Rapid formation of new migration route and breeding area by Arctic geese

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Current Biology

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Graphical abstract

Highlights

- We observe a population of Arctic geese in the making in real time

- The colonization of new distinct breeding grounds was enabled by recent warming

- Social transmission appears to be a key driver behind the rapid development
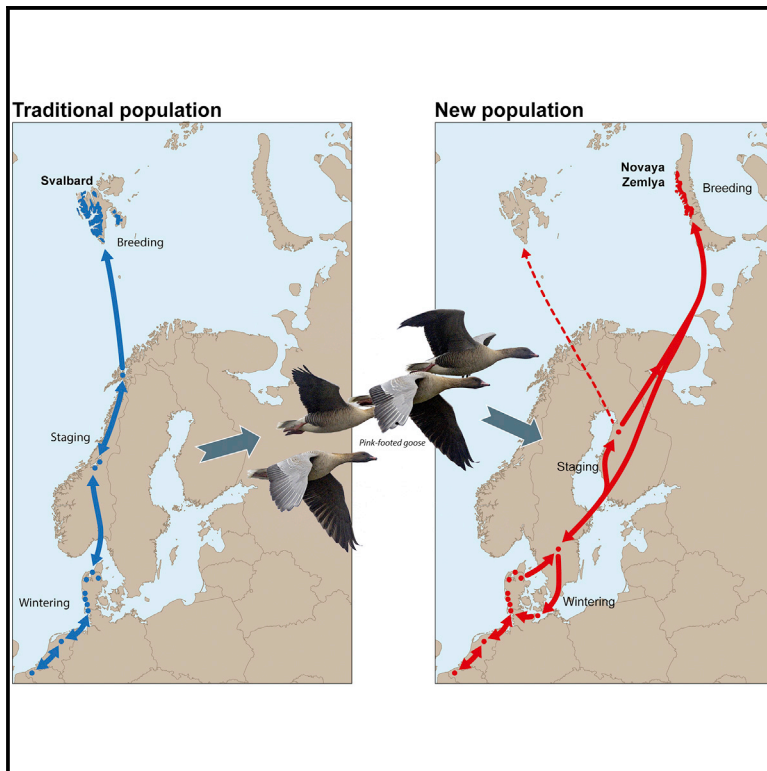
Authors

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In brief

Madsen et al. observe a population of Arctic geese in the making in real time, with distinct breeding grounds and a new migration route being established within a decade. Social transmission between conspecifics and closely related species appears to be a key driver behind this fast development.

CellPress

Report

Rapid formation of new migration route and breeding area by Arctic geese

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SUMMARY

Many Arctic-breeding animals are at risk from local extirpation associated with habitat constriction and alterations in phenology in their Arctic environment as a result of rapid global warming.[1] Migratory species face additional increasing anthropogenic pressures along their migratory routes such as habitat destruction, droughts, creation of barriers, and overexploitation.[2,3] Such species can only persist if they adjust their migration, timing of breeding, and range.[4] Here, we document both the abrupt (~10 years) formation of a new migration route and a disjunct breeding population of the pink-footed goose (*Anser brachyrhynchus*) on Novaya Zemlya, Russia, almost 1,000 km away from the original breeding grounds in Svalbard. The population has grown to 3,000–4,000 birds, explained by intrinsic growth and continued immigration from the original route. The colonization was enabled by recent warming on Novaya Zemlya. We propose that social behavior of geese, resulting in cultural transmission of migration behavior among conspecifics as well as in mixed-species flocks, is key to this fast development and acts as a mechanism enabling ecological rescue in a rapidly changing world.

RESULTS AND DISCUSSION

While many Arctic-breeding migratory animals are threatened by global warming and other human-induced pressures, evidence for changes in migratory behavior that may buffer detrimental impacts is accumulating. Some involve adjustments in phenology of arrival and breeding,[5,6] expansion of breeding range as well as extension of migration routes,[4] breeding in traditional wintering areas,[7] and vagrancy in response to climate change.[8] Underlying mechanisms may be fast genetic adaptations,[9] enhanced by assortative breeding,[10] or phenotypic plasticity allowing for adjustments of behavior. Herd or flock-forming species, where migration routes are learned and culturally transmitted, are particularly likely to rapidly adjust migratory behavior.[11–14] Effects of such cultural interactions between individuals on the ability of species to cope with global change are rarely addressed,[15] but some recent studies have found evidence for its importance in changes of migration within a traditional route.[13,16]

Here we report on a spectacular example of a species, namely a migratory social high-Arctic goose species that has both rapidly colonized a new breeding area far away from its traditional range and established a totally new migratory route, including new staging and wintering sites. A long-term population monitoring and Capture-Mark-Recapture (CMR) program enabled us to follow this development from an early phase, and by deploying GPS tags were we able to map the locations of birds and document nesting behavior in these new remote environments.

The focal population of pink-footed geese traditionally breeds in Svalbard and migrates via a narrow corridor to staging sites in Norway and onward to wintering grounds in western Denmark, the Netherlands, and Belgium.[17] Abundance increased from around 45,000 in 1990 to a level fluctuating around 80,000 individuals since 2010 (Figure 1A).

New migration route

In the 1990s, single individuals or small flocks (≤100 birds) of pink-footed geese, dispersed among taiga bean geese (*Anser f. fabalis*), were reported by the goose counting networks in southern Sweden during autumn and spring and in western Finland during spring. Since the early 2000s, observations of flocks have become more regular and numbers have increased in both countries. So far, peaks of 5,970 and 4,147 individuals were observed in Finland (spring 2020) and Sweden (autumn 2020), respectively (Figure 1A).

Pink-footed geese marked with neckbands in the traditional range (since 1990; see STAR Methods) were only occasionally resighted by observers in Sweden and Finland during the
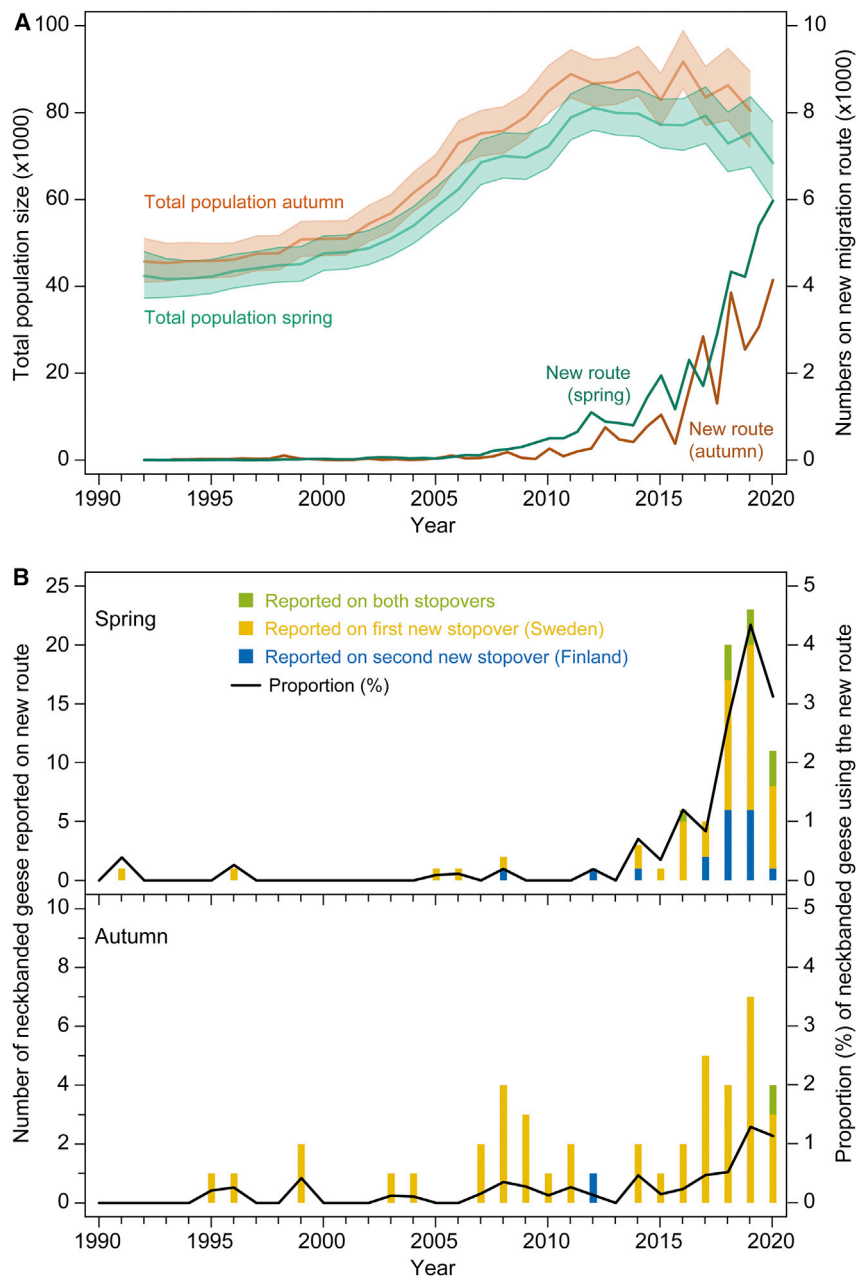
Figure 1. Development in overall population size and numbers of pink-footed geese using the new migration route via Sweden-Finland, 1990–2020

