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### Geese colonising New Land

*Causes and mechanisms of range expansion in an Arctic-breeding migrant*

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*"We simply must balance our demand for energy with our rapidly shrinking resources. By acting now, we can control the future, instead of letting the future control us. (...) Our target is to have 20 % of all the energy that we consume in this nation, come directly from the sun by the year 2000."*

Pres. Jimmy Carter (1977),

who installed 32 solar panels on the White House roof on 20 June 1979,  
which were removed in 1986 by the Reagan administration.  
Currently, solar energy accounts for 3.4 % in the U.S. energy mix (EIA 2023).



# Chapter 1

## General introduction

Kees H.T. Schreven

### **The role of ecology in the relation of people with nature**

One may argue that ecology was one of the first fields of science. Ever since the first hunter-gatherer communities, some knowledge must have existed on where and when to find certain animals, plants and fungi, and how to anticipate the behaviour of game species. The understanding of how species interact with each other and the environment must have deepened when people started to farm and manipulate nature. Finally, our exploitation and manipulation of nature grew beyond the limits of manpower (and horsepower) during the industrial revolution and nowadays human activities affect nature on a global scale, directly and indirectly. From using nature to our own benefit, we have moved to protecting nature to safeguard our own future. The importance of staying within the limits of natural systems has long been recognized on population level, e.g. when harvesting fish or other non-farmed populations. However, global environmental changes have transformed ecology, 'the science of the household', into a science which now often necessarily adopts a global perspective to understand processes, and which is crucial in *predicting* our global effects on nature, to stay within the limits of the 'household' Earth (Rockström et al. 2009).

### **Global environmental change**

Two prominent anthropogenic environmental changes that occur on a global scale, are land cover change and climate change. Land cover is changing generally in favour of habitats where people live or which provide us with food, at the expense of all other habitats. As such, large expansions have occurred in the surface area of urban areas (Seto et al. 2013) and agricultural lands (Winkler et al. 2021), parallel with decreases and fragmentation of e.g. afforested areas (Keenan et al. 2015). When we express the rate of change in land cover as total size of the country Netherlands per year (called 'NL/y'), we see that globally, over the past decades, forests have disappeared at a rate of 1.3 NL/y (during 1992-2020), while urban areas gained 0.5 NL/y (during 1990-2015) and agricultural land first increased by 2.4 NL/y (during 1961-2001) but now decreases by 1.7 NL/y (during 2001-2020; World Bank Open Data 2023).

In the changing climate, an important aspect is the increase in temperature, known as global warming, by an increase in greenhouse gasses (IPCC 2001). The rate of warming varies geographically and is highest in the Arctic, known as Arctic amplification (Cohen et al. 2014). At the same time, weather extremes are becoming more common. For example, in the Netherlands, temperatures are increasing and periods of drought are becoming more common, even though annual precipitation is also increasing (Selten 2022). This is because there is less precipitation in summer, while individual showers are getting heavier (Selten & Siegmund 2022).

Climate change may induce land cover change, since the optimal locations for certain human activities may shift. For example, crops can now be cultivated at higher latitudes (Cho & McCarl 2017), and coastal and riverine areas can become less safe as living place because of an increased flooding risk (Winsemius et al. 2016). In addition, land use can also shift seasonally, as farmers are now able to work their arable lands earlier in the year (Grusson et al. 2021). In turn, land cover changes can further speed up climate change, for example because large-scale deforestation lowers carbon sequestration (Prevedello et al. 2019).

The effects of these global changes on people and nature are plenty. Not only do these environmental changes cause e.g. sea level rise (IPCC 2013), more flooding (Milly et al. 2002), more forest fires (Gillett et al. 2004), a less secure human food supply (Schmidhuber & Tubiello 2007) and could catalyze regional human conflicts (Buhaug et al. 2008), they may also jeopardize the stability of the ecosystem Earth itself, e.g. due to the loss of biodiversity (Hautier et al. 2015). These unsustainable developments are worrying, especially for younger generations, who demand more political action (Sanson & Bellemo 2021).

### **Environmental change and animal ecology**

To pursue a sustainable way of life, it is essential to know how and if the living natural world is able to cope with these changes. Species that can adapt to the (semi)urban environment thrive, while species dependent on large pristine habitats are in jeopardy of extinction (Thomas et al. 2004, Rigal et al. 2023). Within agricultural land use, also the intensity of the agriculture has effects (Rigal et al. 2023). Species that benefit from intensive agriculture, such as geese which eat the crops rather than the natural herbs or insects present besides the crops, generally do well while bird species that are dependent on nutrient-poor natural open landscapes decrease (e.g. in the Netherlands, Sovon 2018). Land cover changes also cause fragmentation of natural habitats, which can limit effective population sizes and genetic exchange (Keyghobadi 2007), making populations more vulnerable.

