

Bean Goose migration shows a long-term temporal shift to earlier spring, but not to later autumn migration in Finland

Pihla Kortesalmi, Salli Pääkkönen, Janne K. Valkonen & Ossi Nokelainen*

P. Kortesalmi, S. Pääkkönen, J. K. Valkonen, O. Nokelainen, Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

O. Nokelainen, Open Science Centre, University of Jyväskylä, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

**Corresponding author's e-mail: ossi.nokelainen@jyu.fi*

Received 3 June 2022, accepted 24 March 2023



Climate change can challenge the inherited or learned behavioural patterns that were useful in the past. In particular, it may change the spatio-temporal dynamics of migratory behaviour in birds. Here, we explored a 40-year-long time series of Bean Goose (*Anser fabalis*) observations using a citizen science database (tiira.fi – BirdLife Finland) to link the timing of the migration across last forty years and with the large-scale temporal weather fluctuation described by an index of North Atlantic Oscillation (NAO). During 1978–2018, the peak of spring migration of the Bean Goose has advanced approximately a month, whereas the timing of autumn migration has remained more similar across the years. The NAO index was associated only with spring migration. Strong temporal changes of the Bean Goose migration are evident as they adjust their migratory behaviour to changing spring conditions.

1. Introduction

Migration is an adaptation to a seasonally changing environment (Herrera 1978). It is a widespread phenomenon throughout animal kingdom and is known to occur among many taxa such as birds, fish, insects, and mammals (Shaw & Couzin 2013). Migratory birds move between breeding and wintering grounds following availability of resources (Cox 2010). In the northern hemisphere, where winter weather conditions limit the availability of resources, birds move to lower latitudes in autumn and return when the resources in the

north become available again (Newton & Brockie 2008). Spring migration back to breeding areas may increase the breeding success of migrants due to more resources (*i.e.*, food and nest sites) available and possibly less competition in north (Newton & Dale 1996). Generally, similar resource-seeking migratory behaviour among birds is globally widespread and exists in all continents (Newton & Brockie 2008).

Climate change can challenge the inherited or learned behavioural patterns that were useful in the past, such as spatial as well as temporal dynamics of migratory behaviour in birds (Mayor

et al. 2017). Global warming has shortened the period with cold temperatures in the northern hemisphere (IPCC 2018) and as a consequence, many birds return to their breeding sites earlier and leave to the south later (Saino *et al.* 2011, Kolářová *et al.* 2017, Mayor *et al.* 2017, Usui *et al.* 2017, Nuijten *et al.* 2020). Temperature affects the timing of migration by influencing the availability of resources such as food and water (Newton & Brockie 2008). Also, local weather conditions (*e.g.*, wind, precipitation) impact the timing of migration in birds (Erni *et al.* 2002) and as many species use local weather as a cue to migrate, migration is broadly affected by dynamic high- and low-pressure weather systems along the migration route (Dokter *et al.* 2011).

The ability to respond to changing environmental conditions, however, varies between species (Usui *et al.* 2017). Previous studies have reported the connection between climate change and the migratory behaviour of birds (Saino *et al.* 2011, Usui *et al.* 2017), and especially a trend of advancing spring migration has been recorded in many species (Kolářová *et al.* 2017). Short-distance migrants are usually more responsive to climate change than long-distance migrants (Kolářová *et al.* 2017) because short-distance migrants can follow the changing temperatures while long-distance migrants use more endogenous cues such as circadian rhythm to time their migration (Mayor *et al.* 2017, Usui *et al.* 2017). Population declines have been observed, particularly in migratory birds that do not adapt to increasing spring temperature and advancing phenology (Møller *et al.* 2010). Therefore, information on how well species adapt their migration behaviour on long-term is important for understanding species' adaptability to large-scale environmental changes.

Here, we examined the Bean Goose (*Anser fabalis*) migration timing in Finland using observation data collected in southern Finland over the last 40 years. Bean geese observed in Finland belong to two subspecies, the Taiga Bean Goose (*Anser fabalis fabalis*) and the Tundra Bean Goose (*Anser fabalis rossicus*). Both were included in the study and were not separated in the analysis (as separating them may be unreliable, refer to methods).

