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Outflying climate change

Optimal timing of migratory geese breeding in a warming Arctic

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CHAPTER 1

General introduction

From their very first appearance on this planet, organisms have been struggling for their survival by adaptation to the changing conditions around them. By a continuous development of traits and capabilities that allowed them to survive these changes, it can be safely stated that the animals currently inhabiting the globe are the product of past environmental change. While the earth has seen many cycles of climatic changes, including periods with temperatures up to 14 °C higher than today and, in the past million years, strong fluctuations in temperature between glacials and interglacials, climatic changes have typically shown gradual trends over time. In the current geological time period, aptly called the Anthropocene, we see strong and sudden changes in climatic conditions, set in motion by humankind itself as it started to change their own environment after having adapting to it. Anthropogenic climate change will possibly turn into the largest threat to the continued existence of humans on this planet, but it also poses a challenge for other organisms to make quick adaptations. Indeed, we see strong shifts in the phenology of flowering of plants and reproduction period of animals, as the optimal conditions shift forward in the season under temperature increase. As climate warming is especially pronounced high up in the Northern hemisphere, the Arctic region, we should expect organisms that live here to show the largest phenological adjustments to warming conditions. However, as many of the animals living in this environment are migratory, their rate of adaptation in the Arctic depends on their ability to adjust their migration from southern wintering areas. In this thesis I study how Arctic climate warming alters the phenology of migration and reproduction of migratory animals breeding in the Arctic, and how this can affect their fitness.

Rapid climate warming in the Arctic

As a consequence of the increase in levels of CO_2 and other greenhouse gasses in the atmosphere, temperatures have been rapidly increasing during the last decades on a global scale, and will continue to increase during the 21st century (Parry et al. 2007; Stocker et al. 2013). The increase in temperature is however not homogeneous across the globe, and is especially pronounced in the Arctic region (ACIA 2004). By storing greenhouse gasses and reflecting a large part of the solar radiation which passes the atmosphere, the Arctic has for a long period functioned as the refrigerator for our planet. At this moment, climatic changes seem to have broken through a threshold, triggering positive feedback mechanisms which lead to a rapid warming of the Arctic, and eventually our planet as a whole. Due to increasing temperatures, the surface area of sea ice and snow are diminishing more rapidly in summer, which results in a lower albedo, in turn leading to a further temperature increase in the Arctic but also on a global level. Already, the cover of Arctic sea ice over the past 30 years has declined by 15% per decade (Parkinson & Comiso 2013) and it is expected that the Arctic Ocean will be free of ice in late summer before the year 2050 (Massonnet et al. 2012; Notz & Stroeve 2016). In late