To understand the main effects of climate change, we zoom in on phenology. Rising temperatures cause temperature sums to be reached earlier in the year (Twardosz et al. 2021) and snow to melt earlier (Stone et al. 2002), thus vegetation to start growing earlier (Schwartz 1998, Zhang et al. 2007) and invertebrates to emerge earlier in the year (Visser et al. 1998, Høye et al. 2007). In turn, species higher up in the food chain, which eat plants or invertebrates, are expected to advance their timing in line with their food availability. The food availability is usually characterized by a seasonal peak (e.g. larva abundance or vegetation nitrogen content, Visser & Both 2005, Doiron et al. 2015) and birds tune the timing of their costly reproductive period to the time when food is most plentiful (Lack 1968a). Because such reproductive decisions are made well in advance of the food peak, animals can only use cues that predict the moment of the food peak, in order to time their reproduction optimally. Although these cues may have been a correct predictor in the past, they could have lost their value in a changed climate if the prey responds to other cues (e.g. Visser & Holleman 2001). For example, daylength may function as cue but the correlation with temperature has changed due to climate change. Consumers may lag behind on the phenology of their resource (Both et al. 2009, Thackeray et al. 2016) and offspring food demand is not synchronized with the food availability: a trophic mismatch (Visser & Gienapp 2019).

Trophic mismatches are likely to be one of the driving factors behind the three main responses of animals to climate change: phenological shifts (Visser & Both 2005, Cohen et al. 2018), range shifts (Parmesan & Yohe 2003, Chen et al. 2011), and body size shrinkage (Gardner et al. 2011, Shediran & Bickford 2011). Other explanations involve e.g. staying in a thermal niche (Socolar et al. 2017). Besides the possibility that these responses are phenotypically plastic adjustments, some of these responses could also result from evolutionary change, i.e. if climate change intensifies the selection for reproducing early in spring (e.g. Visser et al. 1998, Both & Visser 2001).

### **Climate change and migration**

Migratory animals depend on multiple areas during their annual cycle. This further complicates adjustments to climate change, as migrants need to predict the optimal timing of arrival to the breeding grounds in advance and from a long distance. In other words, the environment of selection (breeding success and survival) differs from the environment of the decision making (migration timing), not only in time but also in space (see also Visser et al. 1998).

Migrants face the challenge that the rate of climate change varies geographically. Spring may advance in breeding grounds, but not on the stopover areas (e.g. Clausen & Clausen 2013), and weather in both locations may be uncorrelated (e.g. Kölzsch et al. 2015). Because of the absence of spatial correlation over long distances, migrants may have evolved to use a fixed migration schedule (e.g. depending on internal clocks, Gwinner 1996, Åkesson et al. 2017).

These migration schedules have hardly advanced (Schmalljohan & Both 2017) which may explain why long-distance migrants were found to decline more than short-distance migrants and residents in the same habitats (Both et al. 2010). Also, even when there is selection for earlier migration, constraints may prevent this evolution. If the timing of fuelling on the stopover cannot advance because the spring has not advanced there, migrants cannot accumulate enough body stores to travel earlier. These factors make that climate change may disrupt annual cycles of migrants. To enable migrants to advance, the stopover quality becomes crucial, as the food abundance determines the fuelling speed (Rakhimberdiev et al. 2018).

In addition to these challenges in the spatial and temporal predictability of spring onset, migrants face other challenges by climate change. Due to the larger climate warming in the Arctic than in temperate regions, spring may also advance more in the Arctic. Vegetation phenology has advanced more in colder areas (Ma et al. 2018, Rozenfeld et al. 2021). As a result, spring onset may occur more synchronized along a migration route, which gives migrants less opportunity to follow a 'green wave' of vegetation growth. Rather, they would encounter a 'green flash'. Further, some bird migrations are only possible due to prevailing wind patterns (Gill et al. 2014), but these are likely to change (IPCC 2007). In addition, increasing extreme weather events might affect migrants at times when they are vulnerable, e.g. when crossing a barrier without opportunity to rest or refuel. For example, dust storms in the Sahara are now more frequent (Niang et al. 2008) and can cause migrants to break off migration and retreat (Strandberg et al. 2010).

Because of these pressures on migrants, the phenomenon of migration itself may also become vulnerable (Wilcove & Wikelski 2008). The link between the different areas from which migrants used to benefit throughout their annual cycle may become less feasible. In addition, environmental change in the wintering area (e.g. increased food availability) can allow part of a migratory population to become resident (van der Jeugd et al. 2009, Boom 2022).

### **Challenges for Arctic migratory birds**

Since climate change occurs at the fastest rate in the Arctic, especially Arctic migrants are expected to be under pressure of climate change. A rapidly advancing spring requires fast adjustments in consumers as well. If this is not possible, due to constraints outlined above, this would cause a growing trophic mismatch especially in the Arctic. However, a review combining various bird species found no indications yet that mismatches are larger in the Arctic than at lower latitudes (Zhemchuzhnikov et al. 2021).

The alternative, i.e. adjustment in space rather than time, is also limited as the Arctic is already at the extreme in climate and spring onset, having one of the coldest and latest springs (Wauchope et al. 2017). Smaller-scale spatial adjustments may give some respite for certain species, for example a shift in elevational range (Chen et al. 2011). However, for some species such as migratory Arctic geese, this may only benefit the nesting stage and not the chick rearing stage: nests may be located on slopes, but geese with goslings congregate in flocks in lush lowlands close to water, for safety from predators on land (Madsen & Mortensen 1987).

Also the penalties of arriving too early or too late to the breeding grounds are expected to be large for Arctic-breeding migratory birds. The conditions change steeply throughout the season. Birds laying eggs late may face a time constraint by the short Arctic summer (Barry 1962). On the other hand, birds arriving too early encounter harsh conditions (snow cover, low temperature, low food abundance), and rely on their capital resources. However, breeding prospects decline when more of the capital is used up (Spaans et al. 1999, Spaans et al. 2007). These penalties result in a narrow time window for successful breeding in the Arctic (Tulp &

Schekkerman 2006), although the snow-free season in the Arctic has now become longer (Lameris et al. 2019).