The Taiga Bean Goose starts its spring migration in February from the western Baltic Sea

region, where most of them winter (Heinicke *et al.* 2018). The birds arrive in Finland between March and May. The Taiga Bean Goose breeds mostly in north-west Russia, northern Sweden, and central and northern areas of Finland (Piironen *et al.* 2022a). The birds coming to breed in Finland or passing through the country migrate across entire Finland. The autumn migration of the Taiga Bean Goose occurs between late August and October.

The Tundra Bean Goose migrates across Finland later than the Taiga Bean Goose both in spring and autumn (Piironen *et al.* 2022b). The spring migration occurs between April and May when the birds migrate through southeast Finland to their main breeding grounds in northern Russia. The autumn migration occurs between late September and October. As migrants of the Bean Goose pass through southern Finland annually, long-term migration observations are valuable to be studied from a temporal perspective from this location.

We set out to answer two questions. Our first research question was whether the timing of the Bean Goose migration has changed between the years 1978–2018. We hypothesized that due to warming climate, the spring migration of the Bean Goose has advanced (*i.e.*, masses arriving earlier) and the timing of the autumn migration delayed, as short-distance migrants have been shown to be able to respond to the prevailing climate conditions (Saino *et al.* 2011). The second research question was whether the large-scale weather conditions, described by North Atlantic Oscillation (NAO), during the migration period are linked to the timing of migration. NAO dictates the climatic conditions in Europe (see further methods; Hurrell 1995) where wintering and breeding grounds of the Bean Goose are mostly located (Piironen *et al.* 2022a, Piironen *et al.* 2022b). Thus, it may indirectly influence the timing of migration (Newton & Dale 1996, Erni *et al.* 2002).

2. Materials and methods

2.1. Long-term migration data

We used data from a citizen science bird observation database Tiira of BirdLife Finland (tiira.fi). Tiira is an online portal where anyone

can report their observations. We used all the Bean Goose observations (*i.e.*, *A. f. fabalis* and *A. f. rossicus* were pooled, as identifying them from distance is unreliable) that were made in southern Finland (Kymenlaakso, Southwest Finland, Satakunta, and Uusimaa) between 1.1.1978 and 31.12.2018. We used all the information that is mandatory to report on each observation: date of observation, number of birds observed, location and species. The status of observed birds, *e.g.*, migrating or local, can also be reported but this information is voluntary and not included in all observations. We used all observations, disregarding their status. We assumed the observed birds in our study area in southern Finland to be mostly migrating as their breeding grounds are located further north. This might, however, cause some inaccuracies. If a large group stays in the area for a longer time, it might be observed and counted several times.

Spring and autumn migration periods were processed as separate datasets. Timespan was

chosen as 1.1.–30.5. for spring migration and 1.8.–31.12. for autumn migration. We converted calendar dates to Julian dates (DOY, day of year) to make data easier to handle statistically. We decided to include the observations only from southern Finland to reduce the possibility of counting the same individuals more than once along their migration route as they move through Finland. Also, including only the observations from southern Finland prevents counting the birds that have already arrived at their breeding grounds in central or northern Finland. The number of observations was 34,269 in the spring and 13,877 in the autumn. The sum of the birds observed was 3,613,619 in the spring and 678,150 in the autumn. The mean flock size (number of geese in one observation) was 89.1 (SD± 320). We studied the change in the timing of early, middle, and late phases of migration using dates when 5%, 50%, and 95% of the cumulative sum of migrants was reached (*i.e.*, temporal distribution of masses, rather than early or late observations, Fig. 1).

