

ORIGINAL ARTICLE

When and where to count? Implications of migratory connectivity and nonbreeding distribution to population censuses in a migratory bird population

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Abstract

Migratory connectivity is a metric of the co-occurrence of migratory animals originating from different breeding sites, and like their spatial dispersion, can vary substantially during the annual cycle. Together, both these properties affect the optimal times and sites of population censusing. We tracked taiga bean geese (*Anser fabalis fabalis*) during 2014–2021 to study their migratory connectivity and nonbreeding movements and determine optimal periods to assess the size of their main flyway population. We also compared available census data with tracking data, to examine how well two existing censuses covered the population. Daily Mantel's correlation between breeding and nonbreeding sites lay between 0 and 0.5 during most of the nonbreeding season, implying birds from different breeding areas were not strongly separated at other times in the annual cycle. However, the connectivity was higher among birds from the westernmost breeding areas compared to the birds breeding elsewhere. Daily Minimum Convex Polygons showed tracked birds were highly aggregated at census times, confirming their utility. The number of tracked birds absent at count sites during the censuses however exceeded numbers double-counted at several sites, indicating that censuses might have underestimated the true population size. Our results show that connectivity can vary in different times during the nonbreeding period, and should be studied throughout the annual cycle. Our results also confirm previous studies, which have found that estimates using marked individuals usually produce higher population size estimates than total counts. This should be considered when using total counts to assess population sizes in the future.

KEYWORDS

adaptive management, migration, movement ecology, population census, population monitoring

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1 | BACKGROUND

Reliable, accurate, and regular population size estimates are essential for evaluating the conservation status of populations (Maes et al., 2015), setting targets for management and assessing the impact of population management actions (Madsen et al., 2017). To assess sizes of migratory populations or subpopulations, knowledge about the degree of migratory connectivity (Webster et al., 2002) throughout the annual cycle is essential. Migratory connectivity determines the co-occurrence of birds originating from different breeding sites throughout the annual cycle. This property is high when individuals from same breeding populations remain close throughout their annual cycle and separate from those of other breeding populations, whereas it is low when individuals remain close at one stage of the annual cycle but not at another, so providing a useful measure of how separate elements of a population may remain throughout the annual cycle (Cohen et al., 2017; Webster et al., 2002).

The strength of migratory connectivity between breeding and nonbreeding sites can vary between different phases of the nonbreeding seasons (Knight et al., 2021). Measurements of connectivity help to reveal clustering of the population through the nonbreeding season and its implications for population size assessment (i.e., when and where individuals should be counted to avoid missing any clusters). Similarly, spatial dispersion of the migratory populations can vary substantially during the annual cycle, which has obvious implications for when and where population censuses should optimally be done. Together, measurements of connectivity and spatial dispersion of populations over the annual cycle help identify the most favorable periods for population censusing. Although modern tracking technology provides efficient tools to study these prerequisites for population censuses, we are not aware of any such studies (but see Finger et al., 2016 for a study comparing timing of spring migration and breeding bird monitoring).

A variety of methods have been developed to monitor waterbird populations (Delany & Scott, 2005), but the assessment of goose population sizes is usually based on so-called total counts (Fox & Leafloor, 2018). These counts are often undertaken in mid-winter, when geese are most highly aggregated and when turnover of individuals, more likely associated with migratory staging areas, is considered to be at its lowest. During these counts, birds are censused at as many known different sites as possible (usually during a short period of time) and the population size is estimated as a sum of birds counted from different sites. These counts are based on the assumption that only a negligible amount of birds are

missed in the counts (i.e., all birds are found) or are double-counted (i.e., birds have not moved between count sites during the count). The performance of these schemes are seldom evaluated, although some comparisons with capture-mark-resight estimates (Alisauskas et al., 2014; Clausen et al., 2019; Ganter & Madsen, 2001) and predictions of integrated population models (Johnson et al., 2020) have been made.

In contrast to several other goose populations throughout the globe, the Western Palearctic population of taiga bean goose (*Anser fabalis fabalis*, hereafter taiga bean goose) has declined throughout its range in recent decades (Fox & Leafloor, 2018). The whole population of the subspecies has recently been divided into four flyway populations (or management units, Heinicke et al., 2018; Marjakangas et al., 2015). The main flyway for the taiga bean goose is the Central Flyway (hereafter CF), which breeds in Finland, Sweden, Norway, and North-Western Russia (Heinicke et al., 2018; see also Figure 1). The majority of the CF population is thought to winter in southern Sweden (Nilsson, 2011), but migration patterns and wintering sites of the birds breeding in North-Western Russia remain unknown. In addition, taiga bean geese, thought to be from the CF (Nilsson et al., 1999), winter in Denmark and northern Germany (Heinicke et al., 2018), but their origin and migration patterns are largely unknown (but see Boer, 2019; Mitchell et al., 2016; Nilsson, 2011 for some insights).