2017 Richter-Megne et al. (2017) concluded that the Arctic environmental system has reached a 'new normal', characterized by long-term losses in the extent and thickness of the sea ice cover and strong shortening in the duration of the winter snow cover (Richter-Megne et al. 2017). As such, the Arctic is not expected to be able to return to its original state as a 'reliable frozen region'. This can also be ascribed to another important feed-back mechanism. Due to the melting of permafrost layers across the whole Arctic, high levels of the strong greenhouse gas methane are released, which is expected to be a major source of global temperature increase. The combination of feedback mechanisms leading to amplified warming in the Arctic region is known as 'Arctic amplification' (Serreze et al. 2000; Serreze & Francis 2006a; Serreze & Barry 2011). Current predictions show that the Arctic will warm 2.2 to 2.4 times faster than the global average (Stocker et al. 2013; Figure 1.1), but these predictions might even be underestimating the rate of amplified warming. Although patterns of climatic change in the Arctic are erratic (Stocker et al. 2013), rapid climate warming in the Arctic has already affected plants and insects in the high Arctic, for which temperature is an important trigger for phenological processes (Tulp & Schekkerman 2008; Livensperger et al. 2016), and which show strong advancements during recent years (Høye et al. 2007).
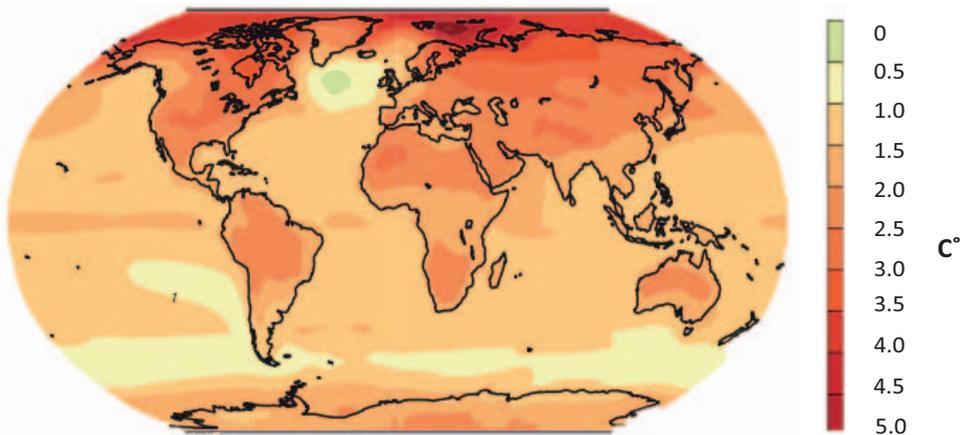
Figure 1.1: Climate warming in 2046 – 2065 under the climate scenario 2A by the IPCC (2007).

Optimal timing of breeding

In order to understand how larger migratory organisms may adjust their phenology to climate warming, we first explore what drives their phenology regardless of climate change. Many larger organisms, such as birds, adjust their reproduction period to the phenology of their food, plants or smaller animals, in order to maximise their fitness (Lack 1968). Typically, offspring survival is strongly linked to the synchrony in timing

of hatch with seasonal peaks in food availability (van Noordwijk et al. 1995), and chicks in nests that hatch too late will experience less beneficial growing conditions due to a mismatch with these seasonal peaks. In addition, earlier hatching chicks have a longer period to attain body condition before the end of the season, necessary to survive the winter. Earlier hatching chicks thus have increased growth and survival rates compared to late hatching chicks (Sedinger & Flint 1991; Prop & Vries 1993; Brinkhof & Cavé 1997; Sedinger et al. 1997; Lepage et al. 1998, 1999, 2000; Verhulst & Nilsson 2008), resulting in a seasonal decline in reproductive success, which favours selection for early breeding (Sedinger & Raveling 1986; van der Jeugd et al. 2009). Most birds however lay ´too late´ to maximise offspring survival (Perrins 1970), suggesting that optimal timing of breeding is not just a matter of laying early. Reproducing itself is costly for an animal, affecting its chances for surviving up to the following year (Drent & Daan 1980). To maximise fitness, an individual should consider both its reproductive success in a given year as well as its survival from one year to the next, given its expected reproductive success in future breeding seasons. Fisher [1930] therefore argued that because early laying might inflict reduced adult survival, laying date might be the result of two conflicting selective forces, one for adult and one for offspring survival. Parents would thus choose not to lay earlier than they do. In extremely unprofitable breeding seasons, this may drive long-lived birds which still have many breeding seasons ahead to forego breeding to ensure their own survival. Alternatively, Perrins (1970) suggested that a shortage of food for the parents early in the season prevents most birds from laying on optimal dates in terms of offspring survival (the 'constraint hypothesis'). In this case, it is hypothesized that a small group of high quality individuals is able to lay early as they can monopolize the little amount of available food, but most individuals cannot lay earlier. This idea has since been proven in a number of experiments with different species (Meijer & Drent 1999), showing that food supply for the female is indeed one of the proximate drivers in laying date (Drent 2006). Parents can improve their body condition by delaying their laying date, which allows them to lay a larger clutch (Ebbinge & Spaans 1995; Prop et al. 2003), but should not delay for too long, as at the same time they experience a seasonal decline in offspring value resulting from reduced availability of food. Depending on their body condition and the prospects for gaining body stores, birds will adjust both their laying date and clutch size, which is the result from a individually optimized trade-off between fitness benefits of breeding early against those of breeding late (Partridge 1989; Tinbergen & Daan 1990; Descamps et al. 2011), known as the 'cost of delay hypothesis' (Reynolds 1972; Drent & Daan 1980). Rowe and colleagues (1994) modelled this hypothesis and predicted that for birds with a similar arrival date on the breeding grounds, individuals in poor condition have more to gain from a delay in terms of an relative increase in potential reproductive success via clutch size. However, due to differences in onset of the condition gain, these birds will still have a lower clutch size than birds with a better condition on arrival,