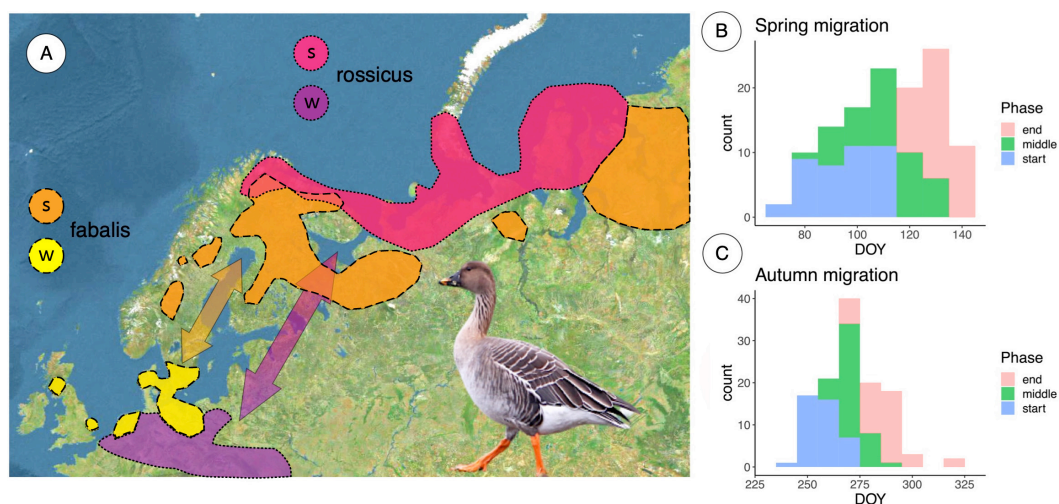


Fig. 1. The western distribution of Bean Goose populations (A). The map is modified for illustrative purposes from Heinicke *et al.* 2018 and should only be considered to highlight the main distribution of the Taiga Bean Goose (*Anser fabalis rossicus*) in comparison to Tundra Bean Goose (*Anser fabalis fabalis*). The map shows summer (s) and winter (w) distributions for *A. f. fabalis* (orange, yellow) and *A. f. rossicus* (pink, purple). Noteworthy, the location of Finland is central to bean goose migration routes (in between the two arrows). In our study however, we focused on both sub-species together, because their separation is not reliable from migrating individuals in our dataset as majority migrates through north Europe. The timing of migration in the data characterized by histogram plots for spring (B) and autumn (C). Analysis included observations from southern Finland (regions Kymenlaakso, Southwest Finland, Satakunta and Uusimaa). The change in the timing of early, middle, and late phases of migration was observed using 5th (start), 50th (middle), and 95th (end) percentiles of the observed migrants, respectively. DOY (here: day of year) refers to Julian days (1.1.= 1). The Taiga Bean Goose (Photo taken on Lista, Norway by Marton Bernsten) image was modified from Wikimedia Commons and used under CC BY-SA 3.0 licence.

Citizen data typically contains weaknesses that may reduce its reliability (Callaghan *et al.* 2019). Data is not collected systematically, and observation effort is usually spatially and temporally unevenly distributed. We studied the timing of migration, and therefore temporal shifts in observation efforts may affect our results. In our analysis, we assumed that the activity of bird-watchers has not changed considerably across the years so that it would have resulted in differential detectability of a large waterfowl, which bird-watchers have been traditionally used to identify. Another weakness in this data is the impossibility of controlling the expertise of the birdwatchers and therefore all the identifications may not be correct. Due to large number of data points, we estimated that the patterns of migration were not substantially impacted by the incorrect observations.

2.2. Large-scale weather conditions

North Atlantic Oscillation (NAO) is a large-scale atmospheric circulation pattern that describes the weather oscillation (*i.e.*, atmospheric pressures, wind directions, precipitation) on the Northern Atlantic Ocean (Hurrell 1995). It is measured by an index that describes the monthly difference in atmospheric pressure at sea level between the Icelandic Low and the Azores High. For example, positive NAO correlates with warm and moist winters in Europe, and negative NAO correlates with cold and dry winters.

