were found to winter much further north where they benefit from garden feeding sites (van Doren et al., 2021), and multiple species show a northward shift in breeding range which has been related to increasing spring temperatures (Potvin et al., 2016). Ultimately, changes in environmental conditions can alter the cost-benefit balance of migration and result in changes in life history strategy where migrants become residents or vice versa (Alerstam et al., 2003; Wilcove & Wikelski, 2008). Which adaptations are necessary for such a radical change and what the role of phenotypic plasticity and genetic change is in this process remains unclear. To start answering such questions, we first need to understand what makes migration a viable life history strategy and how this might change.

To this end, we can use the natural variation in life history strategies and investigate the differences between birds with a migratory and resident lifestyle, to study the costs and benefits of migration. These differences also provide insight into the adaptations that come with a migratory life history strategy. Such a comparative approach is most informative when using populations of the same species, because species are bound to differ in multiple aspects including phylogeny, morphology and ecology.

Aim and study species

The aim of this thesis is to understand the costs and benefits of migration and the adaptations to a migratory life history strategy. To this end, I apply a comparative approach using natural variation within a metapopulation of the barnacle goose (Branta leucopsis), in which migratory and resident birds of the same species can be compared. Because migratory and resident barnacle geese differ also in breeding environment, the comparisons
made in this thesis concern an integrative approach, where a migratory life history strategy is associated with breeding at higher latitudes, including the Arctic. The barnacle goose is originally a long-distance migratory bird with its traditional breeding areas located on cliffs and rocky islands in the Arctic. The white and grey plumage of the barnacle goose, offers perfect camouflage against the rocky backgrounds with partial snow cover that are typical for this breeding habitat (Ogilvie, 1978). Incubation is solely carried out by the female, while the male is responsible for guarding the nest against the various predators that attempt to take the eggs (Syroechkovskiy et al., 1991). On the traditional Arctic breeding grounds the main egg predators concern the Arctic fox (Vulpes lagopus), skuas (Stercorarius spp.) and several gull species (Larus spp.). These predators remain a threat after the eggs have hatched, when the parents take their self-feeding goslings to the foraging grounds (Loonen et al., 1998). Here, the goslings feed on the highly nutritious forage plants, while protected by their parents who by that time commence wing moult. The adults regain their flight capabilities around the time the juveniles are able to fly, allowing them to migrate south together. While breeding in the Arctic, barnacle geese winter along the North Sea coast. Here, they forage on natural grasslands as well as agricultural pastures during the winter months, until the increasing day lengths and rising spring temperatures indicate that it is time to migrate north again.

Within the world population of the barnacle goose, three major flyways are distinguished with spatially separated breeding and wintering areas: 1) Greenland-Ireland, 2) Svalbard-Scotland and 3) Barents Sea-Baltic-North Sea (Madsen et al., 1999). Of these three, the Barents Sea-Baltic-North Sea flyway has the largest number of birds, currently holding 90% of the world population (Fox & Leafloor, 2018). Since the 1950s the population within this flyway has grown exponentially from ca. 20,000 individuals until over 1.2 million today (figure 1.1). This spectacular population growth has coincided with a southwards expansion of the breeding range along the migration route (Feige et al., 2008). In the early 1970s barnacle geese started breeding in the Baltic region, establishing a breeding population on Gotland (Larsson et al., 1988). A decade later, in the 1980s, breeding populations also established in the South-western part of the Netherlands, on the original wintering grounds (Ouweneel, 2001). By colonizing new breeding areas along their flyway, barnacle geese also adopted new life history strategies. While individuals breeding in the Russian Arctic remain long-distance migrants, Baltic breeders shortened their migration, and birds breeding along the North Sea coast became residents. The geese from these three breeding populations still share the same wintering grounds along the North Sea coast. Furthermore, genetic exchange exists among the three populations, and it is likely that both the Baltic and North Sea breeding population originate from the Barents Sea population (Jonker et al., 2013).

The range expansion of the barnacle goose and coinciding change in life history strategy provides a natural experiment in which we can compare migrants and residents within the same species to study the costs and benefits of migration. Partly because of this, few goose
species are studied as intensively as the barnacle goose. Over the years this has resulted in extensive knowledge on the species’ behaviour and ecology (see Black et al., 2014), and first comparisons among migratory and resident populations have been made (see Box 1.1). More importantly, long-term datasets on reproduction and moult are being collected in both migratory and resident populations of this species, and in recent years, individuals of migratory and resident populations have been tracked with GPS-transmitters.