(A) Development in peak numbers observed in spring (Finland) and in autumn (Sweden), compared to the overall population size estimated on basis of an IPM (spring and autumn, with 95% credible intervals).

(B) Numbers of neckbanded individuals observed in Sweden, Finland, or both countries during spring and autumn, respectively (bars), and the proportion of neckbanded geese in the two countries out of the total number of alive banded individuals in the population (line).

See also Figures S1, S3 and Table S3.

least 1 year after capture but then made a permanent switch to the Swedish-Finnish route.
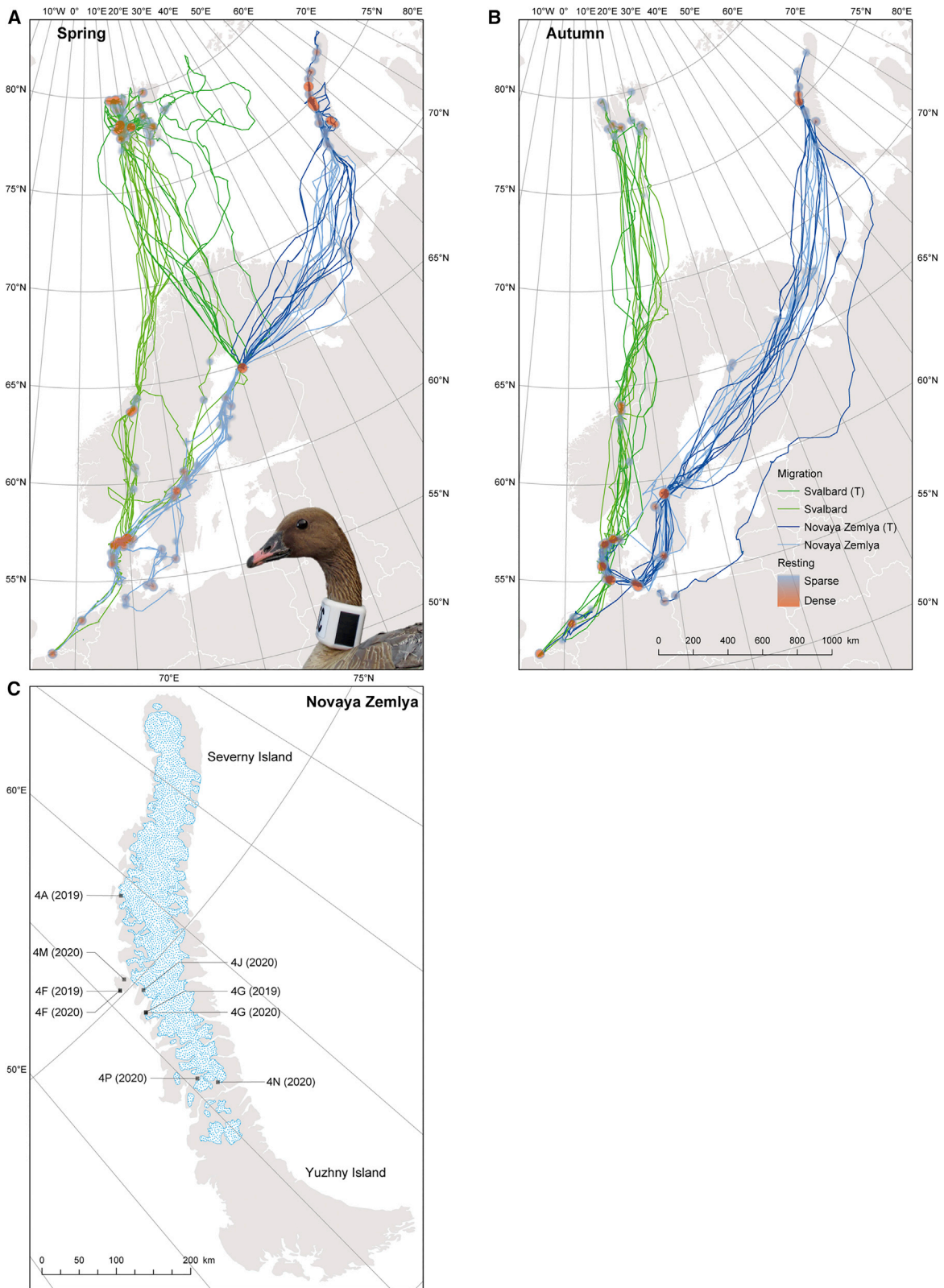
In late April to early May of 2018 and 2019, we tagged a total of 21 pink-footed geese (primarily adult females) with GPS transmitters mounted in neckbands, near Oulu, Finland (see STAR Methods and Table S1). We received GPS signals from the onward migration of 19 individuals. Nine of these migrated to Svalbard while 10 migrated to Novaya Zemlya in northern Russia. Most geese flew almost nonstop to their final destinations over the boreal and tundra zones in northern Fennoscandia, followed by crossing of the Barents Sea (Figure 2A).

In autumn, all of the GPS-tagged geese returning from Svalbard migrated south along the traditional migration corridor to Norway, Denmark, the Netherlands, and Belgium (Figure 2B), whereas nine out of 10 geese from Novaya Zemlya flew via northern Fennoscandia (some nonstop, others stopping on the Kanin Peninsula and Kola Peninsula in Russia or western Finland) to sites in southern Sweden (primarily Örebro County). One individual migrated via Russia, through the Baltic to Poland and Germany (Figure 2B). The nine Novaya Zemlya geese stayed in Örebro County during October–November and, following cold spells, migrated further south to Scania in Sweden and southeast Denmark. From southeast Denmark, most geese eventually joined the Svalbard population on the west coast of Denmark and some traveled to Germany, the Netherlands, and Belgium.

Among 15 individuals tracked for consecutive years (until autumn 2020), all Novaya Zemlya individuals (n = 9) consistently migrated via the new route. Among the Svalbard geese, one out of six individuals consistently used the new route while the remaining individuals switched to the traditional route (Table S1).

The abrupt development of this new migration route follows a recent period when the pink-footed geese have had to cope with

1990s and 2000s. During the 2010s, both the number of individuals and the proportion of banded individuals observed increased exponentially in Sweden and Finland in spring (Figure 1B). In autumn, the number and proportion of banded individuals seen in Sweden more than doubled (Figure 1B). The consistency in using the new Swedish-Finnish migration route by marked individuals also increased (Figure S1A).

