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### Geese colonising New Land

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

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#### Publication date

2023

[Link to publication](#)

#### Citation for published version (APA):

Schreven, K. H. T. (2023). *Geese colonising New Land: Causes and mechanisms of range expansion in an Arctic-breeding migrant*. [Thesis, fully internal, Universiteit van Amsterdam].

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*It's not about the destination, it's not about the journey, it's about the company on the way.*

Unknown



## Chapter 10

### Synthesis

Kees H.T. Schreven

### **Can Pink-footed geese cope with environmental and climate change?**

The vast and rapid range expansion of Pink-footed geese into a new migration route and breeding area allowed us to study whether these developments are a way of geese to cope with changes in their environment. Climate change, especially in the Arctic, and land use changes and intensified competition pressure were of specific interest. We defined ‘coping’ here as maintaining fitness and/or reducing the experienced change.

The geese on the new migration route and breeding area indeed seem to maintain fitness levels similar to those of geese in Svalbard. On population level, the breeding propensity, nesting success and the percentage of chicks in autumn flocks are similar. This is striking, because a factor limiting population productivity in Svalbard is the onset of spring, with earlier springs resulting in a higher production of juveniles (Jensen et al. 2014). As spring starts later in Novaya Zemlya than in Svalbard, this suggests that geese reproduce in fact better in Novaya Zemlya, given the circumstances in the breeding area. This was also shown directly for individual nesting success, which was higher in Novaya Zemlya than Svalbard at a given onset of spring.

Another aspect of maintaining fitness is population vulnerability. The total Pink-footed goose population probably has become more resilient now that it occupies a wider geographical range. However, founder populations generally start off small and can be subject to inbreeding, drift, or severe consequences of erratic environmental conditions (Whitlock 2000). The Novaya Zemlya subpopulation has grown steadily to 3-4000 birds and stayed connected to the Svalbard population by overlap in wintering areas and continued exchange. Genetically, they can still be seen as the same unit.

The new migration route and breeding area have also enabled geese to reduce their experienced change. This occurred in four aspects of change. First, spring onset in the breeding area. In Svalbard, spring has advanced rapidly, while in Novaya Zemlya the spring occurs later. Colonising Novaya Zemlya allowed Pink-footed geese to go 40 years ‘back in time’ in terms of spring in Svalbard, which may allow them to produce chicks that grow up with a smaller mismatch. Second, the interval between spring on the last stopover and the breeding area. On the Norway-Svalbard route, this interval has shortened because spring has not advanced on the Norwegian stopovers. On the Finland-Novaya Zemlya route, a positive and larger interval was maintained, possibly enabling migration to be better in line with the progression of spring (see e.g. Van der Graaf et al. 2006). Thirdly, the predictability of arctic spring from the last stopover. Spring onset in Svalbard and Norway used to be uncorrelated, but turned to negatively correlated in the last two decades. This may complicate arriving at the optimal time for breeding in Svalbard, for a bird which likely times its migration partly based on body stores and vegetation phenology (Duriez et al. 2009). Fourth, competition with other geese during spring migration. Geese had fewer aggressive interactions on the stopover in Finland than in Norway, and goose densities were also lower. This may also resemble a situation in the past, as goose populations have increased.

In comparison with (breeding) range expansions that occurred in other species, there are some differences. Barnacle geese (*Branta leucopsis*) have started to breed in their wintering area, but these geese were found to enlarge their mismatch rather than reduce it (van der Jeugd et al. 2009). On the other hand, they had a higher breeding propensity and nesting success (Boom et al. 2022). So, range expansion of geese to the north versus south may be related to benefits in the late versus early stages of breeding (see also Nolet et al. 2020). Another example of birds starting to breed in their wintering area comes from Barn swallows (*Hirundo rustica*) in Argentina (Winkler et al. 2017). These were found to have similar clutch sizes as in their traditional range, but lower breeding success due to increased predation and parasite load, indicating that other benefits must have caused their increase in Argentina (Gandoy et al. 2019).

An expansion in wintering range was recorded in Blackcaps (*Sylvia articapilla*) which started wintering in Britain rather than southern Europe (Berthold et al. 1992). Also, Richard's pipits (*Anthus richardi*) have recently started to winter in Europe rather than Asia (Dufour et al. 2021). Both of these developments were explained by improved wintering conditions, which may have been discovered by vagrants. This mechanism could be similar to that in Pink-footed geese, but in a different annual cycle stage (see more below).

In the case of Pink-footed geese, can we say whether the environmental and climate change were also the causes of the range expansion? Pink-footed geese have been rare migrants in Finland already since 1970s. Why did they suddenly increase here, and why not earlier? To understand this, we dissect the world of Pink-footed geese into factors facilitating and driving range expansion, then look at their interplay and possible cascading effects.

### Factors facilitating range expansion

One important factor facilitating range expansion in Pink-footed geese is probably the climate. In Novaya Zemlya, spring used to be cold and probably started too late to allow for (successful) reproduction in geese. Freezing conditions, which maintain snow cover, used to persist there throughout May, but nowadays May has above-zero temperatures, which enables breeding (Johnson et al. 2014, Madsen et al. 2023).

Geographically, the presence of a suitable stopover location between Jutland and Trøndelag, namely at Örebro, has probably enabled lowering the pressure on these other two stopovers. In addition, snow melted earlier in Örebro than in Trøndelag, which might fit the schedule of the geese well, since geese have started to leave Jutland earlier and arrive to Trøndelag earlier. The onset of spring can determine stopover site choice and staging times (Bauer et al. 2008). The use of Örebro may then have facilitated a more eastern orientation during further migration.

Regarding land cover, geese have started to exploit crop spills (Cramp & Simmons 1977, Cottaar 2009, Nilsson & Kampe-Persson 2013, Clausen et al. 2018b). The locations where crops can grow are shifting northward (Kenny et al. 1993, Olesen et al. 2011) from which geese may benefit. This may play more on the new route than the traditional route. In Trøndelag in spring, Pink-footed geese use grasslands, stubble fields and newly sown grain fields, whereas potatoes are of negligible importance (Chudzinska et al. 2016). Nilsson & Kampe-Persson (2013) reports for Sweden that Pink-footed geese are mixed with Taiga bean geese (*A. f. fabalis*), which occur on cereal and grass fields but have increasingly used potato and sugar beet fields in winter and spring over the last 20 years. In Örebro, Pink-footed geese mainly eat growing grass in newly sown pastures or meadows, growing winter cereal, and grain from stubble fields or places where Whooper swans (*Cygnus cygnus*) are fed (pers. obs. K. Halttunen). In Oulu, Pink-footed geese mainly feed on grass in meadows and fallow ground, clover, grass and sprouting grain from stubble fields, and potato spill (pers. obs. K. Schreven).