We studied the effect of large-scale weather phenomena on long-term migration dynamics by examining the relationships between the timing of migration and the NAO index. We used the daily NAO index to calculate the average NAO for the spring and autumn migration periods for each year. Average NAO between January and May was used for spring migration and average NAO between August and December for autumn migration. Several studies have found a connection between the average NAO index during the migration period and the timing of the migration (Gunnarsson *et al.* 2006, Van Buskirk *et al.* 2009, Kim *et al.* 2015). NAO index we used was provided by the Climate Analysis Section, NCAR, Boulder, USA. Measuring points are in Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland.

2.3. Statistical analyses

We used Pearson product-moment correlation to study the temporal trend in the timing of migration during the last 40 years. We studied the year and early, middle, and late phases of the migration. We used observation date as a response variable and year as a predictor variable.

To study the relation between NAO index and the migratory behaviour of the Bean Goose, we used linear regression. We built models separately for the early, middle, and late phases of migration. We used observation day as a response variable, and year and average NAO as predictor variables.

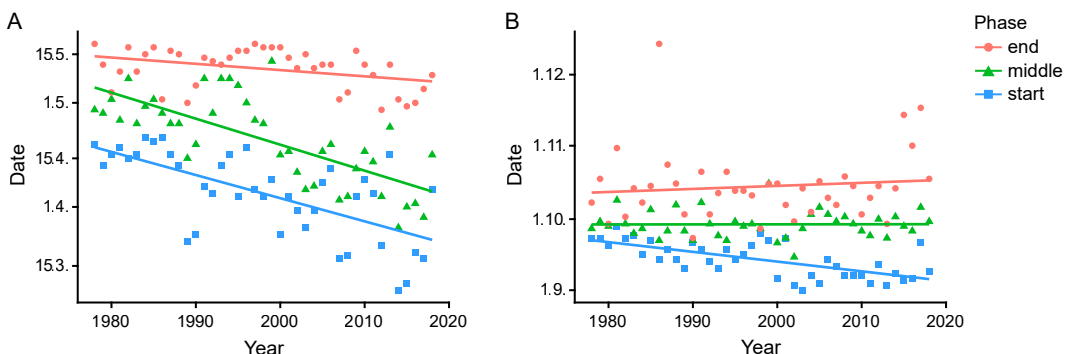


Fig. 2. Bean goose migration shows a long-term shift to earlier spring migration but not to later autumn migration. Relationship of spring (A) and autumn (B) migration dates to the observation year when 5% (start), 50% (middle), and 95% (end) of the cumulative sum of birds had been reached for that year.

We included the year to account for the temporal change in the timing of migration using the regression analysis. All analyses were performed with R program version 4.1.2 (R Core Team 2021).

3. Results

Over the 40-year-long research period the Bean Goose spring migration has advanced in all the phases of migration (Fig. 2A). The change, *i.e.*, days per year, was strongest in the early ($r=-0.66$, $n=41$, $p<0.001$) and middle ($r=-0.72$, $n=41$, $p<0.001$) phases. The timing of migration has also advanced in the latest phase of the migration ($r=-0.37$, $n=41$, $p=0.02$), although much less so. Specifically, the early phase of spring migration has advanced 26 days ($p<0.001$, $SD\pm 4.5$), the middle phase has advanced 30 days ($p<0.001$, $SD\pm 4.9$) and the late phase has advanced 7 days ($p=0.02$, $SD\pm 2.9$). In the spring, NAO index

correlated with the early phases of migration (Table 1).

Regarding the autumn migration (Fig. 2B), the timing of autumn migrants had only changed in the early phase ($r=-0.66$, $n=41$, $p<0.001$), by advancing by 17 days ($p<0.001$, $SD\pm 3.3$) for the entire 40-year period. A temporal trend of later (or earlier) migration was non-significant for the middle and late phases. In the autumn, NAO index was not found to be associated with the timing of migration (Table 1).

4. Discussion

We show that during the past 40 years the spring migration of the Bean Goose has advanced by nearly a month. The beginning of autumn migration has advanced by two weeks. In spring, the timing of migration was also affected by NAO index in the early phase of migration.

Table 1. Relationship of spring and autumn migration dates to the observation year and the average NAO index. The connection was tested separately on days when 5%, 50%, or 95% of the cumulative sum of birds had been reached. We used a linear regression analysis as a statistical model.