Out of 87 individuals marked in the traditional range and subsequently recorded using the new route, 30 were of known age (i.e., marked in their first winter of life). These geese primarily shifted to the new route in their second and third years of life when they were still sexually immature (Figure S1B). Birds making the move were disproportionately males. Five males (three adults and two immature birds) used the traditional route for at

A Spring

B Autumn

Migration
— Svalbard (T)
— Svalbard
— Novaya Zemlya (T)
— Novaya Zemlya
Resting
Sparse
Dense

0   200 400 600 800 1000 km

C   Novaya Zemlya

Severny Island

4A (2019)

4M (2020)   4J (2020)
4F (2019)   4G (2019)
4F (2020)   4G (2020)

4P (2020)   4N (2020)

Yuzhny Island

0   50   100   200 km

(legend on next page)

several anthropogenic changes in their environment along the traditional flyway. These include the effects of increasing spring temperatures allowing for earlier spring migration and the establishment of spring stopover sites in mid Norway since the 1990s;[18] organized scaring by farmers in key spring stopover sites in northern Norway leading to the near-abandonment of these key pre-nesting fueling areas;[19] agricultural changes with the introduction of winter cereals in the 1990s and maize in the 2000s in Denmark leading to shortstopping and winter range expansions, particularly in Denmark;[20,21] habitat loss in the form of large-scale nature restoration projects flooding key farmland areas used by the geese in Denmark;[22] increased food competition with barnacle geese (*Branta leucopsis*) in northern Norway in spring;[23] and changes in goose hunting regimes in Norway and Denmark resulting in increased harvest.[24] Geese rapidly adjusted migration behavior and site use to the modified environmental conditions, demonstrating increasingly exploratory behavior,[25,26] most predominant among immature males but manifested across sexes and age classes.

The migration distance from north Jutland in Denmark to Severny Island on Novaya Zemlya (approximately 3,050 km) is 24% longer than the distance to Svalbard via the traditional route and 9% longer than the Sweden-Finland-Svalbard route. The additional flight energy costs associated with the use of the new route may be critical for these high-Arctic capital breeders, which rely on acquisition of body reserves and production of follicles on their final spring staging areas as a prelude to nesting and chick-rearing in the short high-Arctic summer.[27] As the spring stopover conditions on the traditional route have become less attractive due to anthropogenic perturbations and interspecific competition for food, it may have become advantageous to explore new migratory routes. Shortstopping by families, e.g., in the Oulu area in autumn, and increasing numbers observed in western Poland in recent winters[28] indicate that the process is still ongoing.

New distinct breeding grounds

The GPS tracking provided proof of successful breeding in Novaya Zemlya. Based on accelerometry data and GPS positions,[29] we identified nest locations, nesting attempts, and nest success. 10 geese nested (2018: none, 2019: three, 2020: seven including two repeats from 2019), all located on Severny Island (Figure 2C). We judged four nests to have hatched (all in 2020). All four females were observed with young in Sweden in the following autumn. We observed 5.2% and 26.6% juveniles in the flocks in Örebro County in October 2019 and 2020, respectively. In comparison, the proportion of juveniles in the Svalbard population was 9.0% and 18.4% (Table S2).

For Svalbard, a positive relationship exists between spring temperatures, calculated as the number of days in May with

average daily mean temperature above 0°C ("thaw days") and the proportion of juveniles in the subsequent autumn flocks.[30] During 1981–2020, thaw days ranged 0–27 (mean of 9) in Svalbard and 0–9 (mean of 2) on Novaya Zemlya (Figure 3A). For both areas there was a significant positive trend in thaw days, although annual thaw days were not correlated between the two areas. Currently, spring weather conditions on Novaya Zemlya resemble those in Svalbard decades ago (Figure 3A). An analysis of snow cover based on MODIS satellite imageries from western Severny Island on Novaya Zemlya, May 2008–2020 (Figure S2), reveals a negative correlation between thaw days and snow cover (Figure 3B), a pattern also found in Svalbard.[30] Hence, in relatively early years, suitable nest sites are probably available in May.

Historically, pink-footed geese have occurred only incidentally in Finland, northwest Russia, Novaya Zemlya, and Franz Josef Land.[31,32] Some observations suggest potential breeding on Novaya Zemlya, but it has been confined to Yuzhny Island.[33,34] However, during several summer expeditions to Yuzhny Island in the last decade, pink-footed geese were not recorded.[35] Notably, the GPS-tagged females nested exclusively on Severny Island, and all tagged geese spent the summer there. Therefore, it seems that Severny Island is the key breeding area. According to climate records, spring conditions on Severny Island were inhospitable prior to the 1990s (Figure 3A), with low probability of successful breeding. Recently, spring conditions in Novaya Zemlya should allow geese to breed successfully, but annual success is likely to be variable depending on temperatures and snow conditions. If spring temperatures continue to increase, it is likely to enhance breeding success.[36]

We have no direct evidence of how the first pink-footed geese settled in Novaya Zemlya, but we suggest that the interaction with other goose species has been key. In the 2000s, pink-footed geese expanded their Danish wintering range,[26] starting to overlap with taiga bean geese in their traditional wintering areas, particularly in one site in Jutland (Lille Vildmose; 56.88° N, 10.20° E). The first flocks of pink-footed geese were observed there in spring 2008 (120 individuals.) and have steadily increased since then (up to 1,800 in spring 2020). Recent GPS tagging of taiga bean geese on that site has shown that these migrate via Örebro in Sweden to staging areas along the Swedish Bothnian coast as well as across to Oulu in Finland. From there they go to breeding grounds in northern Fennoscandia.[37] Furthermore, tracking of taiga bean geese in northern Sweden has revealed that some birds go to Novaya Zemlya on molt migration[38] and, most strikingly, Finnish failed and non-breeding taiga bean geese undertake a molt migration to western Severny Island on Novaya Zemlya.[39] Pink-footed geese could have followed the taiga bean geese. Notably, two pink-footed geese

Figure 2. Migration routes taken by pink-footed geese marked and tagged with GPS transmitters in Oulu, Finland in spring 2018 and 2019 and breeding records in Novaya Zemlya

(A) Spring migration routes (toward Svalbard versus Novaya Zemlya) in the year of tagging (T) and in the subsequent two years (January–August). Insert photo shows individual marked with neckband GPS tag with solar panel.

(B) Autumn migration routes in the autumn after tagging (T) and in the subsequent two years (September–December). A heat map is used to show areas where geese stopped (for resting, foraging, and nesting).

(C) Nest sites of individually GPS-tagged females in Novaya Zemlya, 2019 and 2020, detected via accelemometry data derived from the GPS tracking. Glaciated areas are shown by dotted signature. Frame shows the area used for snow cover analysis based on MODIS imageries.
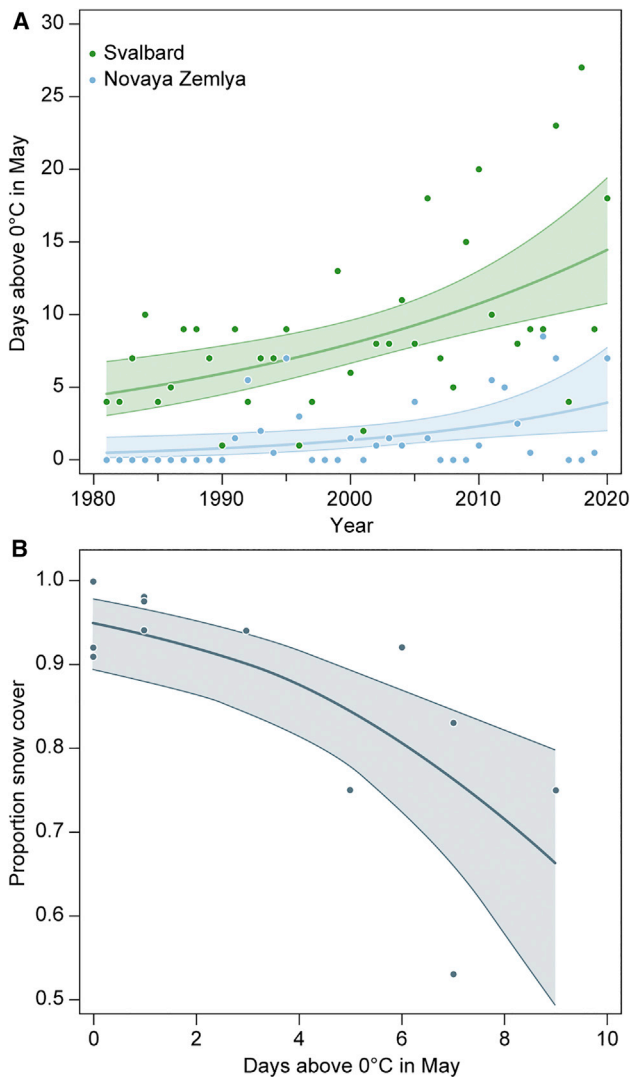
See also Table S1.