Population size assessment is highly relevant for the international adaptive harvest management of the CF population, since a target size for the population is set to 60,000–80,000 individuals (Johnson et al., 2016; Marjakangas et al., 2015). At the start of the flyway-scale management of the population, it was agreed to use mid-January counts to monitor the CF population (Marjakangas et al., 2015). In addition to the mid-winter counts, large-scale, coordinated counts of taiga bean geese were carried out in Swedish staging areas in October (autumn counts; see Nilsson & Kampe-Persson, 2020) and March (spring counts; see Skjyllberg, 2015). It was suspected (but never verified) that at these times the vast majority of the flyway population was present, because these spring and autumn counts always far exceeded those counted in mid-winter (Johnson et al., 2021). Currently, estimates generated by the integrated population model are used to monitor the status of the population, using data from October, mid-winter and March as inputs in the model (Johnson et al., 2021). However, the optimal time of the year for making the most accurate count of the taiga bean goose population remains to be investigated. Likewise, the performance of different counts has not been evaluated with data independent from the counts. Thus, it is unknown, (i) whether the birds from different breeding

areas are mixed with each other during the counts, (ii) how spatially dispersed the population is during the counts, (iii) whether birds (and how many birds) are missed in the counts, and (iv) whether birds (and how many birds) move between sites during the counts and are thereby double-counted.

We use satellite tracking data from the years 2014 to 2021 to study the movements and distribution of the taiga bean goose CF population during the nonbreeding season. First, we describe the overall movements of the flyway population during the nonbreeding season, and also reveal previously unknown migration patterns. Second, we estimate the migratory connectivity of the population to reveal any clustering during the nonbreeding season (and thus, whether some particular clusters could be missed in the censuses). Third, we estimate changes in the spatial dispersion of the population to find the periods favorable for assessing the population size. Fourth, we compare the tracking data to the available census data from 2020 to 2021, to study the current performance of two different (spring and autumn) population censuses. Finally, we discuss the future perspectives to be considered when assessing population size for the taiga bean goose and other migratory populations.

2 | MATERIAL AND METHODS

2.1 | Satellite tracking

We caught taiga bean geese for deployment of global positioning system (GPS) transmitter neck collars in Denmark and Finland in the years 2014–2015 and 2018–2020, respectively. In Denmark, 10 birds (all adult females) were caught using large clap nets at one wintering site, at Lille Vildmose, Jutland (56°54'N, 10°13'E) by decoying wild birds with tame geese.

In Finland, 16 birds (14 females and 2 males) were caught using cannon-netting on spring staging sites at Outokumpu and Liperi (62°42'N, 29°07'E) in North Karelia, and 41 birds (33 females, 8 males) were caught at the breeding sites before breeding, also using cannon-netting. These sites are located at Virrat in South Ostrobothnia (62°22'N, 23°16'E), Lieksa in North Karelia (63°16'N, 30°28'E), Pudasjärvi and Utajärvi in North Ostrobothnia (65°04'N, 26°50'E and 65°12'N, 26°52'E, respectively), and Salla in Lapland (66°51'N, 28°36'E). Another two birds were caught in Lieksa (both females) and two in Utajärvi (both females) during summer when the birds were flightless due to remigial molt. For a more detailed field method description, see Piironen et al. (2021). Before the analysis, we removed two Finnish caught birds (both females) that vanished into Russia quickly after marking. In addition,

we excluded a male that was paired with another tracked bird from the analysis. Altogether, we used tracking data from 68 individuals (59 females, 9 males), which were all adults (at least 2 years old). For birds marked in Denmark ($n = 10$, all adult females), we used “Ibis” solar-powered GPS-GSM (Global System for Mobile Communications) neck collars produced by Ecotone Telemetry. These transmitters weighed 30 g, which added <1% of the body mass of the instrumented birds. GPS resolution was set to 2 h, that is, devices recorded the GPS position every second hour when battery charge levels permitted. The devices transmitted the data via the GSM Short Message Service (SMS). Predeployment calibration demonstrated >90% accuracy to within 10 m of positional data. One Danish bird caught on November 14, 2014 was followed to the Netherlands, subsequently flew to Norway but encountered severe weather and returned to Denmark, where it was retrieved dead in February 2015 (the track of which can be seen in Figure 1) and the GPS collar reused later the same year.