explaining a seasonal decline in clutch size, which is common in birds (e.g. Christians et al. 2001). Birds thus individually optimize their laying date and clutch size depending on arrival time and energy stores on arrival. Bêty and colleagues (2003) indeed showed that female snow geese (*Chen caurulescens*) adjusted both laying date and clutch size to their condition as predicted in the model, and females with high pre-migration condition had an earlier laying date than those in low condition. Consequently, individuals in good condition should be expected to arrive and lay earliest (ensuring good growing conditions for the offspring) and have the largest clutches, thereby achieving the highest reproductive success.

## Optimal timing of migration to the Arctic

By making long migratory flights in spring and autumn, migratory birds can breed at high latitudes in the Arctic region, where increased day length permits longer foraging times (Rose & Lyon 2013), while escaping unfavourable conditions during winter when migrating to mid-latitudes (Alerstam & Högstedt 1982; Alerstam et al. 2003). In the Arctic, birds are however faced with a short breeding season, in which they have to lay and incubate eggs, raise chicks and moult their feathers. As a consequence, they are more time-constrained than birds breeding in temperate regions, and the individual optimized trade-off between late against early breeding also becomes more pronounced. This is particularly the case for larger birds, as their slower pace of life, with longer incubation and chick-rearing periods, makes them more time constrained than smaller birds (Klaassen 2003). Such a strong time-constraint drives birds to lay their eggs early, but in order to do so birds also need to arrive early on the breeding grounds, in a period in which a scarcity of food resources and adverse weather conditions can jeopardize adult survival (Arzel et al. 2006). Optimal timing of breeding may only be possible if birds are also able to optimally time their migration.

As discussed before, early nest initiation can be limited by available resources, and more specifically by the nutrient status of the female (Drent et al. 2006). Decisions on when to breed for migratory birds importantly rely on both the bird's accumulated energy stores and the abundance of food resources in the local environment, which are referred to as capital and income (Drent & Daan 1980; Stephens et al. 2009). While 'income breeders' depend on local food resources on the breeding grounds for acquiring the energy needed for egg production, ´capital breeders´ evade the problem of limited food resources on the breeding grounds early in the season by accumulating these energy stores during migration (Thomas 1988; Stearns 1992; Stephens et al. 2009). In this way, capital breeding migrants have found a solution for the trade-off which resident income breeders face: to use the single peak in food availabillity either for themselves when preparing for breeding, or for their offspring by breeding in front of the food peak. The classification of capital and income breeding strategies is rather a continuum between

two extremes than a sharp dichotomy (Meijer & Drent 1999; Williams et al. 2017), and birds generally use a mixed strategy (Gauthier et al. 2003; Drent et al. 2006, 2007; Klaassen et al. 2006; Nolet 2006). Strategies lying closer to capital breeding are especially expected for larger birds, as for these birds the energetic costs of egg-laying and incubation are relatively small compared to the costs of migration (Klaassen 2003; Klaassen et al. 2006; Nolet 2006). However, even for larger birds such as geese, strategies are not fixed and differ between individuals depending on timing of migration and nesting (Klaassen et al. 2006; Hahn et al. 2011). Taken together, the body stores which a bird can bring to its breeding grounds may be an important predictor for its laying date and, possibly as a consequence, its reproductive success (Prop & Black 1998; Drent 2006).