### **Arctic breeding range expansion by Pink-footed Geese**

With all these challenges for Arctic-breeding migrants, it is important to understand where suitable breeding habitat occurs and how this will change in the future. Pink-footed geese (*Anser brachyrhynchus*) traditionally breed on Greenland, Iceland and Svalbard (Cramp & Simmons 1977). On Svalbard, the amount of suitable breeding habitat was predicted to increase in response to warming, based on distribution models (Jensen et al. 2008). These models found that occurrence was best explained by a combination of three factors, indicative of the start of spring (mean May temperature), the length of the season (number of frost-free months), and feeding conditions (proportion of moist and wet moss-dominated vegetation). As spring onset advances and seasons lengthen with climate change (Karlsen et al. 2014), more breeding habitat becomes available towards the north and east of Svalbard. These areas are generally colder, due to a gradient of sea influences within the Arctic zone, from warm Gulf stream influence in the west to cold Arctic ocean influence in the east (Polyakov et al. 2017). Traditional breeding areas are located on the west coast (Prokosh 1984a, Mehlum 1998), but nesting has also been recorded in other, probably new, areas in the east and north (see Tombre et al. 2012). Although the increased habitat availability is expected to facilitate further population growth, geese in the traditional breeding areas in western Svalbard may face increasing mismatches. The Arctic spring has advanced, but the timing of goose migration has not (Tombre et al. 2008). Thus, the colonisation of new breeding areas may also provide the geese with a smaller mismatch than on the traditional breeding grounds in the west.

To study these processes, the original aim of this project was to compare the breeding performance of Pink-footed geese in traditional and new breeding areas, within Svalbard. This required the capture of breeding geese in both locations, because we would then remotely follow the geese by GPS-tracking. However, when we set out to do this in 30 July – 12 August 2018, we only caught geese in two western sites (Adventdalen, Daudmannsøyra) and were unsuccessful in eastern sites. In the east, flocks of Pink-footed geese were present but largely consisted of adults which could fly already (i.e. in late stages of wing moult) and only few chicks (Table S1). This suggested that some flocks consisted of non-breeders, which had possibly reached the east after moult migration (Glahder et al. 2006) and others of breeders which had mainly failed early. Possibly, the breeding success was lower in the east than in the west in 2018. This ‘plan-A’ part of a methods section usually remains untold and was in our case overshadowed by the unique opportunity to study range expansion on a larger scale, outside Svalbard.

The large-scale range expansion even involved a newly colonised breeding area, Novaya Zemlya, in Russia (described by Madsen et al. 2023; Chapter 5 in this thesis). Some historical records from Novaya Zemlya exist, but should be viewed critically (see Synthesis). The discovery was made by GPS-tracking geese on a newly developing migration route, where Pink-footed geese had increased over the last decades. Although initially not part of this project, the comparison of spring migration routes and these distinct summer areas became the focus of this project and more GPS-tags were deployed on geese in the new route in spring 2019. In the previous year, 2018, no breeding was shown yet by tracked geese on Novaya Zemlya, but breeding was evident there from 2019 onwards.

The new spring migration route goes through Sweden and Finland, whereas the traditional spring route goes through Norway (see below and Figure 1). As the new route was more eastern than the traditional route, we had initially expected that this reflected an

eastward expansion of Pink-footed geese within Svalbard (or perhaps breeding records in north Norway, see Keller et al. 2020). As it turned out, this was partly the case, as half of the geese tagged on the new route still migrated to Svalbard, while the other half migrated to Novaya Zemlya. The birds going to Svalbard via the new route indeed seemed less likely to go to the west and south of Svalbard than the geese tagged in Norway in spring (Box A Supplement).