For birds marked in Finland ($n = 58$), we used OrniTrack-44 (56 birds) and OrniTrack-38 (2 birds) solar-powered GPS-GSM neck collars produced by Ornitela UAB. OrniTrack-44 and OrniTrack-38 weigh approximately 45 and 38 g, respectively, which added <2% of the weight of the body mass of the instrumented geese. These transmitters log GPS positions and send data to the server via a GSM/GPRS network either by e-mail or SMS. To ensure the quality of the tracking data, we excluded GPS noise from the data (i.e., apparently erroneous locations such as 00°00'N, 00°00'E) and locations with hdop (horizontal dilution of precision of the GPS fix) values ≤ 2 . The hdop values were only available for the OrniTrack devices.

2.2 | Migratory connectivity and spatial distribution

We estimated the migratory connectivity of the population during the nonbreeding period using Mantel's correlation (r_M), a correlation between two (distance) matrices (Cohen et al., 2017). The r_M values can range between -1 and 1 , so that 1 expresses full connectivity (individuals that breed close to each other are also close to each other during nonbreeding season), 0 expresses no connectivity (complete mixing of population) and -1 expresses full negative connectivity (individuals breeding close to each other are far away from each other during the nonbreeding season). As the origin of nonbreeding geese is difficult to determine, we used only individuals with at least one breeding attempt during the tracking period ($n = 42$) to estimate the migratory connectivity. For those individuals, r_M was calculated between the breeding site and the