In order to be most efficient in accumulating body stores during migration, it has been proposed that Arctic-nesting geese make optimal use of a seasonal environment during migration by following a climatic gradient of successively delayed flush of grass growth at the onset of spring, known as the 'green wave hypothesis' (Drent et al. 1978; Schwartz 1998). For barnacle geese (*Branta leucopsis*) it has been shown that they indeed track the green wave as they arrive on stop-over sites at the peak of food quality in forage plants (van der Graaf et al. 2006; Figure 1.2a), but continue on migration when quality declines (Prop et al. 2003). To track this green wave, geese seem to be able to use local temperature or vegetation greenness (van Eerden et al. 2005; Eichhorn et al. 2009; Shariatinajafabadi et al. 2014), which together with day length form the most important cues for the timing of migration (Duriez et al. 2009). Also, as should be expected for capital breeders which bring in energy stores from mid-latitudinal stop-over sites to start nesting early, it has become clear that geese can overtake the green wave and reach the breeding grounds before the onset of spring (Shariatinajafabadi et al. 2014; Kölzsch et al. 2015; Si et al. 2015a) in order to make the chicks benefit from the same food peak after hatching (Lepage et al. 1998). Interestingly, barnacle geese which have abandoned a migratory strategy and do now breed as residents at temperate latitudes, do not seem to be able to breed early enough to profit from a local food peak (van der Jeugd et al. 2009), potentially as they cannot make use of a green wave to fuel reproduction.

Long-distance migrants are thus faced with the challenge of optimal timing of breeding on distant Arctic breeding grounds, where they have to arrive early but with enough stores of energy accumulated during migration to start breeding soon after arrival. We have seen that optimal timing of breeding is strongly linked with the optimal timing of migration (Alerstam & Hedenström 1998; Drent et al. 2003), as the arrival time and stores upon arrival necessary for successful breeding are the outcome of an optimal migration strategy. As Arctic geese follow a green wave of peak food availability on stopover sites, Drent and co-workers concluded that these stopover sites, and the migration timing of the birds to make use of these stopover sites, are indeed the weak links to meet the targets for successful reproduction (Drent et al. 2007).
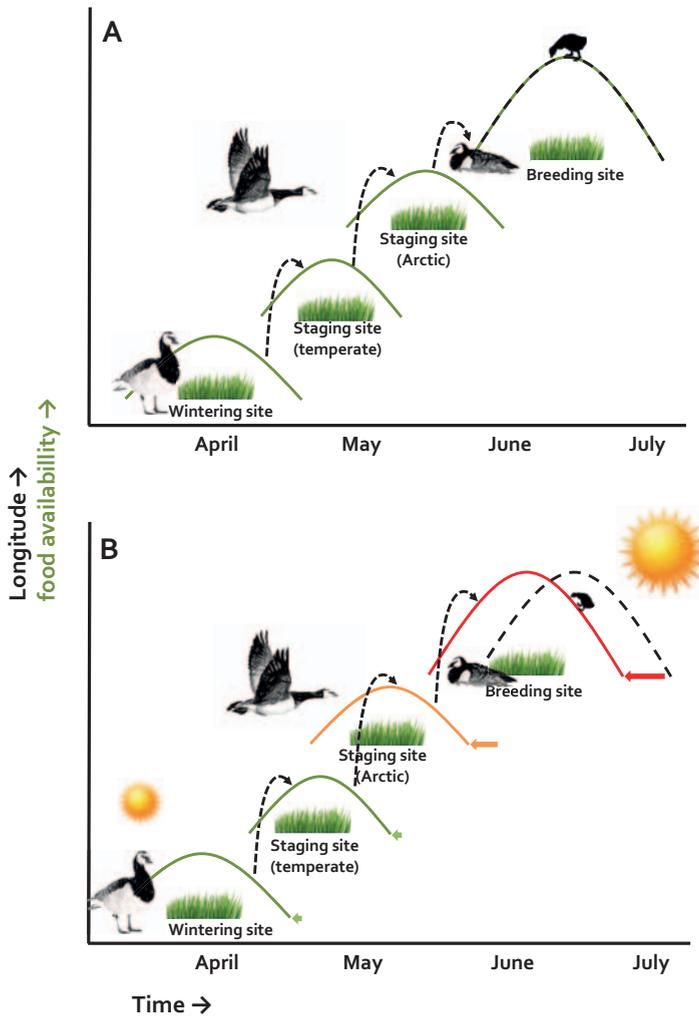
Figure 1.2: (A) Long-distance migrants breeding in the Arctic can follow a 'green wave' of peaks in food quality during migration. Birds leave their wintering site when food quality starts to decline, and they can find higher food quality at a following staging site. By making use of multiple peaks in food quality, birds can arrive at the their Arctic breeding sites and start breeding in front of the green wave. In this way their chicks can profit from high food quality right after hatching. (B) When climate warming is occurring more rapidly in the Arctic than in temperate sites, birds may not be able to adjust their migration schedule accordingly, and as a result arrive too late in the Arctic. If they start breeding late relative to the local food peak, their chicks hatch too late to profit from the peak in food quality, which may reduce their survival and growth.