Apart from crop types, also the agricultural practices may act as facilitator in Oulu. Autumn ploughing is common in Trøndelag (pers. obs. K. Schreven) and Örebro (pers. obs. K. Halttunen), but hardly occurs in Oulu (pers. obs. J. Pessa). Further, in Oulu, grass is often sown at the same time with cereal seeds in spring, to set up grassland over winter, as required by regulations. These practices may cause more plants to grow earlier in spring. This is in line with the result that geese departed from Oulu and Trøndelag at the same time, but in Oulu longer after the local NDVI increase. Thus, in Oulu, geese may have more time to benefit from local vegetation growth and accumulate more resources. Larger body stores were in turn probably required to bridge the longer pre-laying intervals that were registered in Novaya Zemlya. If the

ability to accumulate more resources is an individual trait (e.g. by differences in foraging efficiency), a high individual quality of colonizing geese would also be a facilitator.

Lastly, an effective migration route towards the new breeding area in Novaya Zemlya may have been enabled by the presence of Taiga bean geese, which already used this route during moult migration (Piironen et al. 2021). Taiga bean geese may lead vagrant Pink-footed geese in Novaya Zemlya back south in autumn, but may also attract Pink-footed geese towards the new route in spring. The contact between both species in their wintering areas has likely increased. Taiga bean geese have expanded their range in Jutland (Nyegaard et al. 2022). More importantly, Pink-footed geese have also expanded their range in Jutland and now share an area with Taiga bean geese (Madsen et al. 2023). This may lead some Pink-footed geese to follow Taiga bean geese into Sweden. In Sweden, the wintering areas of Taiga bean geese have moved south, to Skåne, but their autumn distribution shifted north, to the lake region around Örebro (Nilsson 2013). These are the areas that Pink-footed geese use (Madsen et al. 2023) and in Sweden, Pink-footed geese are often in flocks of Taiga bean geese (Nilsson & Kampe-Persson 2013).

### **Factors driving range expansion**

Apart from factors facilitating geese to use alternatives, some factors could drive geese away from the traditional area to explore new areas. One driver could be climate change (thus being both a driver and a facilitator). In the traditional area, we found indications that growing goslings might face a larger trophic mismatch than in the new area (based on NDVI satellite imagery, but not on chick survival data). Being mismatched as a growing chick may stimulate dispersal later in life (Hušek et al. 2014). As juveniles migrate along with their parents for part of the first year, dispersal may occur by splitting off during winter (Gupte et al. 2019) or as late as the next breeding season (own tracking data).

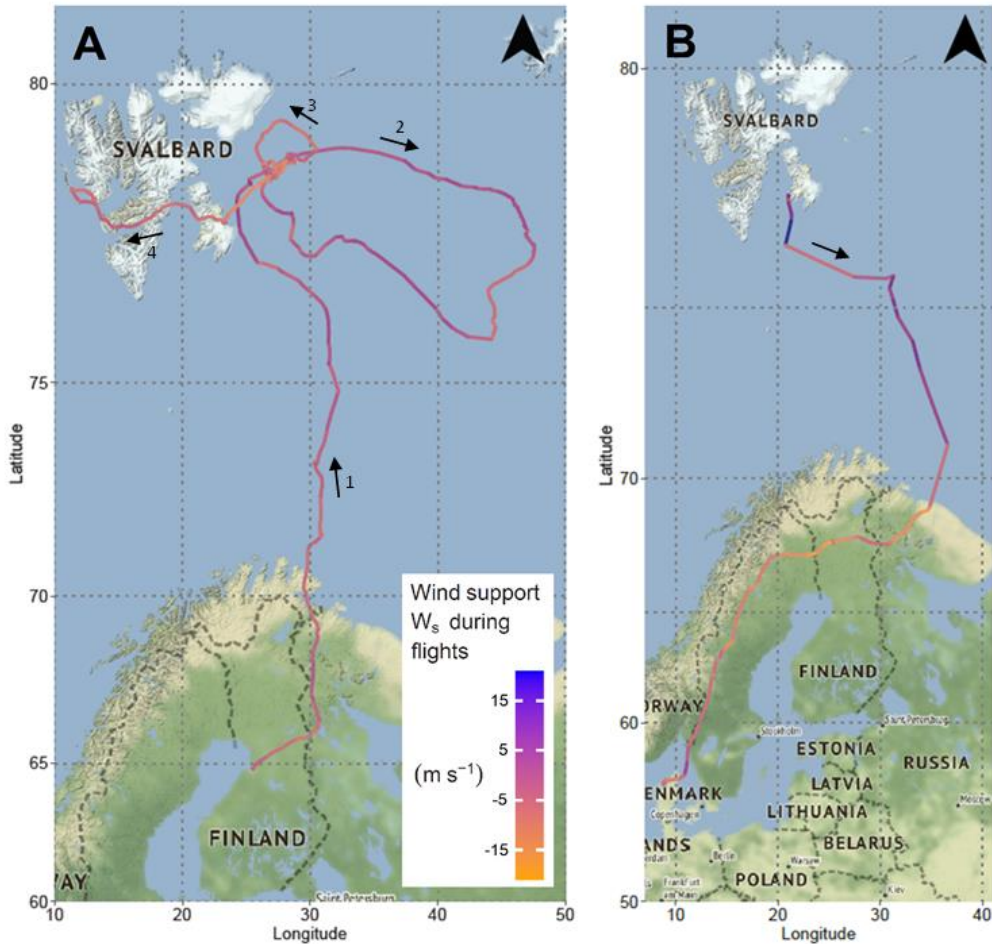
Producing mismatched chicks could also stimulate dispersal in the parents, as they find themselves unable to lead their chicks to high quality food in the traditional breeding area. As laid out in Chapter 6, this would only play for the parents that are capable of starting earlier relative to spring onset, i.e. those geese capable of accumulating and spending more resources. Thus, a high individual quality (Drent et al. 2003) could also be both a driver and facilitator.

On the breeding grounds, other potential driving factors could be increased competition and increased disturbance, but we have not studied these. Competition has likely not intensified in Svalbard, as density-dependence in breeding success has recently disappeared (Jensen et al. 2014), although density-dependence was still detected in Barnacle geese (Layton-Matthews et al. 2020). Disturbance might have increased due to a sharp increase of tourism in Svalbard, including landings in remote areas (Hovelsrud et al. 2023). This can impact geese, which have a flight initiation distance of c. 2 km in remote coastal areas (Madsen et al. 2009).

Driving factors may also occur during migration over sea. Strong winds and adverse weather may cause geese to wander off track (Geisler et al. 2022). This may cause geese to end up in new areas, although we did not find direct evidence for this in our own tracking data. However, we did see signs of disorientation in one goose, which turned frequently above the Barents Sea and crossed its own track once (spring 2019, an adult paired female from Oulu). Further, one 2<sup>nd</sup> calendar year male from Oulu arrived in eastern Svalbard in spring 2018 and made a large loop over the Barents Sea towards Novaya Zemlya and back. Also, one adult female migrated far east in autumn, while almost all geese go straight south in autumn (Geisler et al. 2022). These latter two cases did not seem to be explained by strong winds (Figure 1). Although Pink-footed geese selected the best winds for departure, strong winds have increased in frequency in the Barents Sea region (Crawford et al. 2020).