			Estimate	Std. Error	t-value	p-value
Spring	5%	Intercept	1363	227	5.99	<0.001
		NAO	-14.7	5.27	-2.78	<0.01
		Year	-0.63	0.11	-5.56	<0.001
	50%	Intercept	1589	236	6.74	<0.001
		NAO	-3.99	5.47	-0.73	0.47
		Year	-0.74	0.12	-6.26	<0.001
	95%	Intercept	466	140	3.32	<0.01
		NAO	-5.68	3.26	-1.74	0.09
		Year	-0.17	0.07	-2.38	0.02
Autumn	5%	Intercept	1082	153	7.07	<0.001
		NAO	-0.57	3.48	-0.16	0.87
		Year	-0.41	0.08	-5.39	<0.001
	50%	Intercept	262	158	1.66	0.11
		NAO	0.64	3.59	0.18	0.86
		Year	0.01	0.08	0.06	0.95
	95%	Intercept	-36.4	401	-0.09	0.93
		NAO	9.69	9.12	1.06	0.30
		Year	0.16	0.20	0.81	0.42

Such correlation was not observed in autumn migration.

Our data shows that migrants are arriving earlier in our study area in southern Finland, but we were not able to track the progression of migration along the migration route. This means that while arrival on southern staging grounds has advanced, this does not necessarily mean that arrival on the breeding grounds has also advanced.

The change in spring migration might be the result of the elevated winter and spring temperatures (IPCC 2018, Ruosteenoja *et al.* 2016). As a short-distance migrant, the Bean Goose can possibly react to local weather conditions and follow the progressing spring as they move towards their breeding grounds in higher latitudes. Subspecies Taiga Bean Goose and Tundra Bean Goose differ in their timing as the Taiga Bean Goose starts to arrive in Finland earlier than the Tundra Bean Goose. Yet, all the phases of spring migration have advanced by one to four weeks, and thus, it is likely that there has been a change in the timing of both subspecies.

Migratory birds may shorten their migratory journey in warm winters (Usui *et al.* 2017), and the wintering grounds of the Bean Goose have partly moved closer to its nesting areas (Nilsson 2011). However, there is variation between years as the Bean Goose might migrate further south on cold winters, as shown in a study by Nilsson (2013) where the number of wintering Bean Geese correlates negatively with January temperatures in southern Sweden. The shortening of the migration journey may have some connection to the progressively earlier arrival in Finland. However, in this study, we were not able to determine the migration distance and in previous studies, migration distance has not been shown to explain the advancing arrival on breeding grounds (Gunnarsson *et al.* 2006, Nuijten *et al.* 2020). This could indicate that the advanced arrival in Finland is most likely caused by a shortening stay on wintering grounds.

The early phase of the spring migration was connected to NAO index. Positive NAO index during winter months correlates with warm winter weather in Europe (Hurrell 1995). As the timing of spring migration and NAO index are connected, early spring migration is plausibly a result of warm winters. A similar connection between positive NAO index and spring migration was

observed in a study of Icelandic migrants when several species advanced their migration after mild winters (Gunnarsson & Tómasson 2011).

In the autumn, the Bean Goose showed advanced timing of migration. However, only the start of their autumn has shifted forward. The early migrants are most likely successful breeders from the subspecies Taiga Bean Goose and their offspring, who have advanced the start of their migration from their breeding grounds on boreal zone. Non-breeding and unsuccessfully breeding taiga Bean Geese migrate to moult on Novaya Zemlya in the Arctic Ocean (Piironen *et al.* 2021). Moulting migrants stay on Novaya Zemlya for approximately three months and start their autumn migration later than successful breeders. Moulting migrants form a large part of the population and thus, their movement has a major effect on the observed timing of the autumn migration (Piironen *et al.* 2021). Noteworthy, we must acknowledge that we cannot reliably separate the contribution of the Tundra Bean Goose in our data, and it is possible that their later timing compared to the Taiga Bean Goose (Piironen *et al.* 2022b) may complicate the interpretation of the autumn migration.