Challenges of adapting to climate warming

Climate warming can importantly affect the optimal timing of breeding and migration, as climate dictates the availability and quality of food on stop-over and breeding sites, and is also used by migratory birds as a cue to optimally time their migration. This is especially the case for flyways where rates of climate warming largely differ between wintering and breeding sites, such as is the case for Arctic migrants under Arctic amplification. Already, the short peak in food availability in the Arctic is strongly advancing (Tulp & Schekkerman 2008; Doiron et al. 2014), and some Arctic migrants do not seem to advance their laying dates enough to match these advancing food peaks, resulting in a strongly reduced growth of their chicks (Doiron et al. 2015). It has been proposed that birds do not adapt their migration timing to earlier food peaks on the Arctic breeding grounds, and thus arrive 'too late' to initiate a nest in time (Clausen & Clausen 2013). The pivotal question thus becomes whether birds mistime their reproduction and migration because 1) they cannot use current cues to predict rapid climate warming in their breeding grounds; or because 2) an advancement is limited by revenues for foraging, on the wintering grounds and during migration.

1. Local cues to which birds have access to on their wintering grounds may not enable them to predict the rate of seasonal advancement on their breeding grounds, which may be thousands of kilometers away. Although migrants are known to be able to use yearly variations in local temperature and plant phenology as cues to time their migration (Duriez et al. 2009; van Wijk et al. 2012), the climatic system at their wintering grounds is poorly correlated with that of their breeding grounds, and cannot be used to forecast the advancement of spring in the Arctic (Kölzsch et al. 2015). When using a step-wise migration with multiple stopover sites, birds may become better able to predict conditions on the breeding grounds while aproaching, but environmental barriers such as oceans and mountain chains might then still disrupt correlations between climatic systems in the different areas. As birds are at least to some extent unable to predict climatic conditions on their breeding grounds, they have to time their migration independent from environmental or climatic variables. While these cues may allow for optimal arrival under average conditions, they will not shift together with rapidly advancing onset of spring in the Arctic. The utilization of either one of these cues is likely to lead to a mistimed migration timing under unequal climate warming in the Arctic

2. In order to advance migration timing, birds will need to have acquired enough body stores before departure from their wintering or stop-over site to complete their migratory journey, or at least to fly up to the first stopover site. If birds depend on food peaks at temperate sites or even on a green wave for the first stretch of their migratory journey (van der Graaf et al. 2006), they may simply not be able to accumulate enough body stores to advance their departure for migration. Alternatively, another way to advance migration timing would be to not necessarily advance their departure from the

wintering grounds, but to spend less time feeding on stopover sites, and thus advance the arrival on the breeding grounds (Schmaljohann & Both 2017; Figure 1.2b). Birds may then entirely skip stopover sites, as has been observed for barnacle geese, for which a large part of the population currently skips a historically important stopover site in the Baltic Sea during spring migration (Eichhorn et al. 2006). In this way birds might be able to advance their migration timing, but by spending less time foraging underway it would potentially reduce the capital fat stores which they can bring with them to the breeding grounds. As capital breeders, geese tend to use part of their fat stores for reproduction, and a reduction of their body condition on arrival at the breeding grounds would impact their reproductive output, causing them to either lay less eggs, or delay initiation of breeding as they have to fuel up on the breeding grounds.