**Figure 1. Migration routes of two Pink-footed geese making large detours over the Barents Sea in relation to wind support.** (A) Spring track during 15 May – 19 June 2018 of a 2<sup>nd</sup> calendar year male (code A9) tagged in Oulu, Finland, 28 April 2018. It made a loop from Svenskøya/Kong Karls Land in the direction of Novaya Zemlya and back during 27 – 29 May, including 24 short stops on the water. (B) Autumn track during 6 – 13 Oct 2021 of a paired adult female (code 2S), a failed breeder in that year, tagged in Isdammen, Svalbard, 30 July 2018. For both geese, wind support did not seem to cause the detour. In fact, goose 2S had high wind support towards the south, before stopping on the water and taking an eastern direction, including multiple stops on the water. Direction and sequence of movements is indicated with arrows and numbers.



A driver on the spring stopovers could be competition. The population increase of Pink-footed geese may have intensified intraspecific competition. Goose densities (species combined) were two times higher in Trøndelag than Oulu, and aggressive interactions were four times more frequent. With increasing competition, the geese most affected by competition are expected to be driven out first to search for alternatives. These would be the subordinate, less competitive geese, and we indeed found Svalbard-geese that used the new spring route to be less dominant. However, if a general depletion of a stopover is the driving factor, this may play for all individuals. Increased intraspecific competition may have followed from interspecific

competition. Pink-footed geese mostly skip their northern stopover site in Vesterålen, due to a combination of competition with increasing Barnacle geese and scaring activities (Tombre et al. 2013). Together with the advancing arrival in Trøndelag, this has probably made Pink-footed geese more reliant on Trøndelag.

In the wintering area, a potential driver may be hunting pressure. Although hunting pressure in Denmark did not determine the choice between wintering sites in Denmark or the Netherlands and Belgium (Clausen et al. 2018a), there might be local dynamics within Denmark. Traditions of hunting are less common in inland than coastal Denmark (pers. comm. J. Madsen). Geese may thus benefit from these areas by exploring more east from Jutland. Annual hunting yield in Denmark started to increase from 2006 onwards (Madsen et al. 2018), the year when the use of the new route started growing (Madsen et al. 2023).

Although Pink-footed geese are traditionally site-faithful on population level, by using only a few wintering sites, the individual rate of switching between these sites has increased (Clausen et al. 2018a). This demonstrates an increased flexibility and possibly opportunism to track changes in land use. Pink-footed geese also increasingly use areas outside these traditional wintering sites, such as in Jutland (Clausen et al. 2018a), Friesland (Cottaar 2009) and Flanders (Kuijken & Verscheure 2019). In all cases, an attraction to maize stubble fields was evident. In the Netherlands, geese nowadays increasingly turn up across the country, whereas use of the traditional site Friesland is diminishing (pers. obs. F. Cottaar; own data). This may indicate increased incentives for or pay-offs of visiting the non-traditional area.

### **Interplay of facilitating and driving factors**

For range expansion to occur, facilitating and driving factors are both required. A new area may be suitable, but in absence of drivers no expansion will occur. On the other hand, if there is a driver, but no suitable areas are available elsewhere, no expansion will occur either.

Colonisation may have started from the breeding area, or from the winter and spring stopovers, or from both. In both cases, certain subsets of the population are expected to disperse. Processes in the breeding area would favour dispersal of high-quality geese, while processes in the winter and spring stopovers would favour dispersal of subordinate geese. These subsets likely are not the same, since dominance allows for accumulation of more body stores (Prop & Deerenberg 1991). Our data suggest that the colonisation process has been complex and that both processes may occur. Geese migrating to Novaya Zemlya had larger head lengths, possibly indicating that they have grown up with a smaller mismatch (e.g. Van Gils et al. 2016) and/or with less competition at post-hatching foraging sites. Such individuals may be able to have higher reproductive output (e.g. Larsson et al. 1998). On the other hand, larger geese are expected to be dominant, but Svalbard-breeding geese using the new migration route were less dominant than Svalbard-breeding geese using the traditional route. Thus, the colonisation process of a new flyway may be complex. The process might be comparable with foraging interactions, but then on a larger scale. Like in foraging interactions, subordinate geese may explore new areas first, and subsequently facilitate dominant geese to follow them and benefit from the new area (Stahl et al. 2001, Kurvers et al. 2010).

Further, several cascades of drivers and facilitators during the colonisation process can be hypothesised. First, geese searching areas with a smaller mismatch may initially have relocated within Svalbard, towards the east (e.g. following moult migration, Glahder et al. 2006). Their more eastern orientation may then have increased their likelihood to join groups taking an eastern migration route. Second, winds may have caused vagrancy towards the east also historically (see below), but only recently geese got a foothold in Novaya Zemlya because of climate warming. After joining Taiga bean geese towards the south, they may have stayed in



eastern flocks and again followed them in spring. Third, because of an increased pressure on Trøndelag, the stopover in Örebro may have provided an alternative between Jutland and Trøndelag. In Örebro, the large numbers of Taiga bean geese may then have attracted Pink-footed geese to follow them further east. Fourth, in the wintering area, Pink-footed geese have learnt to exploit maize as a food source. However, geese nowadays seem to prefer maize, since maize availability keeps more geese in Jutland. Although the hunting in Jutland does not drive geese to Friesland and Belgium, it may drive geese to explore other areas within Denmark (in turn, facilitated by the expanded availability of maize), which could lead to increased contact with Taiga bean geese.

### **Plasticity, selection, evolution**

Changes on population level can result from either plastic adjustments in behaviour by individuals, or from selection favouring certain behaviours while an individual's behaviour is fixed. Plasticity itself can also be the result of selection (Charmantier et al. 2008). The extent to which both processes play determines the speed of environmental change that a population can cope with.