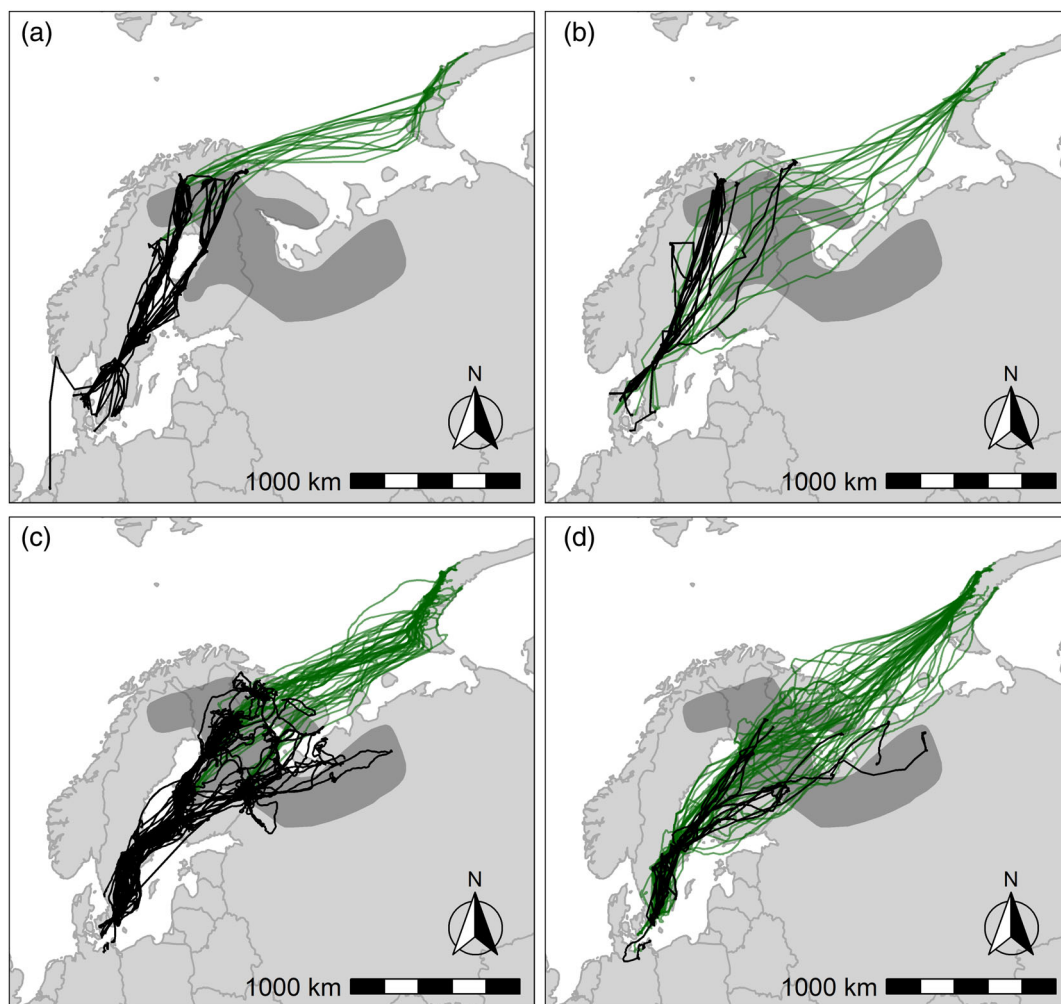


FIGURE 1 Migration routes of taiga bean geese marked for satellite tracking. Map (a) shows individuals marked in Denmark (spring migration), (b) individuals marked in Denmark (autumn migration), (c) individuals marked in Finland (spring migration) and (d) individuals marked in Finland (autumn migration). Figure shows all data from all tracked individuals ($n = 68$) from the years 2015–2021. Maps showing the spring and autumn migration routes include locations from the periods 1 January–30 May and 1 August–31 December, respectively. To ensure figure clarity, migration routes to moulting sites at Novaya Zemlya (1 June–31 July) and back to wintering sites (1 August–31 December) are illustrated by green lines, while black traces show spring and autumn routes taken to and from the breeding sites (i.e. not moult migrants). The shaded grey area denotes the breeding distribution of the Central Flyway population (redrawn after Marjakangas et al., 2015 and Heinicke et al., 2018). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/1365-3113.12143)]

daily locations during the nonbreeding season. For the calculation of r_M , we used one location from each individual per day. We note that the fact that birds were marked at two stages of the annual cycle (at the wintering sites in Denmark and close to breeding sites in Finland) can bias the estimates of migratory connectivity. To account for this potential bias, we calculated r_M not only for all birds, but also to the birds only marked near the breeding sites (see Section 3.2).

For the birds marked in Denmark (all females), we identified the nesting sites using the same method (location revisitation metrics; Picardi et al., 2020) that was previously used to identify taiga bean goose nest sites from the same tracking data (Pironen et al., 2021). However,

we adjusted criteria to fit the GPS resolution (2 h) used for the birds marked in Denmark. In summary, we identified possible nest sites from the period April 15 to June 30 from revisited places with the following criteria: (1) nest site (defined as a 60-m radius to account for small-scale movements around the nest and bias in the GPS locations) must be visited on at least 6 consecutive days (corresponding to average clutch size and laying one egg approximately per day; Cramp & Simmons, 1977), (2) it must be visited in at least 50% of days between first and last visit, and (3) at least 30 locations must be from the site. From the candidate nest sites, we selected the most visited site for each bird and each breeding season as the nest site (bean geese are not known to re-nest after

unsuccessful attempts; Pirkola & Kalinainen, 1994). We note that these criteria include some subjective threshold values, but we believe that the conclusions about nesting based on these criteria are in accordance with what we can clearly see by following the tracks of individual birds. For birds that attempted to breed in several years, we used the centre of the different nesting sites (which were not more than a few kilometers apart from each other) as the breeding site for calculating r_M .

Regarding birds marked in Finland, this study is based on the same satellite tracking data as the previous study by Piironen et al. (2021), so we used individual breeding sites and status provided in that study (see Additional file 2 in Piironen et al., 2021), determined using the same method as used in this study for the birds marked in Denmark. The two birds marked in 2018 in Finland were caught during molt at the breeding grounds from flocks containing adults and their offspring, and we thereby considered them as breeding birds at their breeding sites. As goose pairs move together, their movements are dependent on each other. To ensure independence of the data, we used tracking data from only one member of a goose pair to analyze the connectivity.

We estimated the spatial distribution of the population separately for each day during the nonbreeding season using minimum convex polygon (MCP; Mohr, 1947). We did not calculate the MCP for a period arbitrarily chosen between June 1 and August 31, because some of the birds were marked near their common breeding sites, so the choice of marking sites would affect the MCP during the breeding season. However, as the MCP is nowhere near to its minimum close to this period (Figure 2), the delineation of the excluded period is not critical for the purpose of this study, that is, for finding the optimal period for population size assessment. For the calculation of MCP, we used one location from each individual per day (first location of the day). To find periods when the population is the most concentrated every year (despite the variation between years), we merged the locations from each date (disregarding the year) from the years 2012 to 2021 before calculating the MCPs.

We performed analysis using packages *adehabitatHR* (Calenge, 2006), *MigConnectivity* (Cohen et al., 2017) and related packages in R software version 4.1.1 (R Core Team, 2020).