While climate warming is causing an advancing onset of spring in the Arctic, summers may also become warmer and longer. Higher summer temperatures have been shown to positively affect chick survival and total reproduction in Artic breeding waders and waterfowl (Meltofte et al. 2007; Dickey et al. 2008; Van Oudenhove et al. 2014; Wood et al. 2016). In longer summers, the period of vegetation growth and insect abundance can be extended (Chapin III et al. 2005), granting offspring a longer period to grow and accumulate body condition before feeding conditions deteriorate, which in turn can increase their chances to survive southward migration (Owen & Black 1989). It has indeed been shown that in seasons with longer food peaks, offspring survival of Sanderlings *Calidris alba* has been higher (Reneerkens et al. 2016). If longer seasons increase offspring survival, the selection pressure to start nesting early is likely to drop (Tomotani et al. 2016), as birds that start nesting relatively late also have a chance to produce viable offspring.

Goals and structure of the thesis

The main goal of this thesis is to examine how Arctic climate warming alters the phenology and fitness of Arctic migrants. I approach this goal by first making predictions how climate warming may alter optimal timing of migration and reproduction, after which I investigate the limitations for Arctic migrants to make these adjustments, and how this affects their fitness. I specifically aim to understand which mechanism is a more important factor limiting advancement of migration and reproduction timing under climate warming – revenues for energy deposition prior to and during migration or predictability of climatic conditions in the breeding grounds.

I investigate these questions by a study on the barnacle goose, an Arctic long-distance migrant which breeds in coastal regions of Greenland, Svalbard and North-Western Russia and spends the winter in North-western Europe. Barnacle geese are one of the most intensively studied migratory waterfowl, with 18 dissertations on the ecology and behaviour of this species published to date (Box 1.1; Black 1987; Choudhury

1992; Ebbinge 1992; Forslund 1992; Larsson 1992; Tombre 1995; Loonen 1997; van der Jeugd 1999; Stahl 2001; Prop 2004; van der Graaf 2006; Portugal 2008; Eichhorn 2008; Jonker 2011; Karagicheva 2011; Kurvers 2011; Sandström 2017; Shariati Najafabadi 2017). Not only has this generated a large body of knowledge on this species (also compiled in two monographs: Black et al. 2007; Black et al. 2014), but also do we now have long-term datasets on migration and reproduction timing of this species. In addition, following a population increase in the 1980s (Madsen et al. 1999), the barnacle goose population has started to expand its breeding range along its flyway, and now breeds down to temperate regions in North-West Europe (Larsson et al. 1988; Meininger & Van Swelm 1994), a region where it used to occur only in winter. This enables to study the characteristics of an Arctic migrant breeding in environmental conditions which differ greatly from its original breeding grounds in the Arctic, as if it has already undergone climate change on its breeding grounds.

In the first part of the thesis I aim to make predictions on effects of climate warming on optimal timing of migration and reproduction. In Chapter 2 we study the effect of climate warming on timing of food peaks, important for timing of migration and reproduction. We use a field-experiment with open-top chambers to study the effect of increased temperatures on quality and growth of forage plants at three sites along their migratory flyway. In Chapter 3 we model migration timing of barnacle goose under unequal rates of climate warming to study whether time needed for energy deposition or the predictability of climate warming on the breeding site is a more important limitation for advancement of migration timing.