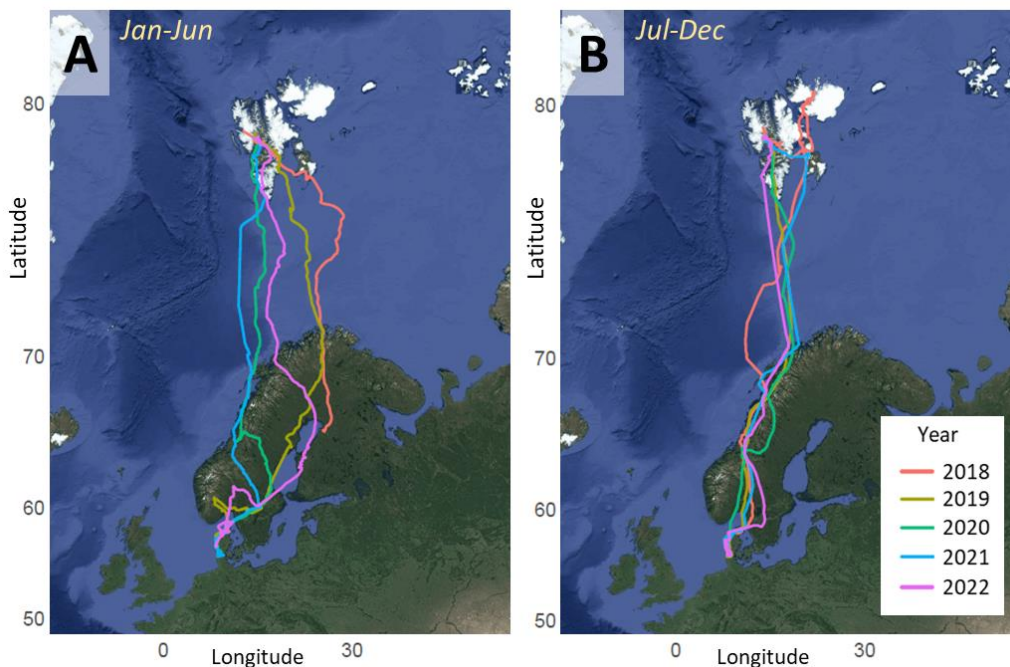
In Pink-footed geese, the plasticity in spring migration route was large. GPS-tracked geese regularly switched between spring routes. Svalbard-breeding geese sometimes used one or two of the new stopovers. On the traditional route, they sometimes skipped the stopover in Vesterålen. In an earlier study on Pink-footed geese on their traditional route, stopover choice was found to relate to body condition in the previous year (Madsen 2001): those migrating in lower body condition were more likely to switch stopover choice next year than those in good condition. This may indicate that geese switch routes in search for energetically better alternatives. Svalbard-geese tagged on the new route were most plastic, possibly because these were caught while exploring a new route. Most of these switched to the traditional route in following years. One individual gradually switched west in during springs of 2018-2021 and jumped back east in 2022, while its autumn routes remained west (Figure 2). Strikingly, the plasticity in spring route was lowest in geese breeding in the new breeding area, Novaya Zemlya. These geese always stopped over in Oulu, and almost always in Örebro as well. This limited plasticity could indicate a high degree of conformity or copying behaviour, as there is no pressure yet (e.g. competition) to explore alternative routes towards Novaya Zemlya. However, they did show more variation and flexibility in site choice during winter than spring, as competition was likely also higher, or as geese may track land use changes (see also Clausen et al. 2018a).

This large plasticity in migration route suggests that innate, genetic components do not play a large role. This is in contrast with e.g. (short-lived) passerines, where the direction of migration is genetically determined (e.g. Wiltschko & Gwinner 1974, Berthold et al. 1992). Still, also short-lived migrants can show remarkable flexibility in their wintering site choice, despite being consistent in their direction during at the start of migration (e.g. Van Wijk et al. 2016). Flexibility in migration routes is more typical of long-lived migrants, such as raptors, and may be a response to annual variation in environmental conditions (e.g. Vardanis et al. 2011), while the timing of migration is usually repeatable, across various bird taxa (Franklin et al. 2022).

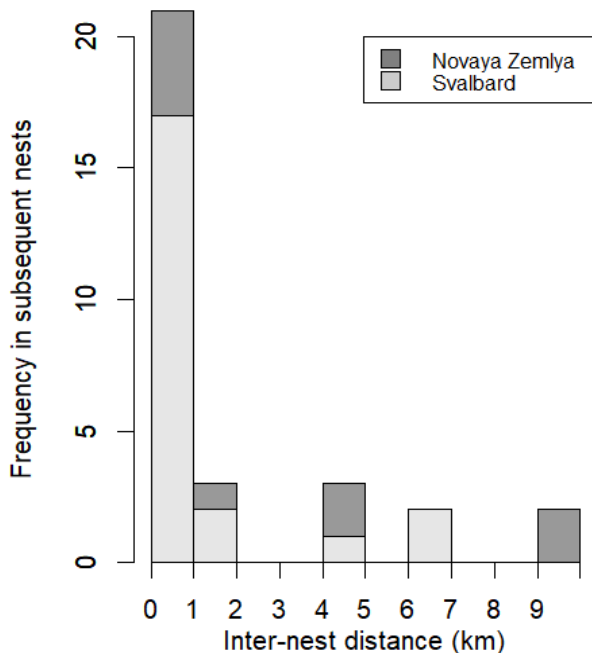
Plasticity regarding breeding area in Pink-footed geese was markedly lower. No switches between Svalbard and Novaya Zemlya occurred in GPS-tracked geese (but, mainly adult females were tracked and males may switch more often). However, integrated population modelling showed that immigration from the Svalbard population to Novaya Zemlya must have been significant. On a smaller scale, nesting locations of individual geese were quite consistent between years. Subsequent nesting attempts were often close to each other (23% within 100

m, 68% within 1 km) but some relocation occurred over large distances, up to 9.5 km (Figure 3). Two geese in Svalbard, both tracked in four years, each used one of their nesting sites twice, but not in subsequent years. The causes of plasticity in nesting site are unknown. Potentially, geese may relocate to another valley in response to snow melt, food abundance, or predation pressure, although Spaans et al. 1998 showed geese may forego breeding altogether in years with high predation pressure.

The remarkable plasticity that Pink-footed geese demonstrated, suggests that they are able to cope with a high speed of environmental change. This benefit itself may have been the selection pressure that resulted in the evolution of plasticity (e.g. Brommer et al. 2005, Charmantier et al. 2008). However, for evolution to occur in migration route and timing, a genetic basis is required for these traits, on which selection can act. The genetic basis of migration route in Pink-footed geese is likely limited, given the important social learning component. Personality, such as the tendency for exploration, is generally heritable (Dochtermann et al. 2015), but so far, we found no relation of migration route with personality traits tested during handling.



**Figure 2. Migration routes of the most plastic Pink-footed goose during five consecutive years.** Goose A4 was tagged in Oulu, Finland, 28 April 2018. (A) Spring routes (Jan-Jun depicted) changed over the years. A4 switched from a route via Finland, to a route via Sweden, to twice a Sweden-Norway route, and finally Sweden-Finland. Strikingly, all spring routes converged in Örebro, Sweden. (B) Autumn routes (Jul-Dec depicted) were more consistent, by always going via Norway and down to Denmark. Strikingly, all autumn routes converged in Trøndelag, Norway. In 2018, A4 was paired with male KG3 (ringed in the same catch) but their breeding attempt failed. In winter 2018/2019, KG3 probably died. In 2019, A4 did not breed but remated with an unringed male in Norway in October. In 2020-2022, A4 and her mate nested successfully each year, but had no juveniles anymore in autumn, except in 2022, when they had one juvenile with them in Denmark.