### **Traditional and new migration routes of Pink-footed Geese**

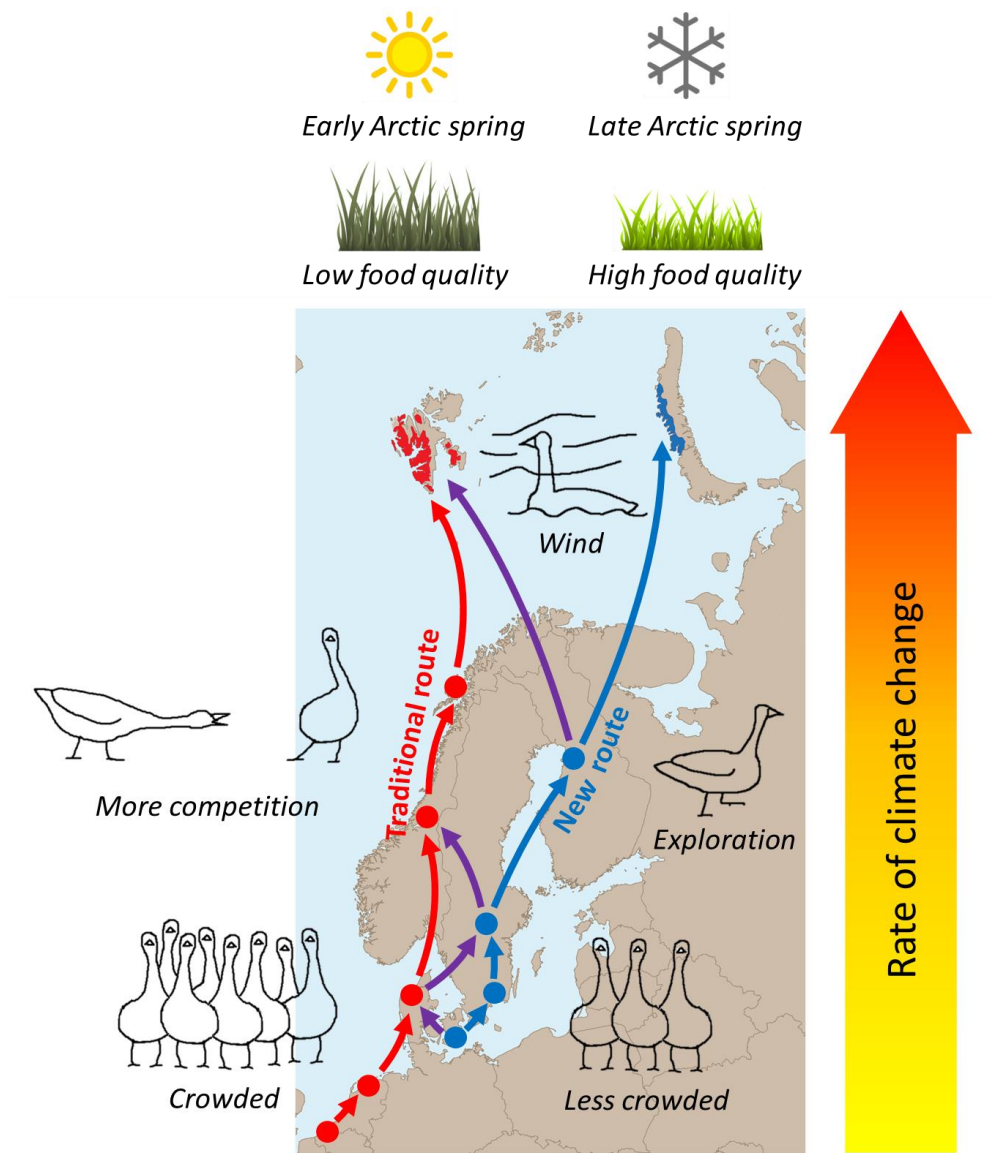
To understand the context in which Pink-footed geese established the new migration route and newly colonised breeding areas in Novaya Zemlya, we now focus on the Svalbard population of Pink-footed geese. Traditionally, this population winters in Flanders (Belgium), Friesland (Netherlands), Jutland (Denmark) and migrates in spring via Trøndelag and Vesterålen (Norway) to Svalbard (Madsen et al. 1999, Figure 1). The newly established route goes via Örebro (Sweden) and Oulu (Finland) from which half of the geese migrate to Novaya Zemlya and half to Svalbard. In Örebro and Oulu, increasing numbers of Pink-footed geese have been observed since 2000, whereas the species used to be a rare migrant here. The development of the new route and the use by geese is described in detail in Chapters 5 and 6. Now, we focus specifically on the changes on the traditional route.

Pink-footed geese on the traditional route have seen many environmental changes. First of all, the population itself has increased in size. For the late 1950s, the population was estimated at 7,000-10,000 (Mörzner-Bruyns et al. 1969) and observations in Denmark suggest that this may have been the case for decades earlier (Madsen 1982). It then rapidly increased and stayed around c. 80,000 since 2011 (Madsen et al. 2018). In western Europe, multiple goose populations increased, which was mainly due to an increased winter survival because hunting pressure was lowered (Rooth et al. 1981, Ebbsinge 1985). The levels at which the populations were kept previously by hunting were likely well below the carrying capacity of the Arctic breeding grounds. Survival may also have increased due to a higher food quality and quantity in wintering areas due to agricultural intensification (Van Eerden et al. 2005, Fox & Abraham 2017).

Along the traditional route, also populations of other goose species have increased. Most important in the wintering grounds are the tremendous increases in numbers of Barnacle geese (*Branta leucopsis*) and Greater white-fronted geese (*Anser albifrons*). Barnacle geese increased in Western Europe from 20,000 in 1960 to 1.2 million in 2015 (Ganter et al. 1999, CAFF 2018) and Friesland is their main wintering area. Greater white-fronted geese (*Anser albifrons*) increased in Western Europe from 18,000 in 1958 to 1.0 million in 2012 (CAFF 2018) and co-occur in Friesland and Flanders. Also in Vesterålen, Barnacle geese (belonging to the population wintering in Scotland) have increased. However, this resulted from a northwards shift in stopover use from Helgeland (Tombre et al. 2013, Tombre et al. 2019). Pink-footed geese likely experience intensified competition due to these increased population sizes. Species that arrive in a site earlier, or those that graze vegetation shorter and can handle shorter vegetation, have a competitive advantage (Buitendijk et al. 2022). Pink-footed geese now mainly skip Vesterålen, as a result of the rise of the Barnacle geese in combination with organized scaring by farmers in the past (Tombre et al. 2013, Tombre et al. 2019). The use of Trøndelag as stopover site has developed since the late 1980s (Madsen 2001). In Denmark, wintering Taiga bean geese (*Anser f. fabalis*) have decreased, but have widened their distribution in Jutland (over 2003-2021; Nyegaard et al. 2022). Pink-footed geese have expanded their wintering range in Jutland (Clausen et al. 2018a) into areas where they now overlap with Taiga bean geese (Madsen et al. 2023).