Because of climate change, also autumns in Finland are getting warmer, though the trend is not as strong as in spring (Ruosteenoja *et al.* 2016, IPCC 2018). Contrary to our prediction, the Bean Goose has not delayed the main timing of the autumn migration, which could indicate slower autumn migration and stopping to feed in suitable sites across the migration route. Migratory birds' responses to climate change are more versatile in the autumn than in the spring, but many short-distance migrants have delayed their autumn migration significantly (Jenni & Kéry 2003).

In autumn, the timing of migration was not connected to NAO index. The breeding grounds of the Tundra Bean Goose reach outside the area that is affected by NAO, which may partly explain this result. The effect of NAO is greatest in winter months (Hurrell 1995), which may also explain why spring migration follows the index more closely. Start of the autumn migration is probably more linked to local weather conditions on breeding grounds.

In spring, advancing the migration to follow the progressing spring is important as the young

plants are important food for birds because of the high nutrition quality (Lepage *et al.* 1998). High-nutrient food is especially important for the survival of goslings (Doiron *et al.* 2015). Autumn migration, on the other hand, is not subjected to a similar selection pressure which may partly explain why the change in the timing of migration is greater in spring than in autumn (Kölzsch *et al.* 2016). The Bean Goose is a single-brooded species and a longer stay on the breeding grounds would probably not improve its breeding success.

Our results are in line with the short-distance migrants' ability to adapt to climate change by adjusting their migration behaviour (Kolářová *et al.* 2017). The ability to change the timing of migration suggests that the Bean Goose has the potential to adapt to environmental changes through its migratory behaviour. A four-week advancement in spring migration is a major shift in a species' migratory behaviour and one of the largest shifts documented so far (see also, Nuijten *et al.* 2020).

Metsähänhen muutto Suomessa on aikaistunut keväällä, mutta ei syksyllä

Ilmastonmuutos vaatii eliöitä mukauttamaan perinnöllisiä tai opittuja käyttäytymismallejaan muuttuviin ympäristöolosuhteisiin. Erittäin alttiita muutoksille voi olla erilaisten habitaatien välillä muuttavat linnut, joiden selviytyminen on yhteydessä muuton onnistuneeseen ajoittamiseen. Tässä tutkimuksessa käytimme metsähänhestä (*Anser fabalis*) avoimeen lintutietopalveluun, Tiiraan (tiira.fi – BirdLife Suomi), kerättyjä havaintoja selvittääksemme, onko lajin muuton ajoituksessa tapahtunut muutosta viimeisten 40 vuoden aikana. Lisäksi selvitimme ajoituksen yhteyttä muuton aikaiseen suursäätötilaan käyttämällä Pohjois-Atlantin suursäätötilaa kuvaavaa NAO-indeksiä. Tutkitulla ajanjaksolla 1978–2018 kevään päämuutto on aikaistunut kuukaudella. Syysmuuton kohdalla muutos oli vähäistä. NAO-indeksi oli yhteydessä vain kevään ensimmäisten muuttajien ajoitukseen. Kevätmuuton voimakas aikaistuminen osoittaa metsähänhen sopeuttaneen muuttokäyttäytymistään vastaamaan kevään muuttuvia olosuhteita.

Acknowledgements. The permission to use the data was granted from BirdLife Finland and its member associations. We thank BirdLife Finland, Tero Toivanen and Teemu Lehtiniemi and the many volunteers who have saved their observations into tiira.fi citizen science database over decades. We thank Anssi Vähätalo, Antti Piironen and one anonymous referee for constructive feedback to improve the quality the manuscript.