**Figure 3. Distance between subsequent nesting attempts of individual Pink-footed geese.**

Subsequent nesting attempts could also occur with a non-breeding year in between. Of all relocations, 23% occurred within 100 m, and two geese in Svalbard each even re-used a nest once. Number of recorded nesting attempts per goose were for Svalbard: two (n=4), three (n=6), four (n=2); for Novaya Zemlya: two (n=2), three (n=2), four (n=1). Geese with only one recorded nesting attempt could not be included (Svalbard: n=6, Novaya Zemlya: n=3, in some cases due to tag failure in subsequent years).

Selection pressures may favour the use of the new spring route. Geese may encounter better feeding conditions on the new stopovers, and possibly reproduce with a smaller trophic mismatch for their goslings in Novaya Zemlya. Also survival is expected to be higher in the new migration route. Hunting rate (annual harvest rate) was six times lower for the Novaya Zemlya population, since hunting is not permitted in Sweden and Finland (Madsen et al. 2023). How the annual survival compares, has not yet been studied.

Occupying a new environment can expose animals to new selection pressures and can lead to local adaptation (Orsini et al. 2013). In Pink-footed geese however, populations of the new and traditional breeding area show continued exchange, which could slow down local adaptation in Novaya Zemlya.

### Adjustment in space rather than time

Pink-footed geese have not advanced their timing of breeding over the past decades, despite fast advancements in the onset of spring. Also longer ago, full clutches were found in Svalbard from early to mid-June with a peak in the second week of June (Bauer & Glutz von Blotzheim 1968). Another decade earlier, laying also commenced in the last half of May and was completed in the first half of June (Løvenskiold 1964 in Cramp & Simmons 1977). Even further back, geese also started their breeding season in early to mid-June (Witherby et al. 1940).

This constant, invariable timing is in stark contrast with the variable migration site choice (see also Madsen et al. 1999, Madsen 2001, Clausen et al. 2018a). Why would Pink-footed geese be largely inflexible in time but highly flexible in space? The answer probably lies in the information that they have for optimal behaviour. In winter and spring, geese can explore different sites and change their route and timing of migration in order to approach optimal decision making, e.g. a strategy to maximise the accumulation of body stores. However, the optimal timing of arrival at the breeding area cannot be forecasted from the stopovers. Thus, geese cannot adjust their timing accordingly to anticipate annual variation in the onset of the

arctic spring. In such circumstances, a fixed migration schedule may evolve (e.g. based on biological clocks, Gwinner 1996, Åkesson et al. 2017). As a result, arrival dates of long-distance migrants have hardly advanced while spring advanced in their breeding areas (Schmalljohann & Both 2017). The fact that the departure dates of Pink-footed geese from Vesterålen advanced slightly (but more slowly than the spring in Svalbard), may indicate a slight selection pressure for earlier migration schedules or a plastic adjustment to long-term experiences in this long-lived bird. If geese would accumulate more body stores in spring than before, departure might also advance (Duriez et al. 2009), as the optimal timing would advance. However, preliminary results rather suggest that geese leave with fewer body stores nowadays than before (unpubl. data J. Madsen). Perhaps, fewer body stores are needed on Svalbard nowadays, because spring has advanced there.

The lack of advance in laying dates in Pink-footed geese contrasts with other species of geese, which did adjust their timing to annual variation in the onset of spring: Greater snow geese (*Anser caerulescens atlantica*, Dickey et al. 2008, Doiron et al. 2015), Lesser snow geese (*Anser caerulescens caerulescens*) and Ross's geese (*Anser rossii*, Ross et al. 2018), Canada geese (*Branta canadensis*, Brook et al. 2015), and Barnacle geese (Lameris et al. 2019). In most of these cases, this can be explained again by predictability of the arctic spring during migration. These species migrate largely over land, without a large sea as barrier. However, Lameris et al. (2019) showed that also Barnacle geese on Svalbard (migrating across the Barents Sea) had advanced their laying date. This may be explained by the different pre-breeding habitat and diet choice of both species. Barnacle geese visit uplands more, while Pink-footed geese visit flat lowlands more (Fox et al. 2009). Also, Barnacle geese eat more moss, while Pink-footed geese eat more below-ground rhizomes (Fox et al. 2007). Both species arrive around the same time, mid to late May (see Prop & De Vries 1993, Kölzsch et al. 2015), but Barnacle geese lay eggs a few days later (on average 3-5 June, Lameris et al. 2019), which may have given more opportunity for plastic advancements.

The fixed migration schedule of Pink-footed geese would probably have evolved to match the optimal timing of arrival and breeding in an average year, or, in the long term. That optimum would be the option best balancing several pressures, e.g. the expected harshness of conditions before and during nesting, the favourability of conditions during chick growth, and the time until the end of the arctic summer (see also Drent et al. 2006). Apparently, migrating in mid-May has evolved because it gives on average the best chances for breeding, which would start in late May and early June (with enough capital resources left), while still facing good growing conditions for goslings and still having enough time before autumn migration. As long-lived species, geese may forego breeding if this favoured timing of breeding cannot be realized, for example when spring start late (Boom et al. 2022).

Earlier spring onset results in a higher breeding propensity and nesting success due to eased conditions for nesting. Still, in the past, Pink-footed geese did not migrate later, which would have given them the same benefit. This may be caused by the other two pressures: a trophic mismatch and shorter time until the winter sets in. In the end of summer, geese face deteriorating feeding conditions, as food quality drops and daylength shortens, which leads them to increase their nighttime foraging (Boom et al. 2023). Preliminary analyses on Pink-footed geese showed that autumn food quality (measured by C:N ratio analyses in droppings) was higher in the east of Svalbard than in the west, which corresponds to a later onset of spring in the east (Karlsen et al. 2014). Geese with a juvenile brood seemed more likely to migrate via the east, possibly to benefit from the better feeding conditions (unpubl. data). Apparently, this benefit also outweighed the cost of the fact that winter started about one week earlier in the east than west, which initiated autumn migration departure (see also Xu & Si 2019). This

suggests that food quality might be limiting for juveniles, not only during growth but also later in the arctic summer.

### **Sociality as key to plasticity**

The fact that Pink-footed geese and Taiga bean geese show similar migration routes towards Novaya Zemlya and in other parts of their annual cycle, does not directly prove interspecific social learning of migration. Theoretically, both species may simply respond to the same environmental conditions, and, both being geese, end up using the same routes. However, both species co-occur in flocks, and (mixed) flock life has benefits (Cohen et al. 2020). For example, birds can have a reduced vigilance (Roberts 1996), a higher food intake rate (Beauchamp 1998), or a lower predation risk (Landeau & Terborgh 1986) and use social information on where food patches are (e.g. Templeton & Giraldeau 1995). This may attract geese to join a flock and thus learn a new migration route.