Pink-footed geese have learned to utilise agricultural crop spills, such as maize, sugar beets and potatoes (Cottaar 2009, Nilsson & Kampe-Persson 2013, Clausen et al. 2018b)





**Figure 1. Environmental, climatic, and intrinsic factors that are hypothesised to play a role in the colonisation of the new migration route and breeding area.** The traditional route goes via Flanders (Belgium), Friesland (Netherlands), Jutland (Denmark), Trøndelag and Vesterålen (Norway) to Svalbard (in red). The newly established route goes via Lolland-Falster (Denmark), Kristianstad and Örebro (Sweden), Oulu (Finland) to Novaya Zemlya (in blue). Some geese use only part of the new route and still breed on Svalbard (in purple).

although this was observed in the UK already for longer (Cramp & Simmons 1977). Possibly also the northward spread of (winter) crops (e.g. Kenny et al. 1993, Olesen et al. 2011) may provide new feeding opportunities (see Therkildsen & Madsen 2000, Clausen et al. 2022). In winter, crop availability was even found to explain the number of Pink-footed geese using a wintering site:

maize kept geese in Jutland, while grass kept geese in Friesland and Flanders (Clausen et al. 2018a). Transformation of agricultural land into restored wetlands in western Denmark resulted in the loss of three major staging sites, but geese redistributed to other parts of Jutland in Denmark (Clausen & Madsen 2016).

Strikingly, Clausen et al. (2018a) did not find that the winter harshness determined winter site choice during the study period of 1990-2015. In the past, winter had a strong effect and harsh winters 'pushed' geese southwards. Maybe this effect has disappeared since winters have become milder in general. The most striking incident occurred in the severe winter of 1955/1956 when for the first time Pink-footed geese came down to Friesland in large numbers (Rooth et al. 1981). Two winters later, Pink-footed geese were also discovered in Flanders (Kuijken 1958). Previously important wintering sites were located in Niedersachsen, especially Emsland and Jadebusen. Here, dramatic changes such a drainage of flooded land (Atkinson-Willes 1961, Prokosch 1984b, Kruckenberg 2021) on top of the severe winter, led the geese to abandon this old wintering site and to keep using the southern alternatives. Further, winter harshness was found to explain the amount of exchange between the Svalbard and Iceland/Greenland population in winter, during 1988-2010, suggesting that winter harshness still affects the movements of geese (Madsen et al. 2014).

Recently, the intensity of hunting has increased again (Madsen 2018). Annually, around 10-15% of the population is shot, in Norway and Denmark during autumn and winter until 31 January. The hunting pressure is regulated in an adaptive harvest management scheme, with a target population size of around 60.000 birds (Madsen et al. 2017). The aim underlying this target is to keep a self-sustaining population that is not jeopardised by recreational shooting, while at the same time limiting conflicts with agriculture and impacts on Arctic tundra vegetation (Madsen & Williams 2012).

Still, hunting pressure apparently did not affect winter site choice and most geese use Denmark as wintering area. This proportion of geese has in fact increased, while the proportion using Friesland has steeply decreased, and the proportion using Flanders slightly decreased (Clausen et al. 2018a). This contrasts with the situation in Vesterålen, where scaring activities contributed to the decreasing use of this stopover (Madsen 1995). Possibly, the effect of disturbance is larger on the more northern spring stopovers, as geese must maintain enough body stores for the upcoming breeding season.

All these factors illustrate the environmental change that Pink-footed geese have experienced in their traditional route: some threats, some opportunities. In such a quickly changing world, an increased general exploration or plasticity is likely favoured (see also Clausen et al. 2018a). Geese are notably social, with extended parental care (e.g. Gupte et al. 2019) and congregation in flocks, sometimes also with other goose species (Cohen & Satterfield 2020). This may facilitate fast exploitation of new opportunities by many individuals.

In summary, whereas climate change may cause important changes in the breeding area, other environmental changes have occurred on the migration routes. These may explain why geese may search alternatives to their traditional route, relating to competition, food availability, survival and disturbance.

### **The choice for a study species: real versus conceptual problems**

Does it make sense to study species that do well, rather than species that are directly threatened by climate and environmental change? Are we not studying the wrong species?

Although it is useful to study pressing issues and species under threat to inform specific conservation efforts, also studying common or increasing species is useful. One might even argue that one should study and understand a species when it is common. Studying species only

when they are in trouble, in decline, or in their last small refugia, may not reveal the causes of their decline or circumstances under which they would thrive better. To understand a biological system, a reference of better times is needed. Also, understanding why a species increases, has merit: is there a trait that enables it to cope well with challenges, while other species without this trait struggle?

Additionally, common or easy-to-study species may serve as conceptual study object ('model system') that can reveal processes that also play for other species. For example, we have learned a lot about the general effects of climate change on reproduction of birds by studying Great tits (*Parus major*, e.g. Visser et al. 1998) and Pied Flycatchers (*Ficedula hypoleuca*, e.g. Both & Visser 2001), both of which are (relatively) common in the Netherlands and have even increased (Sovon 2018).