References

- Callaghan, C.T., Rowley, J.J.L., Cornwell, W.K., Poore, A.G.B. & Major, R.E. 2019: Improving big citizen science data: Moving beyond haphazard sampling. — *PLoS Biology* 17: e3000357. <https://doi.org/10.1371/journal.pbio.3000357>
- Cox, G.W. 2010: *Bird Migration and Global Change*: — Island Press, Washington.
- Doiron, M., Gauthier, G. & Lévesque, E. 2015: Trophic mismatch and its effects on the growth of young in an Arctic herbivore. — *Global Change Biology* 21: 4364–4376. <https://doi.org/10.1111/gcb.13057>
- Dokter, A.M., Liechti, F., Stark, H., Delobbe, L., Tabary, P. & Holleman, I. 2011: Bird migration flight altitudes studied by a network of operational weather radars. — *Journal of the Royal Society Interface* 8: 30–43. <https://doi.org/10.1098/rsif.2010.0116>
- Erni, B., Liechti, F., Underhill, L.G. & Bruderer, B. 2002: Wind and rain govern the intensity of nocturnal bird migration in Central Europe - a log-linear regression analysis. — *Ardea* 90: 155–166.
- Gunnarsson, T. G., Gill, J. A., Atkinson, P. W., Gélineau, G., Potts, P. M., Croger, R. E., Gudmundsson, G. A., Appleton, G. F. & Sutherland, W. J. 2006: Population-scale drivers of individual arrival times in migratory birds. — *The Journal of Animal Ecology* 75: 1119–1127.
- Gunnarsson, T.G. & Tómasson, G. 2011: Flexibility in spring arrival of migratory birds at northern latitudes under rapid temperature changes. — *Bird Study* 58: 1–12. <https://doi.org/10.1080/00063657.2010.526999>
- Heinicke, T., Fox, A.D. & Leafloor, J.O. 2018: A1 Western Taiga Bean Goose *Anser fabalis fabalis*. — In A global audit of the status and trends of Arctic and northern hemisphere goose populations (Component 2: Population accounts). (ed. Fox, A.D. & Leafloor, J.O.): 4–9. Conservation of Arctic Flora and Fauna International Secretariat: Akureyri, Iceland.
- Herrera, C.M. 1978: On the Breeding Distribution Pattern of European Migrant Birds: Macarthur's Theme Reexamined. — *The Auk* 95: 496–509.
- Hurrell, J.W. 1995: Decadal Trends in the North Atlantic Oscillation: Regional Temperatures and Precipitation. — *Science* 269: 676–679. <https://doi.org/10.1126/science.269.5224.676>