**Figure 1.1**: Development of the barnacle goose population of the Barents Sea-Baltic-North Sea flyway including the numbers in the Baltic (yellow) and North Sea (blue) breeding populations. Data from van der Jeugd et al. (2009), Koffijberg et al. (2020), Isaksen (2020). Baltic population counts are incomplete after 2006 (between dashed lines), because no counts from Sweden were available.

**Study populations**

During the past decades, the research efforts on the barnacle geese of the Barents Sea-Baltic-North Sea populations were focussed on breeding biology, and colonies in the Barents Sea, Baltic and North Sea populations have all been studied for multiple years (figure 1.2). These study populations form the foundation of the comparisons between migratory and resident geese in this thesis, and part of the analyses presented have only been possible due to the data collected in previous years.

*The Arctic migratory population breeding on the Barents Sea coast*

Birds of the Arctic migratory population were studied in a colony in close vicinity of the abandoned village Tobseda in the Kolokolkova Bay (68°34’ N, 52°18’ E), west of the Pechora
Delta (figure 1.2). The village of Tobseda was abandoned in the early 1990s, after which a breeding colony of barnacle geese was established. Arctic foxes rarely visit this area, likely due to extensive hunting for fur during the period the village was inhabited. This allows the geese to nest on the mainland as well as on small islands in the Kolokolkova Bay. The foraging grounds for the geese consist of subarctic saltmarshes dominated by Carex subspathacea and Puccinellia phryganodes which provide high quality forage for the geese and their goslings (van der Graaf et al., 2004).

Studies on this colony started in 2002 (van der Jeugd et al., 2003) and focussed on both the migration and breeding ecology of Arctic breeding barnacle geese. During the expeditions to this study site that took place between 2002 and 2017, information on timing of reproduction, clutch size and hatching success were obtained by nest monitoring. Furthermore, goslings and moultling geese were caught, individually marked with coloured leg rings and biometric measurements (i.e., head length, tarsus length, wing length, primary length, and body mass) were taken. The migration routines of geese breeding in this colony were investigated by Eichhorn et al. (2005, 2006, 2009) who used light-level geolocators and satellite telemetry (Platform Transmitter Terminals) to collect information on stopover use and departure time. Lameris (2018) equipped geese of the study colony with GPS-Accelerometer loggers and Light-level geolocators in 2014, to collect data on the behaviour and timing of migration and study the impacts of a warming climate on the migration and reproduction of Arctic breeding barnacle geese (Lameris et al., 2018a; Lameris et al., 2019). Barnacle geese were also equipped with GPS-Accelerometer transmitters on the wintering grounds by Moonen & Buitendijk between 2016 and 2021, for projects focussing on agricultural damage and effects of disturbance. For the research presented in this thesis I visited the study site in the Kolokolkova Bay in 2018 and 2019. We collected data on reproduction and caught goslings and moultling adults for marking and biometric measurements. Furthermore, we equipped geese with GPS-Accelerometer transmitters and heart rate-body temperature (HR-Tb) loggers in 2018, with the aim to collect data on behaviour and energy expenditure.

A temperate migratory population in the Baltic

In the Baltic, barnacle geese breed on small islands along the coast. Historically, the Baltic population was concentrated around the islands of Gotland (57°25’N, 18°53’E) and Öland (56°40’N, 16°36’E), with the most important study site located on the three islands of Lau Holmar (Larsson & Forslund, 1994). While the geese breed on the smaller islands they take the goslings to Gotland or Öland after hatching to forage on lower marshlands which are dominated by Festuca rubra (van der Graaf, 2006).

The establishment of breeding colonies of barnacle geese in the Baltic from 1971 onwards (Larsson et al., 1988) provided the basis of a long-term study on barnacle geese breeding on the islands of Gotland and Öland between 1984 and 2004 by K. Larsson and
general introduction

colleagues (figure 1.2). The population on these islands initially grew exponentially but declined during recent years, likely due to increased disturbance and predation by white-tailed eagles (*Haliaeetus albicilla*) and red foxes (*Vulpes Vulpes*). Throughout the study period, data on timing of reproduction, clutch size and hatching success were collected annually. In addition, adults and goslings were individually marked with coloured leg rings and biometric measurements were taken during moult catches.