Figure 3. Development in spring climate conditions affecting breeding by geese in Svalbard and Novaya Zemlya

(A) Spring temperature trends, Svalbard and Novaya Zemlya, 1981–2020, expressed by the number of days with daily average temperatures above 0°C in May (thaw days) and averaged for two meteorological stations on Svalbard and two sites on western Severny Island, Novaya Zemlya. For both areas there was a significant positive trend in thaw days (Svalbard: τ = 0.320, p = 0.005; Novaya Zemlya: τ = 0.325, p = 0.006). The annual thaw days were, however, not correlated between the Svalbard and Novaya Zemlya (r = 0.125).

(B) Relationship between thaw days and snowcover in late May on Admirality Peninsula, western Severny Island, Novaya Zemlya, 2008–2020 (r = −0.72, p < 0.01). Shading shows 95% confidence intervals.

See also Figure S2 and Table S2.

tagged in Oulu have subsequently stayed in Lille Vildmose in spring, and one individual took off from there on the new route to Novaya Zemlya via Örebro and Oulu. The molt migration of taiga bean geese mainly takes place throughout June[39] at a time when almost all pink-footed geese have already left western Finland (GPS-tagged pink-footed geese departed from Oulu on average on 13 May ± SD 2.0 days, range 9–18 May, n = 31 in 2018–2020). However, some pink-footed geese, presumably

non-breeding individuals, might leave later, as corroborated by an observation of a flock of 17 birds in eastern Finland (7 June 2017), including a 2cy neckbanded female, marked in Norway in the same spring. Furthermore, the pink-footed goose has incidentally been observed on pre-breeding sites of taiga bean geese on bogs in eastern Finland, even apparently in a mixed-species pair (A. Piironen, personal communication). Assuming that late immature pink-footed geese joined taiga bean geese, this may have provided a pathway to Novaya Zemlya. Taiga bean geese on molt migration arrive to Novaya Zemlya mainly throughout June,[39] which is still before the initiation date of about half of the nests of pink-footed geese (average 1 June ± SD 6.3 days, range 27 May–17 June, n = 10 in 2018–2020). Further, following taiga bean geese may take the pink-footed geese back to Örebro County in the autumn because this is the route that taiga bean geese take on their return migration from Novaya Zemlya.[39] This possibility implies interspecific transmission of information, a phenomenon also implied in songbirds.[40,41]

Other phenomena may have contributed to the colonization as well. Pink-footed geese may have drifted on adverse westerly winds to Novaya Zemlya during crossing of the Barents Sea on spring migration (which was observed in two tagged individuals, although they eventually returned to Svalbard; Figure 2A).[42] This possibility assumes that pairs settled, found suitable breeding conditions in Novaya Zemlya, and were able to establish a new migration route south and then back.

Population size, demographics, and immigration

Assuming that around half of the geese observed in Oulu in spring migrate to Novaya Zemlya as suggested by the GPS tags, the current Novaya Zemlya population constitutes around 3,000 individuals in spring. Recent resightings of banded geese and GPS tracking suggest that the geese observed in southern Sweden in autumn are almost all Novaya Zemlya birds. Hence, the current autumn population is estimated at approximately 4,000 individuals, i.e., including juveniles. Based on peak autumn counts in Sweden, the Novaya Zemlya population increased annually by 24% between 2000 and 2020, faster than the entire population (2%).

We analyzed the likely demographic variables behind this difference in growth rates by use of an integrated population model (IPM).[43] In recent years, the harvest rate in the total population has reached a level (0.12) that is likely controlling population size,[43] but we can only indirectly estimate the harvest rate for the Novaya Zemlya population. The pink-footed goose is protected in Sweden and Finland but hunted in Denmark (September–January), and we assume that no geese are shot in remote Novaya Zemlya. The mean arrival time of GPS-tagged Novaya Zemlya individuals to Denmark was 13 December; hence, the hunting exposure period was 49 days (SD 23.26). Assuming that the Novaya Zemlya geese were exposed to the same daily level of harvest as the as the entire population while in Denmark during these months, this results in a mean annual adult harvest rate of 0.022 (SD 0.003). At this harvest rate, the Novaya Zemlya population must have had values of natural survival and productivity well above the IPM estimates if it were to follow the observed growth rate without immigration; if natural survival was 0.931 (i.e., IPM estimate), productivity has to be 0.374. If productivity was 0.224 (i.e., IPM estimate), the Novaya

Table 1. Summary of population status, demography, migration distances, and environmental factors that have affected geese in the ranges of the traditional versus newly established population

Variable	Traditional route and breeding area	Newly colonized route and breeding area
	BE - NL - DK - NO - Svalbard	*SE - FI - Novaya Zemlya*
Population status and demography		
Population size	68,000 (spring), 105,000 (autumn)	3,000 (spring), 4,000 (autumn)
Population increase per year (2000–2020)	2%	24%
Survival (IPM)	0.931	Not available
Reproduction (IPM)	0.224	Not available
Proportion of juveniles in autumn, 2019 and 2020	9.0% and 18.4 %	5.2% and 26.6 %
Exchange between routes during 2000–2020	immi- and emigration	1,309 geese net immigration
Migration distances		
Distance from Jutland (wintering area Denmark)	2,450 km	3,050 km
Length of sea crossing	670 km	590 km
Environment		
Recent climate on breeding grounds (number of thaw days in May; 2018–2020)	14 (SD 5) days	4(SD 3) days
Climate change on breeding grounds (trend in thaw days in May)	+10 days over 40 years	+4 days over 40 years
Agricultural change on stopovers and wintering grounds	Cultivation of winter cereal (1990s) and maize (2000s)	None[a]
Habitat destruction	Wetland restoration, Denmark (1990–2010)	None[a]
Organized scaring	Vesterålen, Norway (1990s–2000s)	None[a]
Increased competition with other goose species	Barnacle geese, north Norway, spring (2000s–2010s)	None[a]
Harvest impact (annual adult harvest rate, based on IPM)	0.12	0.02

[a]Based on expert judgment (J. Pessa for Finland and K. Halttunen for Sweden).

Zemlya population could not grow at the observed rate (Figure S3). Thus, the growth of the Novaya Zemlya population was likely partly due to net immigration, resulting from the exchange between the traditional and new route, as evidenced by neckbanded birds. We can estimate this immigration, assuming that the Novaya Zemlya population follows the same year-specific estimated median values of natural survival and productivity as in the IPM, as well as a constant median differential harvest vulnerability, while using the estimated annual harvest rates of the Novaya Zemlya birds. Hence, from 2000 to 2019 we estimated a total net immigration of 1,309 (SD 213; range 615–2,344) birds, or an average annual emigration rate of 0.001 (SD 0.011) from the total flyway population to the Novaya Zemlya population. In Table 1 we summarize the main characteristics of the demography and geography of the two populations, including environmental changes that may have affected the development of the new population.