In the second part of the thesis I deal with the most important research technique used to study animal migration, the application of electronical tracking devices. In Box A we demonstrate our method of attaching tracking devices to geese, and in Chapter 4 we study whether attachment of tracking devices in this way has effects on survival, migration and reproduction in three species of Arctic-breeding geese. In Chapter 5 we review the potential effects of tracking device attachment for waterfowl in general and study to what extent these are reported in research papers. In Box B we present the results of our tracking study in 2015 on the spring migration of barnacle geese using GPS-loggers, showing detailed patterns in migration timing and stopover site use.

In the third part of the thesis I study the limitations for barnacle geese to adjust migration and reproduction timing, and how this affects their fitness under current climate warming and climatic variation in the Arctic. In Chapter 6 we use time budgets derived from this study to investigate whether Arctic barnacle geese can advance fuelling for migration in the wintering grounds, by comparing fuelling rates of the Arctic population with the resident population. In Box C we further dive into this fuelling period by investigating what drives geese to make a shift in habitat use during fuelling along the North Sea coast. In Chapter 7 we use the yearly climatic variation in the Arctic

and long-term data on migration and reproduction data to study how geese adjust migration and reproduction timing under warmer Arctic springs, and whether mistimed reproduction has fitness consequences. In Chapter 8 we consider the potential benefits of climate warming on fitness through earlier breeding, which we study using long-term data on reproduction timing and reproductive output in three colonies of barnacle geese in the low and the high Arctic. In Chapter 9, I take the findings from previous chapters together to find an answer to the initial question of this thesis – how Arctic climate warming alters the phenology and fitness of Arctic migrants.

Box 1.1 Dissertations on the ecology and behaviour of barnacle geese

The first studies on barnacle geese have been initiated in the geese's wintering grounds in North-Western Europe, most notably in Scotland and in the Netherlands. The first dissertation in which barnacle geese features as a study species was defended by Jeffrey **Black** (thesis defence: 1987) at Oxford University, who studied barnacle geese in their wintering grounds in Scotland under supervision of Myrfyn **Owen**. This study was focussed on the unique social life of geese: the long-lasting pair bonds and the relationship with offspring which stay together with their parents for almost a year. Sharmilla **Choudhury** (1992) continued this work under supervision of Black, to study the formation of these pair bonds, and to what extent barnacle geese choose their mates based on their own experience, body size and the familiarity with their new partner.

At the same moment a long term study on breeding barnacle geese in Gotland and Öland, from the emerging breeding population around the Baltic Sea, was initiated from Uppsala university. Kjell **Larsson** (1992) and Pär **Forslund** (1992) used this population to study the influence of density dependent processes on reproduction and population growth in this colony. Forslund focussed on the additional effects of age on reproductive success, and how the experience of a bird, but also that of its partner, affected reproductive success. Larsson found that traits such as body and egg size were heritable, and simultaneously affected reproductive success of geese. Supervised by Larsson, Henk **van der Jeugd** (1999) continued the study on the Baltic population. He found that colony size was the main determinant for reproductive success, with large colonies producing more, but also smaller offspring. At the same time, reproductive success was importantly affected by climate.

By then, the study of barnacle geese from Scotland had been extended with expeditions to the breeding grounds in Arctic Svalbard, where Norwegian, Dutch and British scientists collaborated in the study of breeding barnacle geese. One of the first to visit this region to study barnacle geese was Barwolt **Ebbinge** (1992), who visited Nordenskioldkysten in 1975 and used his study on the breeding ecology and population dynamics of wintering geese to investigate the cause of the enormous population growth of several goose populations in western Europe in the 20th century. He concluded that the main cause of this population increase was primarily

improved survival, resulting from hunting restrictions and not necessarily improved feeding conditions in the wintering region, because goose numbers were also much higher in the first half of the 20th century. Ingunn **Tombre** (1995) and Maarten **Loonen** (1997) continued the work in Svalbard and worked together in the Kongsfjorden, where they studied several aspects of reproductive success in Arctic-nesting barnacle geese. While the studies around the Baltic Sea had put the main focus on the conditions in the colony and the experience of birds, Tombre focussed on the importance of timing of laying and the body mass of individual females prior to breeding on their clutch size, aspects which may be especially important in the Arctic. Loonen investigated what happened after the chicks had hatched, and found that earlier hatch dates but also larger broods positively affect the growth rate of goslings. Jouke **Prop** (2004) initiated a long term study of barnacle geese breeding at the Nordenskioldkysten in 1977, which makes this colony the longest term study site for barnacle goose breeding studies. In his research, Prop showed the importance of individual differences in foraging success, both in wintering, stopover and breeding sites for the fitness and survival of barnacle geese.