A temperate resident population on the North Sea coast

Most breeding colonies along the North Sea coast are situated in the south-western part of the Netherlands, where the barnacle geese breed in the Delta area (51°47’ N, 4°08’ E) since 1982 (Ouweneel, 2001; Lensink *et al.*, 2013). The geese breed on several islands in the Haringvliet and Krammer-Volkerak, but also in nature areas on the mainland, likely because few ground predators are present in this part of the Netherlands. In addition to natural foraging areas on salt marshes containing *Festuca rubra*, the geese also have access to agricultural pastures which are dominated by *Lolium perenne* (Bos & Stahl, 2003).

Studies on the barnacle geese breeding in the Netherlands were initiated in 2004 focussing on the colony on the Hellegatsplaten, which was one of the largest breeding colonies at the time (Pouw *et al.*, 2006). Fieldwork was later relocated to the colony breeding on the Westplaat Buitengronden (figure 1.2). In both colonies data on timing of reproduction, clutch size and hatching success were collected. Moulting barnacle geese and their goslings were caught annually on the moulting grounds around the breeding sites to collect biometric data and to individually mark the birds. Individuals of the colony breeding on Westplaat Buitengronden have been equipped with GPS-Accelerometer loggers in 2015 and 2016 by Lameris (2018), collecting information on movements and behaviour of resident barnacle geese. The study site at Westplaat Buitengronden was also used for the work presented in this thesis. In addition to collecting data on reproduction and biometrics, we equipped birds with GPS-Accelerometer transmitters and HR-Tb loggers in 2018, with the intention to collect data on behaviour and energy expenditure of geese from the resident population.
Figure 1.2: Map showing the breeding locations of the three study populations of the barnacle goose used in this thesis. Insets depict the location of the main study colonies for the Barents Sea (red), Baltic (yellow) and North Sea (blue) populations, in which data on breeding biology is collected.

Outline of the thesis
This thesis aims to unravel the costs and benefits of a migratory life history strategy by comparing migratory and resident barnacle geese. I) In the first part of this thesis, I focus on the stages that occur on the breeding grounds (e.g. reproduction and moult) to assess the potential benefits of migrating to the Arctic to breed. II) In the second part, I investigate the behavioural adaptations that are associated with a migratory life. To this end, I studied the differences in activity between migratory and resident geese, focussing on the migration period specifically, as well as adopting a full annual cycle approach.

I. Reproduction and moult
Understanding how reproductive success varies in response to the environment is an important step in evaluating the potential benefits of a life history strategy. Breeding propensity (i.e. the probability that a female breeds in a given year) is a key component of reproductive success, which is generally difficult to estimate, because non-breeding individuals are less conspicuous or might leave the breeding area before being observed. In
Chapter 2 we apply a novel method to estimate breeding propensity based on tracking data. We relate breeding propensity to local spring phenology and timing of arrival, and investigate whether this relationship changes with breeding latitude. Differences in conditions at the breeding grounds also affect the offspring. In Chapter 3 we analysed differences in postnatal growth rate of goslings in relation to breeding latitude and life history strategy. We focus on how the differences in growth rate are shaped by environmental conditions experienced by the goslings on the breeding grounds. In addition to breeding, geese also moult their primaries on the breeding grounds, leaving them temporarily flightless. Migratory geese might therefore be time constrained to complete both breeding and wing moult in time to leave for autumn migration, especially in the Arctic, where the summers are short. This time constraint might differ between sexes, because only females bear the costs of egg laying and incubation. In Chapter 4 we investigated the relation between timing of breeding and timing of wing moult in male and female barnacle geese breeding at different latitudes. In addition, we explored the flexibility in timing of these annual cycle stages by looking into the timing of breeding and wing moult of individuals that switched population.

II. Rhythmicity and activity
Geese need to adapt to different environmental conditions during migration. When migrating along a latitudinal gradient, birds experience rapid changes in light conditions, and for diurnal birds like geese, daylight largely determines the time available for foraging. In Chapter 5 we measured body temperature in free living barnacle geese, using implanted loggers, to study the circadian rhythms of migratory and resident geese. We analysed how rhythmicity of geese from both populations changed during the period of spring and autumn migration in relation to changing light conditions. A migratory life history strategy does not only require changes during the migratory period but impacts the complete annual cycle due to potential carry-over effects. In Chapter 6 we use tracking data to compare foraging activity of migratory and resident barnacle geese throughout the entire annual cycle to investigate if and when migratory geese compensate for the energetic expenses of migration. By comparing the period during which migratory and resident geese are active longer than the available day length, we evaluate if migratory geese experience a stronger energetic bottleneck.