This case study shows that range expansions can be fast and far (not only gradual and short) when conditions allow and prompt for it, likely facilitated by social information transmission among flocking birds. This probably makes such species more adaptable to a rapidly changing world. Younger individuals copying older individuals has been shown in two recent studies describing changes in migration within the traditional routes. In whooping cranes (*Grus americana*), flocks containing older individuals were more likely to winter about halfway through

the original route than flocks just consisting of young individuals, suggesting that experience drove this innovation.[16] Similarly, a recent northward expansion of a sping staging area by migratory barnacle geese, which has happened in response to global warming and food competition, was largely explained by young individuals switching, copying older individuals.[13,23] Our study shows that these migratory changes can also happen over longer distances and include the formation of new routes and breeding areas outside the traditional annual range, possibly partly through the cultural transmission across (closely related) species.

The observed rapid development is relevant for conservation and population management. On the one hand, breeding numbers at newly colonized sites are small, rendering them potentially vulnerable to adverse conditions. On the other hand, the species as a whole may become more resilient, as individuals face different circumstances by occupying a wider range. Cultural adjustments are likely the first steps in a process that can expose individuals to new selection pressures, favoring specific phenotypes, potentially leading to the prevalence of certain genetic adaptations and ultimately speciation. In the case of pink-footed geese, the colonization has happened over few generations and with an immigration from the original flyway population. Hence, we are still in the early phase of a potential speciation process. Nevertheless, according to conservation definitions, the new Novaya Zemlya group qualifies as a separate

biogeographic population.[44] Our observations also make a case for preserving local biodiversity (i.e., multiple species sharing common foraging areas and roosts) because migratory social species, like geese, ungulates, or whales, can learn new migration routes from each other,[45] thereby enabling rescue from local extirpation in a rapidly changing world.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2023.01.065.

AUTHOR CONTRIBUTIONS

Conceptualization: J.M., K.H.T.S., and B.A.N.; methodology: J.M., K.H.T.S., B.A.N., F.A.J., G.H.J., J.P., and L.N.; investigation: J.M., K.H.T.S., B.A.N., F.A.J., G.H.J., J.P., and L.N.; visualization: J.M. and G.H.J.; project administration: J.M.; supervision: J.M. and B.A.N.; writing – original draft: J.M., K.H.T.S., G.H.J., F.A.J., B.A.N., J.P., and L.N.; writing – review & editing: J.M., K.H.T.S., B.A.N., and F.A.J.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

REFERENCES

1. Gilg, O., Kovacs, K.M., Aars, J., Fort, J., Gauthier, G., Grémillet, D., Ims, R.A., Meltofte, H., Moreau, J., Post, E., et al. (2012). Climate change and the ecology and evolution of Arctic vertebrates. Ann. N. Y. Acad. Sci. *1249*, 166–190. https://doi.org/10.1111/j.1749-6632.2011.06412.x.

2. Wilcove, D.S., and Wikelski, M. (2008). Going, Going, Gone: Is Animal Migration Disappearing. PLoS Biol. *6*, e188. https://doi.org/10.1371/journal.pbio.0060188.

3. Bairlein, F. (2016). Migratory birds under threat. Science *354*, 547–548. https://doi.org/10.1126/science.aah6647.

4. Lameris, T.K., Hoekendijk, J., Aarts, G., Aarts, A., Allen, A.M., Bienfait, L., Bijleveld, A.I., Bongers, M.F., Brasseur, S., Chan, Y.C., et al. (2021). Migratory vertebrates shift migration timing and distributions in a warming Arctic. Anim. Migrat. *8*, 110–131. https://doi.org/10.1515/ami-2020-0112.

5. Saalfeld, S.T., and Lanctot, R.B. (2017). Multispecies comparisons of adaptability to climate change: A role for life-history characteristics? Ecol. Evol. *7*, 10492–10502. https://doi.org/10.1002/ece3.3517.

6. Lameris, T.K., Scholten, I., Bauer, S., Cobben, M.M.P., Ens, B.J., and Nolet, B.A. (2017). Potential for an Arctic-breeding migratory bird to adjust spring migration phenology to Arctic amplification. Global Change Biol. *23*, 4058–4067. https://doi.org/10.1111/gcb.13684.

7. Winkler, D.W., Gandoy, F.A., Areta, J.I., Iliff, M.J., Rakhimberdiev, E., Kardynal, K.J., and Hobson, K.A. (2017). Long-Distance Range Expansion and Rapid Adjustment of Migration in a Newly Established Population of Barn Swallows Breeding in Argentina. Curr. Biol. *27*, 1080–1084. https://doi.org/10.1016/j.cub.2017.03.006.

8. Dufour, P., de Franceschi, C., Doniol-Valcroze, P., Jiguet, F., Guéguen, M., Renaud, J., Lavergne, S., and Crochet, P.-A. (2021). A new westward migration route in an Asian passerine bird. Curr. Biol. *31*, 5590–5596.e4. https://doi.org/10.1016/j.cub.2021.09.086.

9. Berthold, P., Helbig, A.J., Mohr, G., and Querner, U. (1992). Rapid microevolution of migratory behaviour in a wild bird species. Nature *360*, 668–670. https://doi.org/10.1038/360668a0.

10. Bearhop, S., Fiedler, W., Furness, R.W., Votier, S.C., Waldron, S., Newton, J., Bowen, G.J., Berthold, P., and Farnsworth, K. (2005). Assortative Mating as a Mechanism for Rapid Evolution of a Migratory Divide. Science *310*, 502–504. https://doi.org/10.1126/science.1115661.

11. Newton, I. (2008). The migration ecology of birds (Elsevier).

12. Németh, Z., and Moore, F.R. (2014). Information acquisition during migration: A social perspective. Auk *131*, 186–194. https://doi.org/10.1642/auk-13-195.1.

13. Oudman, T., Laland, K., Ruxton, G., Tombre, I., Shimmings, P., and Prop, J. (2020). Young birds switch but old birds lead: How barnacle geese adjust migratory habits to environmental change. Front. Ecol. Evol. *7*, 502. https://doi.org/10.3389/fevo.2019.00502.

14. Sutherland, W.J. (1998). Evidence for flexibility and constraint in migration systems. J. Avian Biol. *29*, 441–446. https://doi.org/10.2307/3677163.

15. Buchholz, R., Banusiewicz, J.D., Burgess, S., Crocker-Buta, S., Eveland, L., and Fuller, L. (2019). Behavioural research priorities for the study of animal response to climate change. Anim. Behav. *150*, 127–137. https://doi.org/10.1016/j.anbehav.2019.02.005.

16. Teitelbaum, C.S., Converse, S.J., Fagan, W.F., Böhning-Gaese, K., O'Hara, R.B., Lacy, A.E., and Mueller, T. (2016). Experience drives innovation of new migration patterns of whooping cranes in response to global change. Nat. Commun. 7, 12793. https://doi.org/10.1038/ncomms12793.

17. Madsen, J., Kuijken, E., Meire, P., Cottaar, F., Haitjema, T., Nicolaisen, P.I., Bønes, T., and Mehlum, F. (1999). In Pink-footed Goose Anser brachyrhynchus: Svalbard In Goose populations of the Western Palearctic: A review of status and distribution, J. Madsen, G. Cracknell, and A.D. Fox, eds. (National Environmental Research Institute), pp. 82–93.

18. Tombre, I.M., Høgda, K.A., Madsen, J., Griffin, L.R., Kuijken, E., Shimmings, P., Rees, E., and Verscheure, C. (2008). The onset of spring and timing of migration in two arctic nesting goose populations: the pink-footed goose Anser bachyrhynchus and the barnacle goose Branta leucopsis. J. Avian Biol. 39, 691–703. https://doi.org/10.1111/j.1600-048X.2008.04440.x.