The social learning of migration, both inter- and intraspecific, has probably been the key to fast rise of the new flyway. Apart from living in flocks, other behaviours of geese show that they have a highly social life. First, they exhibit mate fidelity (e.g. Black 2001). In species where partners are only faithful to their mate upon returning to the nesting site, the mate fidelity can in fact be nesting site fidelity (Furness 1987). However, in geese, one can speak of 'true' mate fidelity as partners also migrate together (e.g. Rees 1987, Rohwer & Anderson 1988). Second, geese exhibit extended parental care, as chicks stay together with their parents and migrate along as juveniles, at least until autumn or winter (e.g. Gupte et al. 2019). In birds, such extended parental care has also consequences for the adults, potentially costs, e.g. a slower migration speed (Byholm et al. 2022) or not migrating at all (Palacín et al. 2011).

Why are geese social? Does the extended parental care and collective pair migration provide benefits that weigh up against potential costs? Possible benefits relate to three aspects: the short arctic summer, longevity, and diet and within-flock food competition. Pair migration prevents having the cost of mate absence upon arrival in the breeding grounds. Mate absence could preclude breeding as there is little time to find another mate. Being long-lived, geese may gain benefits of long-lasting pair bonds, such as a higher reproduction (Black 2001) and a higher survival (Nicolai et al. 2012). For herbivores, food availability is often concentrated in specific areas, both in the tundra or on agricultural fields in winter, where geese in turn congregate. Within a flock, individuals compete for food and gain dominance benefits when operating in a unit of multiple individuals (a pair or a family, Klaassen et al. 2006; also juveniles join efforts to chase other units away, pers. obs.). This in turn provides the benefit to accumulate more body stores (Prop & Deerenberg 1991), which enables the female to prepare for the breeding season in the short arctic summer. The female may also gain foraging time since the male is most vigilant (Lazarus & Inglis 1978). Such cooperation between partners in the competitive flock environment may be the key to the long-term pair bonds (Black 2001).

These benefits of being paired outside the breeding season are likely to promote pair formation outside the breeding season, which occurs in many waterfowl species (Rohwer & Anderson 1988). In addition to the effect of flock life, this may in turn promote genetic exchange and information sharing between breeding areas, given that the non-breeding areas overlap.

### **Is Novaya Zemlya really 'New Land' for Pink-footed geese?**

Given the dynamic distribution of a species over time, how certain is it that Novaya Zemlya is a new breeding area of Pink-footed geese? Have the geese now colonized or recolonized it? Or has a small population remained unnoticed there, as some sources suggest?

First, we look how the migration routes have developed since the last ice age. Although nowadays, Pink-footed geese breed in the high Arctic, they must have bred in more southern areas during the last glacial maximum, from which they have (re)colonized the arctic regions and established migration routes. Based on climate and vegetation reconstructions, the potential glacial refugia of Pink-footed geese are believed to have been in northern Norway, the southern North Sea area and the shelf area off western Iceland (Ploeger 1968). Based on the present lack of geographic variation in morphology, it is assumed that Pink-footed geese occupied only one of these potential refugia, or that populations in different refugia kept contact in the wintering area. Genetic studies have indeed suggested that the refugial population was genetically a single population, from which different populations arose after the last glacial maximum (Ruokonen et al. 2005, Pujolar et al. 2017). However, when identifying which population now represents the ancestral gene pool, analyses of mitochondrial DNA indicate Svalbard (Ruokonen et al. 2005) while whole-genome analyses indicate Iceland (Pujolar et al. 2017).

Evidence for the spread of Pink-footed geese into Russia only comes later. The first records consist of archaeological finds on Vaygach, bone remains from the 7<sup>th</sup> to 12<sup>th</sup> century (Kalyakin 2016). Out of 310 goose bone remains, 115 (of at least 40 birds) were morphologically identified as a 'bean goose' species, of which 2 as Pink-footed goose. More recent historical records with harder evidence are from the 19<sup>th</sup> and 20<sup>th</sup> century. A Svalbard-ringed goose was shot 120 km north of Moscow on 7 Oct 1956 (Webbe 1958) and a Dutch ringed goose was shot 790 km NE of Moscow on 3 May 1992 (Sotnikov 1998). One goose was shot at the Yenisey river close to Dudinka on 11 Sept 1894, 2700 km NE of Moscow (Webbe 1958). Other sources report the species on Kolguyev (Zhitkov & Buturlin 1901), Yugorsky peninsula on 9 Jun 1983 (Kalyakin 2016), the Ob river mouth (Kalyakin 2016) and the Gulf of Finland close to Saint Petersburg (Van Impe 2008). There are also records higher north in Russia, even at the North Pole at 85°N and on Franz Josef Land in August 2018 (Mizin 2019). Regarding Franz Josef Land, Kalyakin (2001) argues that the shot geese on photographs taken by Jackson (1899) show Pink-footed geese. On Franz Josef Land, two eggshells were collected on Alger Island in 1990, which Kalyakin (1995) presumed to be of Pink-footed geese, but also Barnacle geese breed there (obs. J. de Korte, a pair with four goslings at the isthmus east of Rubini Rock, Hooker Island, early July 1994). Further, Pink-footed geese have been reported to nest on Kola Peninsula, where four goslings were captured in 1880 (Pleske 1886, Van Impe 2000).

Specifically for Novaya Zemlya, Spitsyn et al. (2020) mention that Pink-footed geese were not observed in the 19<sup>th</sup> century, but were present as vagrant species in the 20<sup>th</sup> century. Kalyakin (2001) reports for the south island, that an adult male was collected at Gribova Bay on 21 Sep 1948 and a juvenile from a non-flying brood at Gusina Land on 28 Aug 1993. Other records are more indirect. Two skeletons were found near the Savina river in 1985, which were first identified as either Tundra bean goose or Pink-footed goose (Kalyakin 2016), but later as Pink-footed goose (Kalyakin 2001). Two nests were found in rocky hills on the south island (in one of which four chicks hatched later), and based on similarity of the nesting habitat with that of Pink-footed geese in Svalbard, it was assumed that these nests were of Pink-footed geese (Kalyakin 2001). Further, in 1994-1999, some groups of 'bean geese' were observed annually on the south island, during aerial surveys (Kalyakin 1999). Because they seemed to nest in the foothills and kept close to inland water bodies, it was again assumed that they were Pink-footed geese, since Tundra bean geese would not nest in hills and would flee to sea rather than to inland lakes (Kalyakin 1999). The same inference was made longer ago, by Bilkevich (1904), based on observations by local Nenets. Finally, on a lake on the Mednoya peninsula, a female that had a brood was caught on 4 Aug 1997. This female was first described as "most consistent



with Pink-footed goose” (Kalyakin 1999), but later more detail was given (Kalyakin 2001). It was then presumed to be a hybrid of Pink-footed and Tundra bean goose, given the pink-coloured but long bill, yellow feet, and short neck. Pink-footed geese with yellow or orange legs have incidentally also been observed in the Netherlands and Iceland (see Webbe 1958).