In Chapter 7, I synthesize the results of these studies and reflect on their significance to our understanding of the costs and benefits of migration. I discuss the impact of environmental changes on the cost-benefit balance of migration and evaluate the requirements for migratory birds to adopt a resident life history strategy.
Box 1.1 Comparative studies on the barnacle goose populations in the Barents Sea-Baltic-North Sea flyway

The range expansion of the barnacle goose has provided the opportunity to study the differences between migratory and resident geese. Over the years data have been collected in breeding colonies in the Arctic (Barents Sea) and in the newly established temperate populations (Baltic and North Sea). Nonetheless, true comparative studies among these populations remain scarce. Here I provide a brief overview of the results of studies that applied a comparative approach using migratory and resident populations in the Barents Sea-Baltic-North Sea flyway.

Van der Jeugd et al. (2009) were the first to compare major life history characteristics of barnacle geese of the Barents Sea, Baltic and North Sea populations (Table 1.1). They revealed population differences in timing of reproduction (hatch date) and moult, showing that both temperate populations had advanced the timing of reproduction and moult. Temperate breeding geese likely had advanced reproduction as much as possible to match hatching with the local food quality peak, which occurs earlier at temperate latitudes. In addition, post-fledging survival was markedly lower in the Barents Sea population (0.55 compared to 0.90 and 0.97 in the temperate populations) and depended strongly on local timing of breeding. During the post-fledging period, the duration of parental care was found to be 21% shorter in the North Sea population compared to the Barents Sea population (183 vs 233 days, Jonker et al., 2012) because migration and non-migration differ in expectations of future reproductive success as a result of differential adult and/or offspring mortality. Here we studied how a recent emergence of non-migratory behaviour has affected the duration of parental care in the previously (until the 1980s, presumably because prolonged parental care in the resident North Sea population is not necessary to enhance offspring survival. Eichhorn et al. (2010) respectively focussed more specifically on the first phase of reproduction using the North Sea and Barents Sea populations in a comparison of clutch size and incubation behaviour. Clutch size was shown to decrease with latitude resulting in a larger clutch size in the North Sea population (5 eggs) compared to the Barents Sea population (4 eggs). Although egg volume was larger in the Barents Sea population, this did not fully compensate for the lower clutch size, thus resulting in a lower clutch volume in the Arctic. Additionally, Eichhorn et al. (2010) respectively found that temperate breeding female barnacle geese in the North Sea population started the incubation period with a higher body mass and lost about 23% of their body mass during incubation, whereas females in the Barents Sea population only lost 15%. Barents Sea females were found to increase
nest recess time to forage in order to supplement the energy expended during incubation. Recently, Eichhorn et al. (2019) revealed differences in Resting Metabolic Rate (RMR) in adults during the moult period and in growing juveniles, when RMR of migratory geese was found to be higher than the RMR of resident geese. Fokkema et al. (2020) complementary to traditional concepts, as to why certain species show seasonal migration. We describe how demographic processes (survival, reproduction and migration combined published and unpublished parameters on reproduction and survival collected in the Barents Sea, Baltic and North Sea populations in a matrix population model, to derive the population growth rates. They found that the Arctic migratory population (Barents Sea) was growing slowly over the period of 2003-2014 ($\lambda = 1.034$). The temperate resident population (North Sea) was growing rapidly during the same period ($\lambda = 1.139$, 2004-2012) and showed comparable growth as the temperate migratory population (Baltic) during the period 1984-2001 ($\lambda = 1.157$).

Table 1.1: Overview of the breeding and wintering latitudes of the barnacle goose populations used in comparative studies

<table>
<thead>
<tr>
<th>Population</th>
<th>Life history strategy</th>
<th>Breeding latitude</th>
<th>Wintering latitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barents Sea</td>
<td>Long-distance migratory</td>
<td>68-72 °N</td>
<td>51-54 °N</td>
</tr>
<tr>
<td>Baltic</td>
<td>Short-distance migratory</td>
<td>56-61 °N</td>
<td>51-54 °N</td>
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<tr>
<td>North Sea</td>
<td>Resident</td>
<td>51-53 °N</td>
<td>51-54 °N</td>
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