19. Drent, R., Both, C., Green, M., Madsen, J., and Piersma, T. (2003). Payoffs and penalties of competing migratory schedules. Oikos 103, 274–292. https://doi.org/10.1034/j.1600-0706.2003.12274.x.

20. Therkildsen, O.R., and Madsen, J. (2000). Energetics of feeding on winter wheat versus pasture grasses: a window of opportunity for winter range expansion in the pink-footed goose Anser brachyrhynchus. Wildl. Biol. 6, 65–74.

21. Clausen, K.K., Madsen, J., Nolet, B.A., and Haugaard, L. (2018). Maize stubble as foraging habitat for wintering geese and swans in northern Europe. Agric. Ecosyst. Environ. 259, 72–76. https://doi.org/10.1016/j.agee.2018.03.002.

22. Clausen, K.K., and Madsen, J. (2016). Philopatry in a changing world: response of pink-footed geese Anser brachyrhynchus to the loss of a key autumn staging area due to restoration of Filsø Lake, Denmark. J. Ornithol. 157, 229–237. https://doi.org/10.1007/s10336-015-1271-9.

23. Tombre, I.M., Oudman, T., Shimmings, P., Griffin, L., and Prop, J. (2019). Northward range expansion in spring-staging barnacle geese is a response to climate change and population growth, mediated by individual experience. Global Change Biol. 25, 3680–3693. https://doi.org/10.1111/gcb.14793.

24. Madsen, J., Williams, J.H., Johnson, F.A., Tombre, I.M., Dereliev, S., and Kuijken, E. (2017). Implementation of the first adaptive management plan for a European migratory waterbird population: The case of the Svalbard pink-footed goose Anser brachyrhynchus. Ambio 46, 275–289. https://doi.org/10.1007/s13280-016-0888-0.

25. Madsen, J. (2001). Spring migration in pink-footed geese Anser brachyrhynchus and consequences for spring fattening and fecundity. Ardea 89 (Supplement), 43–55.

26. Clausen, K.K., Madsen, J., Cottaar, F., Kuijken, E., and Verscheure, C. (2018). Highly dynamic wintering strategies in migratory geese: Coping with environmental change. Global Change Biol. 24, 3214–3225. https://doi.org/10.1111/gcb.14061.

27. Klaassen, M., Hahn, S., Korthals, H., and Madsen, J. (2017). Eggs brought in from afar: Svalbard-breeding pink-footed geese can fly their eggs across the Barents Sea. J. Avian Biol. 48, 173–179. https://doi.org/10.1111/jav.01364.

28. Wylegała, P., Krąkowski, B., and Nowak, B. (2018). Występowanie gęsi krótkodziobej Anser brachyrhynchus w Wielkopolsce w latach 1997–2017. Ptaki Wielkopolski 5, 60–65.

29. Schreven, K.H.T., Stolz, C., Madsen, J., and Nolet, B.A. (2021). Nesting attempts and success of Arctic-breeding geese can be derived with high precision from accelerometry and GPS-tracking. Anim. Biotelemetry 9, 25. https://doi.org/10.1186/s40317-021-00249-9.

30. Jensen, G.H., Madsen, J., Johnson, F.A., and Tamstorf, M.P. (2014). Snow conditions as an estimator of the breeding output in high-Arctic pink-footed geese Anser brachyrhynchus. Polar Biol. 37, 1–14. https://doi.org/10.1007/s00300-013-1404-7.

31. Bauer, K.M., and Glutz von Blotzheim, U.N. (1968). Handbuch der Vögel Mitteleuropas – Band 2 (Akademische Verlagsgesellschaft).

32. Bent, A.C. (1925). Life histories of North American wildfowl: order Anseres (Govt. Print. Off.).

33. Kalyakin, V.N. (1999). Birds of Novaya Zemlya region and Franz Josef Land. Material for the distribution of birds in the Urals, the pre-Urals and Western Siberia (Smamey collection) (Yekaterinburg, Russia: Yekaterinburg publisher).

34. Kalyakin, V.N. (2001). New data on bird fauna of Novaya Zemlya archipelago and Franz-Josef Land. Ornithologia 29, 8–28.

35. Spitsyn, V.M., Glazov, P.M., Anufriev, V.V., and Rozenfeld, S.B. (2020). An updated annotated list of birds of the Novaya Zemlya archipelago. Biharean Biologist 14, 98–104.

36. Jensen, R.A., Madsen, J., O'Connell, M., Wisz, M.S., Tømmervik, H., and Mehlum, F. (2008). Prediction of the distribution of Arctic-nesting pink-footed geese under a warmer climate scenario. Global Change Biol. 14, 1–10. https://doi.org/10.1111/j.1365-2486.2007.01461.x.

37. Piironen, A., Fox, A.D., Kampe-Persson, H., Skyllberg, U., Therkildsen, O.R., and Laaksonen, T. (2022). When and where to count? Implications of migratory connectivity and nonbreeding distribution to population censuses in a migratory bird population. Population Ecology. https://doi.org/10.1002/1438-390X.12143.

38. Nilsson, L., de Jong, A., Heinicke, T., and Sjöberg, K. (2009). Satellite tracking of Bean Geese Anser fabalis fabalis and A. f. rossicus from spring staging areas in northern Sweden to breeding and moulting areas. Ornis Svec. 29, 184–189.

39. Piironen, A., Paasivaara, A., and Laaksonen, T. (2021). Birds of three worlds: moult migration to high Arctic expands a boreal-temperate flyway to a third biome. Mov. Ecol. 9, 47. https://doi.org/10.1186/s40462-021-00284-4.

40. Seppänen, J.T., and Forsman, J.T. (2007). Interspecific Social Learning: Novel Preference Can Be Acquired from a Competing Species. Curr. Biol. 17, 1248–1252. https://doi.org/10.1016/j.cub.2007.06.034.

41. Farine, D.R., Aplin, L.M., Sheldon, B.C., and Hoppitt, W. (2015). Interspecific social networks promote information transmission in wild songbirds. Proc. Biol. Sci. 282, 20142804. https://doi.org/10.1098/rspb.2014.2804.

42. Geisler, J., Madsen, J., Nolet, B.A., and Schreven, K.H.T. (2022). Sea crossings of migratory pink-footed geese: seasonal effects of winds on flying and stopping behaviour. J. Avian Biol. 2022, e02985. https://doi.org/10.1111/jav.02985.

43. Johnson, F.A., Zimmerman, G.S., Jensen, G.H., Clausen, K.K., Frederiksen, M., and Madsen, J. (2020). Using integrated population models for insights into monitoring programs: An application using pink-footed geese. Ecol. Model. 415, 108869. https://doi.org/10.1016/j.ecolmodel.2019.108869.

44. AEWA (2005). Proposal for guidance on the definition of biogeographical populations of waterbirds In AEWA_Secretariat, ed. 3rd Session of the Meeting of the Parties to the Agreement on the Conservation of African-Eurasian Migratory Waterbirds, 23 – 27 October 2005 (Secretariat of the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA)).

45. Cohen, E.B., and Satterfield, D.A. (2020). 'Chancing on a spectacle:' co-occurring animal migrations and interspecific interactions. Ecography 43, 1657–1671. https://doi.org/10.1111/ecog.04958.

46. Pujolar, J.M., Dalén, L., Hansen, M.M., and Madsen, J. (2017). Demographic inference from whole-genome and RAD sequencing data suggests alternating human impacts on goose populations since the last ice age. Mol. Ecol. 26, 6270–6283. https://doi.org/10.1111/mec.14374.