Kalyakin (2001) did estimate that a few hundred to a thousand Pink-footed geese would nest in Novaya Zemlya, but this was a daring extrapolation based on only his two nest finds in the hills and aerial surveys on the south island. Strikingly, our GPS-tracking has not given any evidence of breeding on the south island. Some GPS-tagged Pink-footed geese did pass this area, but rarely stopped there. Thus, it is unlikely that a substantial breeding population of Pink-footed geese would exist on the south island. No historical records exist from their current breeding area on the north island, which is partly due to restricted access, as it has been a nuclear military testing site since 1955 (Andrianov et al. 2004). Although Van Impe (2008) makes a good point that Russian literature is overlooked in western countries, he unfortunately quotes Kalyakin’s extrapolation as a real observation in English (even though his French text uses a more correct wording), which may have caused confusion.

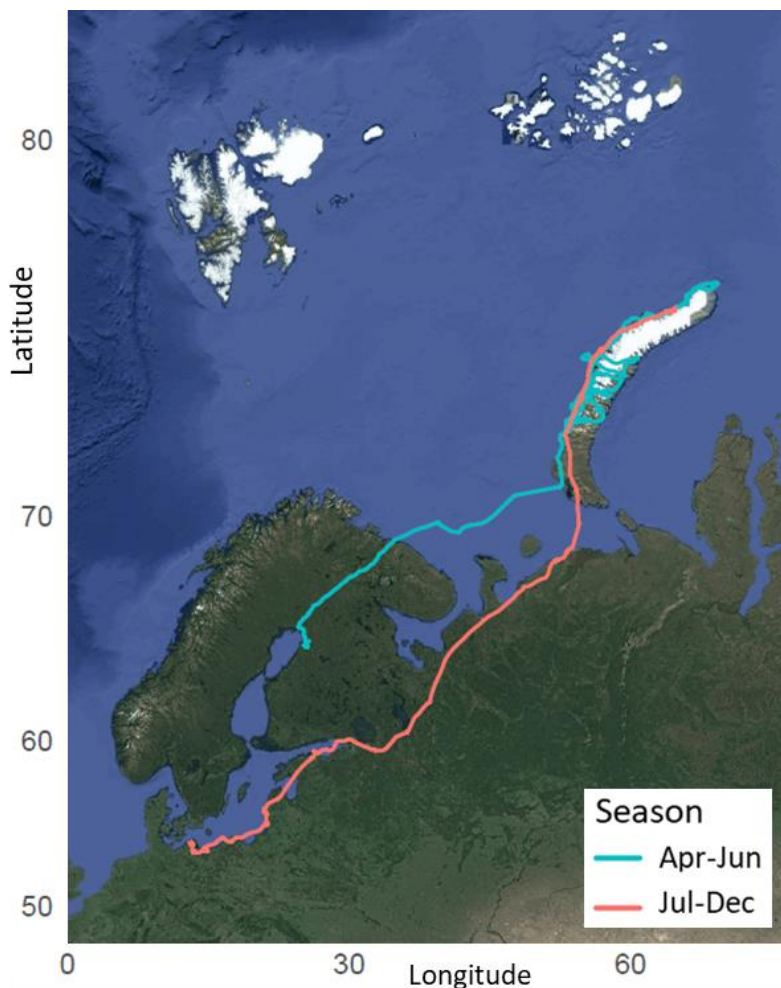
Concluding, historical breeding records of Pink-footed geese in Russia are sporadic and records from Novaya Zemlya unverifiable, as identification methods were questionable and poorly substantiated. However, there is evidence of Pink-footed geese occurring historically as vagrants across Russia. As Sotnikov (1998) assumed, they may have migrated along with other species. Pink-footed geese have occasionally also turned up in other parts of eastern Europe and as far south as North Africa (Bauer & Glutz von Blotzheim 1968, Cramp & Simmons 1977, Faragó 1991).

### **Future changes for Pink-footed geese**

The population developments on the new migration route are still ongoing. The latest simultaneous counts of geese on the Swedish-Finnish route indicated a new record peak number of c. 7850 geese on 5-7 May 2023. This ongoing increase suggests that the capacity of these stopovers may be reached in the future. As a consequence, the potential benefit of competition avoidance may attenuate and geese may once again explore alternative sites and routes. Even though Novaya Zemlya has been colonized recently, the tracked Pink-footed geese have shown remarkably consistent routes towards it. However, other species of geese reach Novaya Zemlya via a different route over the mainland of Russia, such as Greater white-fronted geese (*A. albifrons*, Van Wijk et al. 2012) and Barnacle geese (de Boer et al. 2014). Pink-footed geese may join these geese, potentially starting from Novaya Zemlya, and explore these alternative routes. In fact, in 2018, one GPS-tracked adult male was unpaired and visited various unusual parts of Novaya Zemlya, including the north tip, the east coast, and the south (Figure 4). It migrated in autumn via Russia, the Baltic states, Poland, Germany to Denmark. In Poland, it was among c. 10,000 Bean geese *A. fabalis* and Greater white-fronted geese, and one Red-breasted goose (*Branta ruficollis*, obs. Ł. Jankowiak et al., 50 km north of Szczecin, 19 Oct 2018). However, in the following spring, it took the Sweden-Finland route again. Nevertheless, Pink-footed geese do increase in western Poland in spring and mainly occur there in early March (Wylegała et al. 2017). They increased from 1 to 100-180 individuals during 1997-2017, and always occur in large flocks of Bean geese and Greater white-fronted geese. Pink-footed geese occurred in 32% of cases as singletons and in 41% as a group of 2-3, indicating that also pairs may explore this route. Migrating via central Europe and mainland Russia may give the benefit of a better predictability of spring in Novaya Zemlya (Kölzsch et al. 2015).

The continuing increase of Pink-footed geese in Sweden-Finland also complicates the population management scheme (Madsen & Williams 2012). The population was hitherto

**Figure 4. Migration and summer movements of a Pink-footed goose in Novaya Zemlya.** Goose A8 was an unpaired adult male. It was tagged in Oulu, Finland, 28 April 2018. In Novaya Zemlya, this goose undertook excursions to areas, where thus far no GPS-tracked goose have nested: several areas on the east coast, and the north tip, where it probably moulted. A8 was the only GPS-tracked Pink-footed goose recorded to migrate south in autumn, via mainland Russia and eastern Europe. In Poland, it was the only Pink-footed goose among c. 10,000 Bean geese, Greater white-fronted geese, and one Red-breasted goose. Next spring it migrated via Sweden and Finland again. Depicted in blue is the period April-June and in red the period July-December.



managed as a contained unit (Madsen et al. 2017), but may now become an interplay of two biogeographic populations where only one is managed and where developments in one unit can affect the other unit due to considerable exchange. This also means that threats in one unit can determine developments in another unit. The population management scheme is in the process of being revised to account for this complexity, planned to happen from 2025 onwards (pers. comm. J. Madsen).

With increasing numbers of Pink-footed geese in Novaya Zemlya, also their breeding range may expand there. This may intensify their contact with other geese, such as moulting

Taiga bean geese (Piironen et al. 2021) or breeding Tundra bean geese (*A. f. rossicus*), Greater white-fronted geese, and Barnacle geese (Scott & Rose 1996).