Both Ebbinge, Loonen and Prop were students of Rudi **Drent**, who was one of the main instigators of barnacle goose research in the Netherlands. He was also the supervisor of Julia **Stahl** (2001), who took up the study of foraging in barnacle geese from a different angle, by investigating how social status and location in the flock determine foraging opportunities and energy expenditure of an individual goose. The potential benefits of living in flocks were further investigated by Ralf **Kurvers** (2011), under the supervision of Herbert **Prins**. Kurvers looked into personality of geese, and found that barnacle geese which were less explorative benefitted from copying the behaviour of bolder geese. The topic of foraging was taken up again by Stahl and Drent, who supervised Alexandra **van der Graaf** (2006) who studied foraging along the migration route of barnacle geese breeding in Arctic Russia. She investigated how geese selected foraging sites in space and time, showing for the first time how barnacle geese make use of a green wave of spring grass growth during migration. The green wave hypothesis was more thoroughly explored with the use of satellite imagery by Mitra **Shariati Najafabadi** (2017), who added important evidence that barnacle geese indeed follow a green wave.

Initiated by Mennobart **van Eerden**, Rudi **Drent**, Konstantin **Litvin** and Henk **van der Jeugd**, the breeding colony in the Kolokolkova Bay in Arctic Russia was visited in 2002 and became another location of long-term field study. Under the supervision of Drent, Götz **Eichhorn** (2008) started a study which aimed to connect migration timing and reproduction success. Eichhorn uncovered the flexibility in migration schedules of barnacle geese, but also the importance of feeding prior to and during migration for optimal reproduction timing. The colony structure in this Arctic colony was further investigated by Julia **Karagicheva** (2011), who found that offspring tended to nest close to their parents. The energetics of migration and moult of barnacle geese was investigated by Steven **Portugal** (2008), supervised by Pat

Butler. Portugal used heart-rate loggers to quantify energy expenditure year-round, and found that the moulting period was a much more strenuous period for geese than previously considered.

Although a first comparison between Arctic and temperate (Baltic Sea) breeding geese had been made by Maarten Loonen, this comparison was made more comprehensively by adding a study population breeding in the Netherlands, studied by Henk **van der Jeugd** and Götz **Eichhorn**. It appeared that temperate breeding geese nest too late relative to the local food peak. The comparison between Arctic and temperate breeding geese was used again by Rudi **Jonker** (2011), who was supervised by Herbert Prins. Jonker studied the emergence of the non-migratory barnacle goose population. Using genetical analyses, he found that both populations show large admixture, as there is still gene-flow between migratory and resident populations. The potential benefits of breeding in the Arctic were investigated by Cecilia **Sandström** (2017), who was supervised by Maarten **Loonen** and compared the immune defence of Arctic and temperate breeding geese, and found that Arctic geese have to spend less energy in defending themselves from parasites than their temperate counterparts.

Together, these theses give a comprehensive overview of barnacle geese as a social herbivore, which makes optimal use of its environment prior to and during migration to increase its fitness. The tremendous amount of knowledge generated has paved the way to study how the barnacle goose can cope with a changing environment. Where Prop, Eichhorn and van der Graaf have all shown how geese can adapt to land-use changes, rapid climate warming in the Arctic has now set the scene for a study entirely focussed on the effects of climate change on barnacle geese. This thesis truly stands on the shoulders of giants, benefitting heavily from the extensive knowledge on foraging intake and energy expenditure of barnacle geese, and the data from long-term field studies in the Arctic and temperate breeding areas.