Are geese a suitable study object then, to reveal problems encountered by migratory birds that breed in the Arctic? At first, their increasing population trends may lead one to think that they do not have problems such as a trophic mismatch (see e.g. Rozenfeld et al. 2021). However, it is impossible to read a mismatch from a population trend (see also the Great tit and Pied Flycatcher), because a population trend is the combined result of multiple effects throughout the annual cycle. For example, an effect of a mismatch on reproduction can be offset by e.g. density-dependent juvenile survival during winter (e.g. Reed et al. 2013). Rather, increasing goose populations may indicate that geese cope exceptionally well with environmental changes despite living in the same environment as decreasing species. In fact, in Pink-footed geese, there are indications that the density-dependence in reproductive success has now disappeared, possibly due to an overall increase in arctic primary production and earlier snowmelt providing more nesting habitat (Jensen et al. 2014). However, other types of analyses on Barnacle geese still found density-dependence throughout the annual cycle (Layton-Matthews et al. 2020).

Second, goose populations generally show a higher production of juveniles when the Arctic spring starts early (Nolet et al. 2020), which again can make one believe that geese may not have a trophic mismatch caused by climate change. However, as Nolet et al. (2020) lay out, again it is difficult to infer a mismatch directly from a pattern in productivity on population level. Population productivity is the result of a sequence of effects, and the timing of spring can have opposite effects in different stages of breeding. Early springs may reduce the growth and survival of goslings, (likely) through a mismatch (e.g. Dickey et al. 2008, Brook et al. 2015, Doiron et al. 2015, Lameris et al. 2018a, Ross et al. 2018), but may also increase the breeding propensity in the population through eased breeding conditions (e.g. Reed et al. 2004, Madsen et al. 2007, Boom et al. 2022). On the population level, this gain in breeding propensity apparently far offsets the loss in gosling survival, in many goose populations (Alisauskas 2002, Trinder et al. 2009, Morrissette et al. 2010, Nolet et al. 2013, Jensen et al. 2014, Cleasby et al. 2017; but see Clausen & Clausen 2013). It was probably also this effect, that Bauer & Glutz von Blotzheim (1968, p. 98) were referring to when speaking of 'Klimaverbesserungen im Brutgebiet', as one of the possible explanations for increasing numbers of Pink-footed geese wintering in the United Kingdom; a wording that no biologist would use today.

These contrasting effects of spring onset during different stages of reproduction show that a mismatch does not necessarily mean mistiming (see also Visser & Gienapp 2019). The difference is, that a mismatch occurs when the time of the food demand of offspring does not match the time of food availability, whereas mistiming occurs when a bird does not breed at the time that would result in highest fitness. If fitness components other than the growth of offspring are important and are influenced differently by the timing of breeding, mismatched reproduction can in fact be optimal.

Here, two main trade-offs play a role: the trade-off between quality and quantity of offspring, and the trade-off between current and future reproduction. Laying another egg may result in less food per chick, if the feeding rate is limited by the environment (by an increased mismatch due to later hatch date) or the parents (by a limited brood provisioning rate), but can still outweigh this cost if it results in more (successful) recruits. Also, reproducing in mismatched conditions can still be favoured if reproducing earlier relative to the spring onset is so costly, that it would compromise survival to a future breeding attempt (e.g. in long-lived species). The same holds when waiting for a year in which spring starts late does not pay off because the chances for a future breeding attempt are slim anyway (e.g. in short-lived species). Apart from differences between species, the degree to which these other fitness components play a role may also differ between individuals of the same population. Some individuals may be better able to pay the costs of early reproduction than others (Chapter 6, Drent & Daan 1980), causing a mismatch effect to become (more) limiting for their individual fitness.

Concluding, studying Pink-footed geese can still inform us about potential negative effects of environmental change and of climate change on breeding birds in the Arctic, even though the population of Pink-footed geese is increasing and produces more juveniles when spring starts early.

### **Outline of this thesis**

The aim of this thesis is to study whether Pink-footed geese can cope with environmental and climate change, by colonising the new migration route and the new Arctic breeding grounds. We define 'coping' here as maintaining fitness and/or reducing the experienced change. The thesis is subdivided into three parts. We first focus on methodology, then focus on the Arctic range expansion, climate change and fitness, and finally we focus on possible additional causes and consequences of the colonisation process, such as competition (relating to environmental change), personality, wind effects during migration, and genetic differentiation.

#### *Part I: Studying Arctic-breeding geese with GPS/ACC-transmitters*

The migration routes of Pink-footed geese stretch out over more than 3500 km. On various stopover sites, we are in the fortunate position that people have monitored geese there for decades. These population counts and sightings of individually marked birds allow us to study long-term changes in the timing and routes of migration. However, traditional observational methods are logistically challenging in remote breeding areas, especially when the aim is to compare geese between several areas. In some areas, access is even restricted. Therefore, we deploy modern technologies on the geese, small GPS-tracking devices including various sensors. Such 'bio-logging' provides detailed and continuous observations (position, speed, height, activity, temperature), also in the places and times where we are not able to observe.

Contrasting with this great detail of data about certain geese is the limited knowledge about the context of the data. What does the goose eat in a certain location? Does it have a nest or chicks? Are there other geese or predators around? This makes it important to validate interpretations from the tracking data. On the stopovers, tracking allowed us to observe these birds frequently, because we knew beforehand where to go in order to find them. In the breeding area, however, this was only possible in a small area on Svalbard. This allowed us to understand whether a goose has a nest based on tracking data (**Chapter 3**). Pre-existing methods could identify nesting attempts that took at least 7-11 days, but by combining tracking and sensor data, we could narrow this down to 3 days. This allows us to better distinguish non-breeding from early failed breeding.