A widening breeding distribution in Novaya Zemlya may also expose Pink-footed geese to new adverse conditions. Nuclear tests have been performed in Novaya Zemlya (Andrianov et al. 2004, Khalturin et al. 2005) and nuclear waste has been deposited there (Dahle et al. 2009). Levels of radioactivity are elevated (Miroshnikov et al. 2021). Radioactivity can cause higher mutation rates, abnormal development and lower survival and fertility (Mousseau & Møller 2011). In this context, it is of concern that two geese in Novaya Zemlya incubated their nests for too long, indicating that the whole clutch did not hatch. One goose even showed this in two years (Table 1), which suggests that the pair was probably infertile. If hatching failure is radioactivity-related, sperm defects may be the cause (Møller et al. 2005). Hatching failure in itself is not rare, but complete clutch hatching failure is, as clutches rarely contain only one egg (<5% of complete clutches, Bauer & Glutz von Blotzheim 1968). In Svalbard, one goose also incubated for too long, but was found to have only one egg (possibly due to partial predation). Two years later, it bred successfully, which may also be caused by partner change. Still, on population level, any potential negative effects of radioactivity seem limited in Novaya Zemlya to the present day.

Also other breeding areas may be colonised. The population management scheme aims to maintain a viable population, while taking into account economic and recreational interests. One of their defined key actions is to prevent establishment of breeding colonies on mainland Norway (Madsen & Williams 2012). However, breeding has been confirmed or suspected in several locations across north Norway recently (Nordland and Finnmark, Keller et al. 2020) and this may develop further. Also in Barnacle geese and Greater white-fronted geese, breeding populations have started to develop along the spring migration route or even in the wintering area (Van der Jeugd et al. 2009, Sovon 2018). This breeding expansion towards the south instead of the north may relate to benefits gained in the early stages rather than late stages of breeding (see also Nolet et al. 2020).

**Table 1. Three GPS-tracked Pink-footed geese with extended incubation periods.** Nests of Pink-footed geese hatch after 28-35 days nesting, but these geese showed longer nesting periods (underlined). The number of days of each incubation period per nesting attempt is given. Location of a goose was averaged over all its nest attempts but these were in the same area (max. 9 km apart). Notes: \*On day 43, it had one egg. \*\*It was later observed with 7 goslings. \*\*\*Male identities (individual code) are given in chronological order. Neckband loss of males could not entirely be excluded. No: not neckbanded. Goose 4N died on 15 Feb 2021.

Female	Male***	Area	Location	2019	2020	2021	2022
2M	3xKK9, 1xNo	Svalbard	N 78.19, E 15.79	no nest	<u>44 d</u> *	9 d	31 d**
4J	1xLB3, 3xNo	Novaya Zemlya	N 74.89, E 56.58	no nest	<u>39 d</u>	4 d	<u>54 d</u>
4N	2xLA7	Novaya Zemlya	N 73.45, E 55.94	no nest	<u>41 d</u>	-	-

### Conclusion

The rapid range expansion of Pink-footed geese has enabled them to reduce potential negative effects of environmental and climate change. The new breeding area offers a later spring onset, similar to Svalbard decades ago, which enables geese to have a smaller trophic mismatch for growing offspring. On the new spring migration route, geese carried more body stores, which

probably allowed them to cover the longer pre-laying intervals in the new breeding area. This may have been enabled by better feeding conditions on the new route: vegetation green-up started earlier than on the old route, and competition was likely lower, since goose densities were lower and aggressive interactions rarer.

The reduced mismatch and lower competition may have been drivers behind the colonisation, in addition to vagrancy due to strong winds during migration over the Barents Sea. Facilitators have probably been climate change (thus being both a driver and a facilitator) and the presence of Taiga bean geese, from which the new migration route could be learned socially. The exact colonisation history remains elusive, but may run parallel to processes that play on a small scale during foraging interactions: subordinate geese explore new areas first, but dominant (or, higher-quality) geese may copy the behaviour and benefit from the new area.

Pink-footed geese have displayed remarkable plasticity in migration routes and stopovers, but less so in breeding area (based on repeated tracking of adult females). This plasticity may be adaptive, given that it allows geese to quickly find and exploit benign sites. The lower hunting pressure on the new route may evolutionarily favour geese using this route, but given the (probably) limited genetic basis for route choice, largest developments are expected to come from further plasticity.

The spatial flexibility was in stark contrast with the inflexible timing of breeding, which has remained unchanged for many decades. Geese can probably not adjust their timing of migration plastically in order to arrive at the optimal time in the breeding area, because the arctic spring onset cannot be forecasted from the stopovers. Thus, probably a fixed migration schedule has evolved. The timing of arrival and breeding would be tuned to long-term optima, which best balance several pressures: the expected harshness of (pre-) nesting conditions, the favourability of conditions during chick growth, and the time until the end of the arctic summer. However, in winter and spring, geese can explore different sites and adjust their migration accordingly in space, e.g. to maximise body store accumulation.

The social life of geese has probably been key to the fast population developments. This sociality includes not only flocking (inter- and intraspecific), but also long-term pair bonds and extended parental care. These features are thought to stem from associated benefits in herbivorous flock-living species that are long-lived and breed in the short arctic summer. These benefits likely also promote pair-formation outside the breeding season, which in turn can promote exchange between old and new breeding areas, since the wintering ranges still overlap.

Although some sources suggest that Pink-footed geese have bred in Novaya Zemlya in large numbers already for longer in recent history, we have reviewed the available literature and found this to be questionable. Most records used poorly substantiated identification methods, e.g. based on nesting habitat or fleeing behaviour instead of morphological characteristics. Still, large extrapolations have been made from these findings, and these have subsequently been quoted as observations, which may have caused confusion.

In the future, more Pink-footed geese will probably use the new route and breeding area. This may cause expansion in Novaya Zemlya and expose them to more competition with other geese, or to environmental hazards such as nuclear radioactivity, which might inhibit reproduction. Up to now, these effects seem limited on population level. Increasing competition may also lead Pink-footed geese to explore once again a new route. This route may lead via eastern Europe and mainland Russia, where other goose species migrate to (southern) Novaya Zemlya. In Poland, Pink-footed geese have increased to several hundreds and occur mainly in early March now. New breeding colonies may also further develop in north Norway.

Our studies have shown that, even though efforts are made to understand and predict changes in nature in the Arctic, changes occur on unforeseen scales in time and space, and there is still much to learn about the potential and limits of natural systems.

**Acknowledgements**

I thank Irina Pokrovskaya, Ivan Mizin, Vitaly Spitsyn, Petr Glazov, Maria Gavrilov and Sonia Rozenfeld for information and literature about Pink-footed geese in Russia, and Irina and Ivan for even keeping an extra eye out for geese during their field expeditions at the north tip of Novaya Zemlya. I thank Götz Eichhorn and Thomas Lameris for help with interpreting the Russian literature, and Jan Geisler for help with making figure 1.