47. Madsen, J., Tjørnløv, R.S., Frederiksen, M., Mitchell, C., and Sigfússon, A.T. (2014). Connectivity between flyway populations of waterbirds: assessment of rates of exchange, their causes and consequences. J. Appl. Ecol. 51, 183–193. https://doi.org/10.1111/1365-2664.12183.

48. Ganter, B., and Madsen, J. (2001). An examination of methods to estimate population size in wintering geese. Hous. Theor. Soc. *48*, 90–101. https://doi.org/10.1080/00063650109461206.

49. Bolker, B.M. (2008). Ecological models and data in R (Princeton University Press).

50. Nilsson, L., and Kampe-Persson, H. (2020). Changes in numbers of staging and wintering geese in Sweden: 1977/78 – 2019/20. Wildfowl *70*, 107–126.

51. Clausen, K.K., Balsby, T.J.S., Goma, V., and Madsen, J. (2019). Using re-sighting data to estimate population size of Pink-footed Geese (Anser brachyrhynchus). Ornis Fenn. *96*, 112–123.

52. Clausen, K.K., Schreven, K.H.T., and Madsen, J. (2020). Effects of capture and marking on the behaviour of moulting Pink-footed Geese Anser brachyrhynchus on Svalbard. Wildfowl *70*, 13–29.

53. Brockwell, P.J., and Davis, R.A. (1991). Time Series: Theory and Methods, 2nd Edition (Springer Verlag).

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Survey data	Zenodo	https://doi.org/10.5281/zenodo.7501015
Software and algorithms		
R Statistical Software	R Project	https://www.r-project.org
Contributed R packages	Comprehensive R Archive Network (CRAN)	https://cran.r-project.org
R Code	Zenodo	https://doi.org/10.5281/zenodo.7501015

RESOURCE AVAILABILITY

Lead contact
Further information and requests should be directed to and will be fulfilled by the lead contact, Jesper Madsen (jm@ecos.au.dk).

Materials availability
This study did not generate new unique reagents.

Data and code availability

- All data used for demographic and climate data analyses in this paper has been deposited at Zenodo and is publicly available as of the date of publication. DOIs are listed in the key resources table. GPS-GSM tracking data on pink-footed geese are available at www.movebank.org (ID: 676425507). The Capture-Mark-Resighting data for pink-footed geese that support the findings of this study are deposited in www.geese.org and are available from the lead contact upon reasonable request.
- All original code used for demographic and climate data analyses has been deposited at Zenodo and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study population
The pink-footed goose is an Arctic breeding species which is divided into two flyway populations: a western population breeding in Iceland and East Greenland and wintering in the British Isles, and an eastern population breeding in Svalbard and wintering in Denmark, the Netherlands and Belgium. The two populations are genetically distinct with low degree of gene flow in both directions,[46] in concordance with observations of low rates of exchange of marked individuals, suggesting that the two populations are almost demographically separate.[47] Both the western and the eastern populations have increased during the last 4–5 decades, in the late 2010s reaching a total of approximately 500,000 (https://app.bto.org/webs-reporting/numbers.jsp) and approximately 80,000 individuals (Figure 1A), respectively. The focal Svalbard-breeding population has remained relatively stable during the last decade. This is largely a result of the implementation of an internationally-coordinated harvest-management program with the objective to maintain a stable population in order to reduce damage to agricultural crops and vulnerable tundra vegetation.[24]

METHOD DETAILS

Field surveys
Monitoring of the population size of the Svalbard-breeding pink-footed geese has been coordinated since 1991, based on synchronized counts carried out by a network of experienced observers on all known staging areas on specific dates in November and May (since 2012) (https://calm-dune-07f6d4603.azurestaticapps.net/) and supplemented by citizen science portals (www.dofbasen.dk, www.artsobservasjoner.no). Productivity of the population has been monitored annually since 1981, using counts of juveniles versus older birds in randomly selected flocks observed on the autumn staging grounds in Norway, Denmark, the Netherlands and Belgium; juveniles were discriminated based on plumage characteristics. The age counts were done by experienced observers (annually between 12 October and 4 November).[48] In October 2019 and 2020, productivity was also recorded for the Novaya Zemlya population during their stay in Örebro County, Sweden (Table S2). It should be noted that the proportion of juveniles from Sweden are pre-harvest estimates, whereas some harvest will have occurred when the age counts are carried out in Norway, Denmark, the Netherlands

and Belgium. For both populations the proportion of juveniles was assessed using maximum likelihood estimation. We used a generalized linear model with a logit-link function using a beta-binomial error distribution for the proportion of juveniles.[49] A beta-binomial error distribution was used to account for over-dispersion in the counts.

In Sweden, regular mid-monthly counts of geese have been undertaken in south Sweden in October, November and January since 1977/78 covering all known staging areas for geese by a network of experienced observers[50] and supplemented by accidental observations (www.artportalen.se). In Finland, periodical counts of geese have been undertaken in April and May by a network of experienced observers in the Oulu staging area since 1978. Because the pink-footed goose was a very rare migrant in Finland until 2000, all observations have been reported to the bird observation databases (www.tiira.fi and www.birdlife.fi/havainnot/harvinaisuudet/rk/). Weekly targeted pink-footed goose counts were carried out during peak migration time in April and May since 2000.

CMR and GPS-tagging

A Capture-Mark-Recapture (CMR) program using individually coded neckbands has been operating since 1990. Almost on an annual basis, pink-footed geese were caught, either using cannon-netting on the spring staging grounds in Denmark and Norway or rounding up of flightless flocks during their molt of flight feathers on the Svalbard breeding grounds. Geese were aged and sexed based on plumage characteristics and cloacal examination. Resightings of banded geese, recording of their status (mated/unmated) and breeding output (number of juveniles in the family) were carried out in the field by a network of voluntary and professional observers on the wintering grounds in Denmark, the Netherlands and Belgium as well as on the stopover sites in Norway.[47] Since 1990, a total of 4950 geese have been marked with neckbands, including 71 with GPS-tags (of which 21 were tagged in Finland in 2018 and 2019). Neckbands have produced a total of 414,000 resightings. All marking data and resightings have been stored online on www.geese.org. Based on the CMR program, the number of banded individuals alive each spring can be estimated.[51] If we add the number of newly marked individuals in the spring or summer of a given year, the total number of marked geese in the population in the subsequent autumn can be calculated. The proportion of banded geese going to Sweden and Finland in the autumn and spring, respectively, was calculated as the number of marked individuals resighted in the two countries divided by the total number of marked geese alive in a given season of a year. The consistency of marked individuals using the new Swedish-Finnish migration route was expressed by the number of times they used this alternative route during their life time (number of years observed). Due to the low numbers of resightings, it was not possible to estimate resighting probability as a measure of observer effort in the calculations. However, in both Sweden and Finland there is a long tradition for CMR programs particularly with regard to taiga bean goose since the 1980s, with active observer networks in the field searching for neckbanded geese. Thus, the sites used by bean geese and pink-footed geese have been regularly covered for the last three decades. Therefore, we assume that the observer effort has been stable over time, but the number of banded individuals and the proportion of banded geese using the new flyway may be too low.