Whenever studying birds that are wearing a device, it is also important to verify that these birds still show natural behaviour. We evaluated two potential effects of devices: short-term effects on behavioural budgets, and longer-term effects on migratory and breeding performance. For the first aspect, we compared the time allocation to various activities between tagged geese and geese that were not caught or marked, for the first two weeks after capture on Svalbard (**Chapter 2**). For the second aspect, we compared the timing of migration and breeding, and the success of breeding, between geese that were tagged in spring with geese tagged longer ago (**Box A**).

*Part II: Dispersal as a way to cope with Arctic warming*

Once we know the impact of tracking devices on geese, and how to recognize a nesting attempt and its success from tracking data, we focus on our main questions. These relate to climate change and the migratory and breeding performances of geese on the traditional and newly established routes and breeding areas.

Before we zoom in on our own system, we first review existing literature about the effects of spring onset on breeding geese (**Chapter 4**). On congresses, we had noticed that there was disagreement among scientists from different continents and species, on whether early springs were 'good or bad' for breeding Arctic geese. This led us to think about various processes involved. Finally, we concluded that a relatively simple dichotomy between the early stages (pre-laying, laying, and nesting) and late stages (hatchling, fledgling, and juvenile phase) of reproduction could explain these inconsistencies.

Next, we describe the range expansion and colonisation of a new flyway by Pink-footed geese (**Chapter 5**). Thanks to long-term monitoring throughout northwestern Europe, a mark-resighting program, and GPS-tracking, we could document this development based on many sources of information. This breeding area was previously undescribed (historical records are discussed in the Synthesis) and it was exciting to witness this discovery first-hand. I will never forget the autumn morning in Skogn when we saw the tracks of the pair of A3 and A5 for the first time when they had come back from Novaya Zemlya.

Finally, we compare the traditional and newly established routes in various aspects (**Chapter 6**). First, we describe which stopovers are used by which birds. Then, we evaluate how problematic climate change has possibly been along both routes, by assessing the rate of change and predictability of spring along both routes. We study whether the geese have adjusted their migration and timing and location of breeding accordingly. Finally, we study how the breeding success of the geese relates to their timing and the timing of spring. We apply the framework of Chapter 4 to the within-species level and argue that a mismatch (in the late reproduction stage) can affect fitness of part of the population, while the other part of the population is limited by harsh conditions during breeding (in the early reproduction stage).

*Part III: Further potential causes and consequences of long-distance range expansion*

In this part, we broaden our view from climate-related questions to other pressures that may play in the annual cycle of Pink-footed geese and relate to the observed range expansion.

First, we examine the influence of winds and other weather variables on migrating geese above the Barents sea (**Chapter 7**). If winds influence the geese to a large extent, this may give us part of the proximate explanation how geese ended up on Novaya Zemlya. Strong winds may blow them off course towards new areas (see Synthesis for further discussion). We also study whether stopping on the water is a way of geese to handle adverse conditions, and we compare the costs of migration between spring and autumn.

Next, we evaluate potential alternative proximate causes for geese to move outside the traditional migration route: competition pressure and personality (**Chapter 8**). We assess competition pressure by looking at goose densities and the frequency of aggressive interactions between geese, on both routes. Personality was measured during handling and could play a role if the more 'explorative' types are more likely to establish a new migration route or breeding area. By comparing geese of different routes, on stopovers where they co-occur, we can evaluate on an individual level whether social status (position in a dominance hierarchy) may push subordinate geese towards alternative routes.

Finally, we look at an ultimate result of range expansion into a separate breeding area: genetic differentiation (**Chapter 9**). Are there different subpopulations arising, or can geese of Svalbard and Novaya Zemlya genetically still be seen as part of the same population? Geese from both areas still use overlapping autumn and wintering areas, which could lead to exchange because geese may follow conspecifics of the other breeding area. To put any potential genetic differentiation into context of range expansion that occurred longer ago, we compare geese from both breeding areas with geese from the Iceland/Greenland population.

### Synthesis

In **Chapter 10**, I combine all findings to answer the question whether Pink-footed geese can cope with environmental and climate change by colonising a new migration route and breeding area. I reflect on the general flexibility of geese and ask the question why it would be more beneficial for geese to adjust in space rather than in timing. Further, I explore whether there could be a link between the flexibility in migration routes on the one hand, and the diet and sociality on the other hand. Finally, I reflect on what we have learnt about the ability of the natural world to cope with changes in the climate and the environment.

## Supplement

**Table S1. Observations of geese in remote areas of Svalbard, in 2015, 2018 and 2022.** Trips were made with the MV Ulla Rinman in 2018 and the MV Ortelius in 2015 and 2022 (SEES, [www.sees.nl](http://www.sees.nl)). Species are abbreviated: PFG (Pink-footed goose), BG (Barnacle goose), LB (Light-bellied brent goose, *Branta bernicla hrota*). Observers are: AS (Annette Scheepstra), BN (Bart Nolet), BV (Berend Voslamber), JdL (Joep de Leeuw), JF (John Frikke), JM (Jesper Madsen), KB (Kees Bastmeijer), KdK (Ko de Korte), KS (Kees Schreven), ME (Mennobart van Eerden), ML (Maarten Loonen), OG (Ove Martin Gundersen), PdV (Peter de Vries), RB (Rob Buitter), RH (Renno Hokwerda), RN (Ramsey Nasr), RV (Ronald Visser), RW (René van der Wal), SW (Sip van Wieren). Ages: ad (adult), juv (juvenile, gosling). Captures in Adventdalen and Daudmannsøyra are described in most detail in Chapter 8. Nests found on Tusenøyane are described in Madsen et al. (2019). Location names are based on the Norsk Polarinstitutt map (<https://toposvalbard.npolar.no/>).