2.3 | Comparison of satellite tracking data and census data

We assessed the performance of taiga bean goose population censuses (spring and autumn) by comparing satellite tracks of tagged geese to the positions and timing of the

counts from autumn 2019 (carried out on October 14–25), spring 2020 (February 29 to March 2), and spring 2021 (March 12–16). The autumn counts used in this study were carried out in addition to the standardized mid-October counts (Nilsson & Kampe-Persson, 2020). These counts are so-called total counts, that is, all birds in the population are assumed to be found and counted once, early in the morning when they departed from the roost or later when they were feeding in the fields. The counts are carried out from the ground with spotting scopes and binoculars. The count method was selected to be suitable for different count sites (e.g., small sites were counted from one point, whereas larger sites were counted simultaneously from several points). The count data for autumn counts included date, time, count site (coordinates), and the number of birds counted. For the spring counts, the date is known but exact time of the day was not available. However, at the two major sites, counts were carried out during the roost flight in the morning (5.00 a.m. to 7.00 a.m.). At the other sites, counts were carried out during the day (9.00 a.m. to 2.00 p.m.) on feeding fields. For a detailed description of the count methods, see Kampe-Persson (2017), Nilsson and Kampe-Persson (2020), and Skjyllberg and Tjernberg (2008).

We compared the count data to satellite tracking data from all individuals tracked during the count (for autumn 2019 and spring 2020, $n = 16$; for spring 2021, $n = 40$). For comparison with spring count data, we used locations from the above-mentioned time intervals, as the exact time for counts was unknown. For autumn counts, we used locations from the time window of ± 30 min around count time (as the count time was known). Count sites in the data represent feeding areas where geese were searched for and counted (counts in the field) or the location where geese were counted during the roost flight. For the field counts, we compared the locations of satellite-tracked birds at the above-mentioned time intervals with the location of the feeding areas at which geese were counted. For roost flights, we compared the locations of the tracked birds matched with the location of the roosts, or at feeding sites close to the roost within the above-mentioned time intervals.

3 | RESULTS

3.1 | Migration routes and migration phenology

The migration routes and migration phenology of satellite tracked taiga bean geese are illustrated in Figures 1