- IPCC 2018: Summary for Policymakers. — In Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty (ed. Masson-Delmotte, V., Zhai, P., Pörtner, ... & Waterfield, T.): 3–24. Cambridge University Press, Cambridge, UK and New York, NY, USA.
- Jenni, L. & Kéry, M. 2003: Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. — *Proceedings of the Royal Society B: Biological Sciences* 270: 1467–1471. <https://www.jstor.org/stable/3592127>
- Kim, H., Vega, M.S., Wahl, M., Puan, C.L., Goodrich, L. & Bildstein, K.L. 2015: Relationship Between the North Atlantic Oscillation and Spring Migration Phenology of Broad-winged Hawks (*Buteo platypterus*) At Hawk Mountain Sanctuary, 1998–2013. — *Journal of Raptor Research* 49: 471–478.
- Kolářová, E., Matiu, M., Menzel, A., Nekovář, J., Lumpe, P. & Adamic, P. 2017: Changes in spring arrival dates and temperature sensitivity of migratory birds over two centuries. — *International Journal of Biometeorology* 61: 1279–1289. <https://doi.org/10.1007/s00484-017-1305-5>
- Kölzsch, A., Müskens, G.J.D.M., Kruckenberg, H., Glazov, P., Weinzierl, R., Nolet, B.A. & Wikelski, M. 2016: Towards a new understanding of migration timing: slower spring than autumn migration in geese reflects different decision rules for stopover use and departure. — *Oikos* 125: 1496–1507. <https://doi.org/10.1111/oik.03121>
- Lepage, D., Gauthier, G. & Reed, A. 1998: Seasonal variation in growth of greater snow goose goslings: the role of food supply. — *Oecologia* 114: 226–235.
- Mayor, S.J., Guralnick, R.P., Tingley, M.W., Otegui, J., Withey, J.C., Elmendorf, S.C., Andrew, M.E., Leyk, S., Pearse, I.S. & Schneider, D.C. 2017: Increasing phenological asynchrony between spring green-up and arrival of migratory birds. — *Scientific Reports* 7: 1902. <https://doi.org/10.1038/s41598-017-02045-z>
- Møller, A.P., Flensted-Jensen, E., Klarborg, K., Mardal, W. & Nielsen, J.T. 2010: Climate change affects the duration of the reproductive season in birds. — *Journal of Animal Ecology* 79: 777–784. <https://doi.org/10.1111/j.1365-2656.2010.01677.x>
- Newton, I. & Brockie, K. 2008: The migration ecology of birds. — Academic Press, Amsterdam.
- Newton, I. & Dale, L. 1996: Relationship between migration and latitude among west European birds. — *Journal of Animal Ecology* 65: 137–146.
- Nilsson, L. 2011: The migrations of Finnish Bean Geese *Anser fabalis* in 1978–2011. — *Ornis Svecica* 21: 157–166. <https://doi.org/10.34080/os.v21.22599>
- Nilsson, L. 2013: Censuses of autumn staging and wintering goose populations in Sweden 1977/1978–2011/2012. — *Ornis Svecica* 23: 3–45.
- Nuijten, R.J.M., Wood, K.A., Haitjema, T., Rees, E.C. & Nolet, B.A. 2020: Concurrent shifts in wintering distribution and phenology in migratory swans: Individual and generational effects. — *Global Change Biology* 26: 4263–4275. <https://doi.org/10.1111/gcb.15151>
- Piironen, A., Paasivaara, A. & Laaksonen, T. 2021: Birds of three worlds: moult migration to high Arctic expands a boreal-temperate flyway to a third biome. — *Movement Ecology* 9:47. <https://doi.org/10.1186/s40462-021-00284-4>
- Piironen, A., Fox, A.D., Kampe-Persson, H., Skjyllberg, U., Therkildsen, O.R. & Laaksonen, T. 2022a: When and where to count? Implications of migratory connectivity and nonbreeding distribution to population censuses in a migratory bird population. — *Population Ecology* 1–12. <https://doi.org/10.1002/1438-390X.12143>
- Piironen, A., Piironen, J. & Laaksonen, T. 2022b: Predicting spatio-temporal distributions of migratory populations using Gaussian process modelling. — *Journal of Applied Ecology* 59: 1146–1156. <https://doi.org/10.1111/1365-2664.14127>
- R Core Team 2021: R: A Language and environment for statistical computing. Austria.
- Ruostenoja, K., Jylhä, K. & Kämäräinen, M. 2016: Climate projections for Finland under the RCP forcing scenarios. — *Geophysica* 51: 17–50.
- Saino, N., Ambrosini, R., Rubolini, D., Von Hardenberg, J., Provenzale, A., Hüppop, K., Hüppop, O., Lehikoinen, A., Lehikoinen, E., Rainio, K., Romano, M. & Sokolov, L. 2011: Climate warming, ecological mismatch at arrival and population decline in migratory birds. — *Proceedings of the Royal Society B: Biological Sciences* 278: 835–842. <https://doi.org/10.1098/rspb.2010.1778>
- Shaw, A.K. & Couzin, I.D. 2013: Migration or residency? The evolution of movement behavior and information usage in seasonal environments. — *The American Naturalist* 181: 114–124. <https://doi.org/10.1086/668600>
- Usui, T., Butchart, S.H.M. & Phillimore, A.B. 2017: Temporal shifts and temperature sensitivity of avian spring migratory phenology: a phylogenetic metaanalysis. — *Journal of Animal Ecology* 86: 250–261. <https://doi.org/10.1111/1365-2656.12612>
- Van Buskirk, J., Mulvihill, R.S. & Leberman, R. C. 2009: Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. — *Global Change Biology* 15: 760–771. <https://doi.org/10.1111/j.1365-2486.2008.01751.x>