On 28 April 2018, 27 April and 1 May 2019, we caught pink-footed geese in Tyrnävä, south of Oulu, western Finland (64.83 N, 25.56 E) by use of a cannon-net. In 2018, we tagged 10 and in 2019 11 geese, primarily adult females but also two first-winter males and three adult males. We used solar-powered GPS-GSM transmitter neckbands, type OrniTrack-N38 (Ornitela UAB, Lithuania) with a weight of 38 g (c. 1.5% of body mass). At high battery voltage, the tags recorded a GPS-fix every 10 min.[29] From studies of newly tagged geese caught during molt in Svalbard it is observed that the geese will be temporarily affected behaviorally (particularly more preening activity) by the neckbands but that the effect will be minimal less than one week after marking.[52]

Temperatures and snow cover on Svalbard and Novaya Zemlya

For Svalbard it has been shown that there is a negative relation between the number of days with temperatures above 0° C (thaw days) in May and snow cover in late May.[30] May temperatures, as a proxy for the onset of spring/snow melt, were examined for Svalbard and Novaya Zemlya for the period 1981–2020. For Svalbard mean daily temperatures were derived from Ny-Ålesund and Svalbard Airport meteorological stations, where a mean between the two stations was used. For Novaya Zemlya ERA5-Land model based temperature estimates were derived from a mean of two points on Severny Island, Novaya Zemlya (75.1 N, 55.8 E and 74.1 N, 55.4 E) where nest sites of GPS-tagged pink-footed geese had been identified (https://cds.climate.copernicus.eu/cdsapp#!/home) (Table S2). A Mann-Kendall trend test was used to determine whether or not a trend exists in the two time series of thaw days in May. Furthermore, the year to year correlation between the two areas was investigated by de-trending the two time series and using a cross correlation function.[53]

To analyze if thaw days and snow cover were also negatively related on Novaya Zemlya, distribution of snow cover was analyzed using MODIS satellite images with a resolution of 500 m (MODIS/Terra Surface Reflectance 8-Day L3 Global 500m from https://earthdata.nasa.gov/). These images contain the best possible observation during an 8-day period (centered around day 145/25 May, regarded as the time of egglaying) as selected on the basis of high observation coverage, low view angle, the absence of clouds or cloud shadow, and aerosol loading. We analyzed snow cover for the Admirality Peninsula and mainland east of the peninsula (502 km^2 non-glaciated land area), western Severny Island (Figure S2), which has been identified as a nesting area for pink-footed geese (Figure 2C). Across the three years of tracking, spring arrival times of GPS-tagged geese on Severny Island, Novaya Zemlya and on Svalbard were 19 May (sd 2.8 days) and 16 May (sd 4.7 days) (two-tailed t-test, p > 0.05), respectively. This suggests that using 25 May for analysis of snow conditions is representative for the onset of nesting in both areas.

Snow cover classification was done using visually interpreted training points and a maximum likelihood classification. No less than 50 points were used for the class's snow and water, whereas it was only possible to get 15 points for the land class, due to high

degree of snow cover. However, for the years 2009, 2014, 2017 and 2019 the classification was performed for only snow and water, as no land class pixels where identified (using the spectral profile). Accuracy assessment points independent from the training points were selected using visual interpretation of the scenes. The same number of points was used as for the training points. A standard confusion matrix was constructed for each classification result, resulting in a classification accuracy between 93-100%. The correlation between thaw days and snow cover was analyzed using Pearson's correlation coefficient.

QUANTIFICATION AND STATISTICAL ANALYSIS

Estimation of growth rates

A finite, mean growth rate based on autumn count data from Sweden (peak autumn numbers between 2000-2020; Table S3) was calculated using a log-linear model:

$$log(N_t) = \alpha + \beta(t) + \varepsilon_t$$

$$\varepsilon_t \sim Normal(0, \sigma)$$

where N = peak numbers and t = year. The estimated, average growth rate per year is then $\overline{\lambda} = e^{\beta + \frac{\sigma^2}{2}}$. The growth rate of the total population, including those migrating to Novaya Zemlya, was derived from an integrated population model (IPM),[43] and arises from year-specific values of natural survival rate (θ_t, mean of 0.931, sd 0.024), reproductive rate (pre-hunting ratio of young to adults) (r_t, mean of 0.224, sd 0.011), adult harvest rate (h_t, mean of 0.085, sd 0.009) and a constant ratio of young to adult harvest rates (referred to as differential vulnerability) of d = 2.083 (sd 0.172). The population state equation for the IPM is:

$$N_{n,t+1} = \left[N_{n,t}\left(1 - \frac{r_t}{(1+r_t)}\right)\theta_t(1 - h_t) + N_{n,t}\frac{r_t}{(1+r_t)}\theta_t(1 - dh_t) \right](1 + r_{t+1})$$

where, N_n is autumn population size.

Length of exposure to hunting and harvest rate

Exposure of the Novaya Zemlya population to hunting in Denmark was derived using the mean number of days between the first observation in Denmark of GPS-marked geese until 31 January (when the hunting season closes). In Denmark, the birds from the Novaya Zemlya population were assumed to be hunted at the same rate as the total population. In Denmark, reporting of harvest is mandatory and compiled by the Danish Bag Statistics. Furthermore, wings are submitted to a national wing survey, which gives a measure of the temporal distribution of the bag through the hunting season. The temporal distribution was used to calculate the annual harvest rate of the Novaya Zemlya population during its stay in Denmark (h_t^r). This was done by multiplying the total annual harvest rate in Denmark (h_t^d) with the annual proportion of wings retrieved from the mean arrival date in Denmark until 31 January (α_t):

$$h_t^r = h_t^d \alpha_t$$

To account for uncertainty in these estimates, the annual harvest rates of the Novaya Zemlya population were described as beta-distributed random variables $h_t^r \sim beta(a_t, b_t)$, using the methods of moments to estimate the beta parameters. The annual proportion of wings retrieved from the mean arrival date in Denmark until 31 January (α_t) was described as binomial-distributed random variables $\alpha_t \sim binomial(W_t, w_t)$, where W_t is the total number of wings received during the Danish hunting season and w_t is the number of wings received from the mean arrival date in Denmark until 31 January.

Natural survival and productivity under varying and fixed harvest rates

To investigate what changes in natural survival rate and reproductive rate are needed to duplicate the observed growth rate (λ) in Sweden, the following equation was solved:

$$\lambda = \Delta_1 \overline{\theta}[(1 - \overline{h}^r) + \Delta_2 \overline{r}(1 - d\overline{h}^r)]$$

for $\Delta_{1,2}$ by cycling through potential values of both Δ_1 (0.05-$\overline{\theta}^{-1}$, by increments of 0.05) and Δ_2 (0–2, by increments of 0.02), while using the estimated mean harvest rate of the Novaya Zemlya population aged >1 years (h^r, mean of 0.022). We set θ and r at the mean of year-specific median values from the IPM and d was set at the median constant. The outcome of the analysis is shown in Figure S3.

Estimation of growth rates and net immigration/emigration

We estimated the level of emigration/immigration needed to replicate the observed growth rate in Sweden. This was done using year-specific values of θ_t and r_t, a constant median d derived from the IPM and the estimated annual harvest rate of the Novaya Zemlya population in Denmark. To account for uncertainty in the estimates, the survival rate was described as a beta-distributed random variable $\theta_t \sim beta(a_t, b_t)$, using the method of moments to estimate the beta parameters, based on year specific median values of θ_t and sd_t from the IPM. The reproductive rates were described as a gamma-distributed random variable $r_t \sim gamma\left(\frac{\mu^2}{\sigma t}, \frac{\mu}{\sigma t}\right)$,

using the method of moments to estimate the shape and rate parameters, based on year-specific median values of r_t and sd_t from the IPM. Annual mean values of θ_t, r_t and h_t^r are presented in Table S4.

Using these parameters, the pre-harvest autumn population size in Sweden ($N_{n,t}$) was projected for a 20-year period, starting from the population size in year 2000 (using the population state equation from the IPM).

At the beginning of each annual cycle, the population size was re-set at the observed year-specific count, which then allowed us to compare the annual differences between the observed population size and the projected population size; hence the amount of migration needed to arrive at the observed population size.

The estimated annual migration needed to reach the observed number of geese in a given year is presented in Table S3. To arrive at a net migration across years, the replicates of each year's number of migrants was summed across years for each replicate. Thus, for each replicate, this represents the net migration over the time frame (Figure S4). The estimation of net exchange is conditional on annual productivity estimates matching between the two breeding areas, which remains uncertain. Finally, we estimated the emigration rate by taking the geometric mean over years of the absolute net migration divided by the flyway population in November.