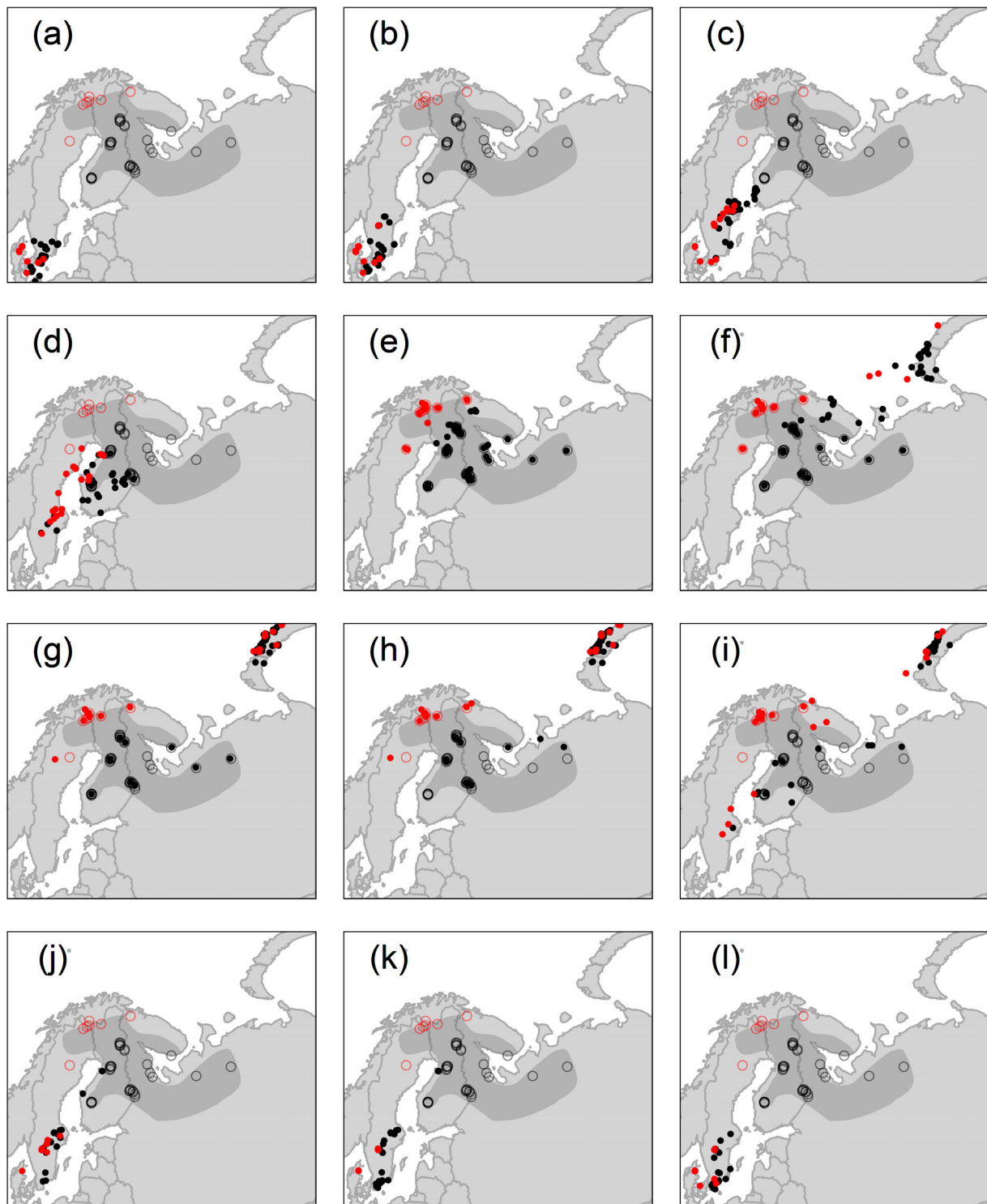


FIGURE 2 Nonbreeding distribution and breeding sites of satellite-tracked taiga bean geese in 2014–2021. The nonbreeding distribution is illustrated as the mid-month positions of individual birds (dots). Figures (a)–(l) denote months from January to December so that (a) = January, (b) = February, and so on. Locations from the same date in different years are pooled to each map, that is, each map contains one location per individual per year on a given date from the years 2014 to 2021. Circles denote the breeding sites for birds with at least one breeding attempt during the study period (note that the map also includes nonbreeding birds, which are not connected to any of the breeding sites). Locations and breeding sites of birds marked in Finland and Denmark are illustrated with black and red, respectively. The shaded gray area denotes the breeding distribution of the Central Flyway population (redrawn after Heinicke et al., 2018; Marjakangas et al., 2015). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/1365-3113.12143)]

and 2. Birds marked in Denmark had breeding grounds in northern Sweden and Norway, in the Kola Peninsula, and in northwestern Finland, more to the northwest than those of birds marked in Finland (Figure 2). Most of them migrated along the west coast of the Bothnian Bay (Baltic Sea) unlike the birds breeding elsewhere in Finland or in Russia, which exclusively migrated through Finland east of Bothnian Bay (Figure 1).

In August, the birds were still at their breeding and molting sites. In mid-September they began to arrive in staging areas in central Sweden, where they stayed for variable time periods until moving further south. The birds marked in Finland gathered in southern Sweden in December–February, with some individuals visiting Denmark ($n = 6$) and Germany ($n = 2$) during winter 2020–2021. The birds marked in Denmark began to arrive at the same sites for wintering in October, but note that one of these birds wintered elsewhere in Denmark (Sjælland) and one in Sweden later during the study period. The birds started to move northwards in early February, and the northward movement increased during February. In mid-March, many birds had already moved to Finland and the majority of the birds that migrate through Finland had left Sweden in mid-April. During March and April, most birds moved step-by-step to the north on either side of the Bothnian Bay, but birds heading east jumped across Finland to their breeding or staging site in eastern Finland. In mid-April, the birds were spread along their spring migration routes, as some birds were still in central Sweden while the first birds were already at their breeding sites.