Date	Location	Geese	Observer	Viewpoint
20-08-2015	Stellingfjellet	75 BG, 10 PFG	BN, BV	land
21-08-2015	Kapp Lee	24 PFG	BN	land
	Rosenbergdalen	115 PFG	BN	land
22-08-2015	Agardhbukta	22 PFG	BN	land
23-08-2015	Barentsøya, Frankenthalvøya	2 PFG, 11 BG	BN	zodiac
	Barentsøya, Frankenthalvøya	135 PFG, 30 BG	RW, ME	land
24-08-2015	Barentsøya, Sundneset	3 pairs BG (ad) with 1,2,2 juv	BN	land
25-08-2015	Habenichtbuka/Russebukta	22 PFG, 97 BG (ad) with 8 juv	BN	land
27-08-2015	Hornsund	7 PFG (ad) with 5 juv, 61 BG	BN, RW, SW	land
03-08-2018	Sorgfjorden	20 PFG (ad) on land	KS, JM, BN	boat
04-08-2018	Barentsøya, NW-Sundneset	60 PFG (ad) fly up and land, 70 BG (ad) on land	KS, JM, OG	land
	Barentsøya, Ureinskagen	Tens of BG (age unknown)	KS, JM	boat
05-08-2018	Kapp Lee	3 PFG (ad)	JM	boat
	Russebukta	Few groups of tens of BG and PFG	KS, JM, OG	land
	Russebukta, lakes Ekrollhamna	5 PFG (ad) with 1 large juv (>half-grown)	KS, JM, OG	land
	Russebukta, lakes Ekrollhamna	4 pairs BG (ad) with 2,2,2,4 juv	KS, JM, OG	land
	Russebukta, lakes Ekrollhamna	Many shed flight feathers PFG and BG	KS, JM, OG	land
06-08-2018	Russebukta, Hassensteinbukta	1 nest of PFG (≥3 egg), predated by bird	KS, JM, OG	land
	Habenichtbukta	20 PFG (ad) with 1 juv + 30 BG (ad), fly away but some PFG walk	KS, JM, JF, PdV, BN	catch attempt
07-08-2018	Zieglerøya	Goose droppings and shed flight feathers	JM, JF, OG	land
	Andréetangen	5 geese	JM	boat
09-08-2018	Lurøya	4 BG (ad), shed flight feathers BG	KS	land
	Dunderbukta	100 PFG (ad + old juv, ad and some juv fly), some BG (ad + juv)	KS, JM, BN	boat; catch attempt
	Reherchefjorden	20 families PFG (ad + old juv), 5 families BG (ad + juv), 20 BG (ad), 8 LB (ad)	KS, JM, BN	boat
10-08-2018	Reherchefjorden	50 families PFG (ad + old juv), 20 BG (ad) fly	KS, JM	boat
	Daudmannsøyra	PFG (ad + juv) flying	KS, PdV, JF	land
11-08-2018	Algehornet	PFG (age unknown) at sea and flying	KS	land
	Daudmannsøyra	10, 20, 100, 500 PFG + BG (age unknown) walk and fly	KS	land
15-07-2022	Rosenbergdalen, coast	15 PFG on land (age unknown)	JdL	boat
	Barentsøya, coast Talaveraflya	46 PFG (ad, 0 juv)	KS	boat
	Barentsøya, Riegdammen	Group of tens of PFG and BG (age unknown)	RH	land
16-07-2022	Rosenbergdalen, coast	4 + 6 + 2 PFG (ad) flying to N, the 2 land at river	JdL, AS, KS	upon landing
	Rosenbergdalen, valley	2 PFG (ad) fly high to S-SW	KS	land
17-07-2022	Barentsøya, N of Riegdammen	35 BG (ad)	KS	boat
18-07-2022	Barentsøya, Riegdammen	28 BG (ad)	KS	boat
	Barentsøya, Zorellvatnet	58 PFG (ad), 27 BG (ad)	JdL	land
	Barentsøya, Andsjøen	5 pair BG (ad) with 13 juv, 1 pair BG (ad, 0 juv)	RH	land
	Barentsøya, Andsjøen	Many droppings of PFG and BG, ad and juv	KS	land
19-07-2022	Russebukta, lakes at Ekrollhamna	40 PFG (ad), 2 BG (ad)	KS	land
	Russebukta, sea at Ekrollhamna	276 PFG (ad)	KS	land
	Russebukta, cliff at Ekrollhamna	1 BG (ad) on nest in cliff, 1 BG (ad) on sea	KS	land
	Russebukta, lake at Martinodden	8 pair BG (ad) with 0,0,1,2,3,4,4,5 juv	KS	land
	Russebukta, westcoast Martinodden	1 pair PFG (ad) with 6 juv (< half-grown)	KS	land
	Russebukta, lakes at Gothavika	300-350 PFG (age unknown)	ML, RN, KdK, AS, RV	land
20-07-2022	Gnålodden, coast	120 PFG (age unknown), 50 BG (ad and juv)	KB	upon landing
	Gnålodden, coast	Group of few tens of BG (age unknown)	RB	land
21-07-2022	Van Muydenbukta, coastal plain	Many shed flight feathers BG	KS	land
	Van Muydenbukta, lake Eungane	185 PFG (ad) and 17 BG (ad)	KS	land