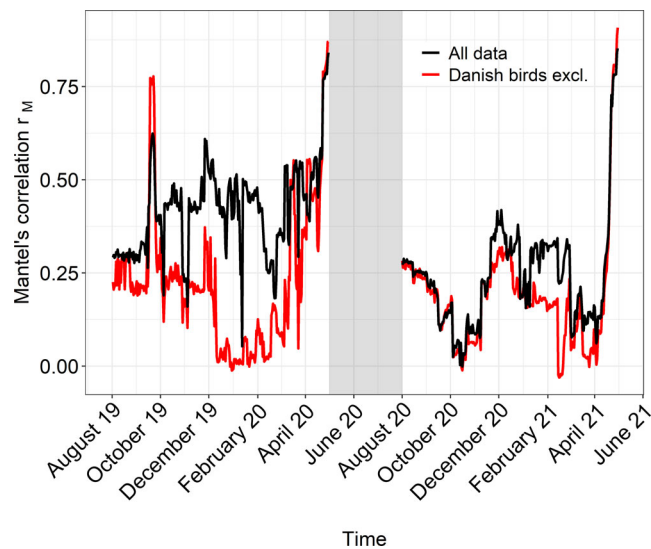


FIGURE 3 Migratory connectivity of the satellite tracked taiga bean geese during the nonbreeding season from August 1, 2019 to April 30, 2021, expressed as Mantel's correlation (r_M). The shaded gray column denotes the breeding season. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

3.2 | Migratory connectivity

The strength of the migratory connectivity of the population expressed as Mantel's correlation (r_M) in the years 2019–2021 is shown in Figure 3. Among all tracked birds, connectivity stayed mainly below 0.5 in August–February, indicating moderate overall connectivity during the nonbreeding season (i.e., birds from different breeding grounds do not completely mix with each other in staging and wintering areas). However, there are periods with very low connectivity ($r_M < 0.2$), especially in the year 2021. Although there was some variation between the years, the connectivity seems to be higher during mid-winter (December–January), than during the autumn migration (September–October) or the beginning of spring migration (late February and March) in both years. Essentially, birds breeding in the northwestern breeding sites (i.e., birds marked in Denmark) show higher connectivity than the birds breeding elsewhere (i.e., birds marked in Finland). We note that this can be, to some extent, an artifact caused by the fact that all birds marked in Denmark were caught from one wintering site in north Jutland, well away from the major wintering areas in southeast Denmark. This might explain especially the high connectivity during the mid-winter, when geese were at their wintering sites (winter site fidelity is known to be high among several goose species; Fox et al., 1994; Wilson et al., 1991). However, as these birds also had somewhat separate breeding grounds (Figure 2) and more defined migration routes than birds breeding more to the east (Figure 1), there was true connectivity between the northwesternmost breeding areas and wintering areas in northern Jutland,

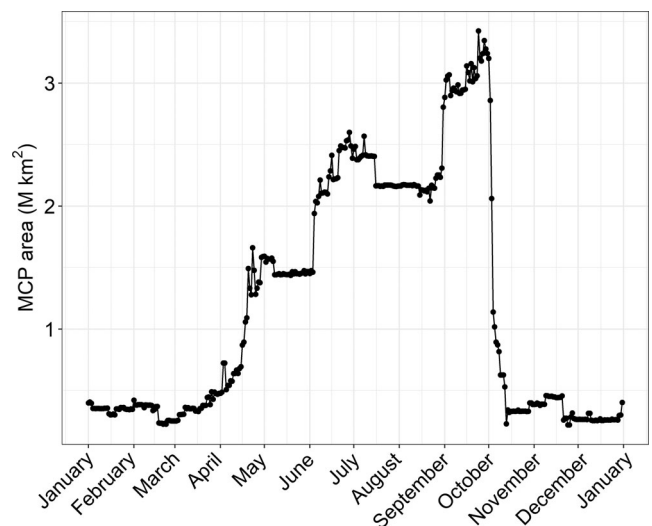


FIGURE 4 The size of the area covered by satellite tracked taiga bean geese during the nonbreeding season, calculated as minimum convex polygon (MCP). For the calculation of the daily MCPs, data have been merged from the years 2014 to 2021.

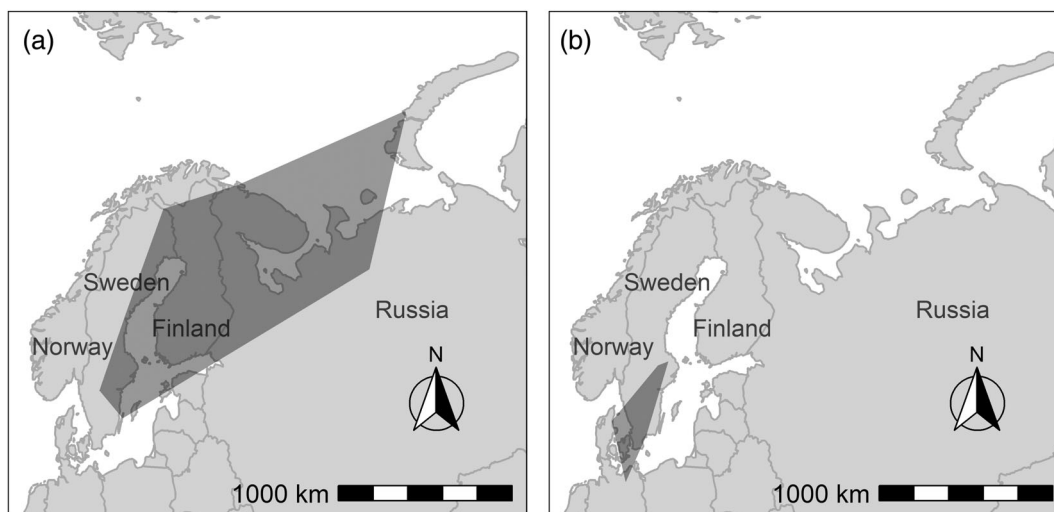


FIGURE 5 The maximum and minimum area covered by satellite tracked taiga bean geese during the nonbreeding season, expressed as a minimum convex polygon (MCP). Map (a) shows the day when MCP is at its maximum (September 24), and map (b) the day when MCP is at its minimum (November 24). For the calculation of the daily MCPs, data were merged from the years 2014 to 2021.

Denmark. Nevertheless, birds from all breeding sites mixed with each other in the Swedish staging sites during the spring and autumn migration (Figure 2), which explains the lower connectivity during these periods.

3.3 | Spatial distribution during nonbreeding season

The within-year variation in the size of the area covered by the distribution of the satellite-tracked taiga bean geese is illustrated in Figure 4. In August, when the birds were still on their breeding and molting sites, the size of the area covered by the population was relatively large. The size of the area reached its maximum in September, when the first birds moved to Sweden, while the rest of the population was still on their breeding and molting sites (Figure 5). The remarkable reduction in the size of the area covered by the birds occurred in early October, when the birds returned from the breeding grounds in Fennoscandia and western Russia and the molting sites in Novaya Zemlya and gathered at staging sites in central Sweden. The population was concentrated into the minimum area between late November and late December (Figure 5).

3.4 | Comparison of count data and satellite tracking data

In the autumn 2019 count, 6 out of 16 of the satellite-tracked birds (37.5%) were present at a count site during the count once (i.e., were on any one count site during

the count). None of the birds were present on two count sites during the counts (i.e., were double-counted) and 10 birds (62.5%) were not present at any count site during a count. In the spring count 2020, 12 out of 16 (75%) of the birds matched with sites covered by a count once, 1 bird (6%) was double-counted and 3 birds (19%) were not present at any count site during a count. In the two sites where the same satellite-tracked individual was present during the counts, 3440 and 2800 birds were counted. In the count in spring 2021, 23 out of 40 (57.5%) matched with a count once, 4 (10%) were double-counted and 13 birds (32.5%) were not near or present at count sites. Out of the total 13 birds that would not have been detected by counts, 2 had already migrated to Finland before the count period, 4 moved to Finland during the count period, and 7 stayed in Sweden during the count period, but were not present at any of the count sites during the counts (i.e., they had moved between the count sites between the counts at different sites).

4 | DISCUSSION

Data from the tracked birds showed moderate to low migratory connectivity between breeding and nonbreeding areas among the CF taiga bean goose population. This has consequences for population genetics as well as future research and conservation needs of the population. Both migratory connectivity and the spatial dispersion (the total area instantaneously containing members of the population) of the tracked birds varied substantially within the nonbreeding season, which influences the most favorable

periods for population size assessment. Comparing satellite tracking and count data indicated that current autumn and spring count schemes likely underestimate true population size, even though spring and autumn counts generally exceed the corresponding winter counts (Johnson et al., 2021). Our findings provide important perspectives to be considered when studying migratory connectivity and assessing the population size of the taiga bean goose population and migratory animal populations in general.

4.1 | Migration patterns and migratory connectivity

Our results showed that the taiga bean geese breeding in northwestern Russia (Karelia, Kola Peninsula, and Arkhangelsk Oblast) have similar migration patterns to the birds breeding in Finland. They migrate via Finland in autumn to winter mainly in southern Sweden, with some movements to southeast Denmark and Germany in some years (Figure 1). Our results also showed that wintering birds from northeastern Jutland in Denmark mainly breed in the westernmost parts of the taiga bean goose breeding range, the majority of which migrated along the west coast of Bothnian Bay, while some birds also migrated through Finland and bred in the Kola Peninsula and northern Finland. Despite the partially different wintering areas, all tracked birds gathered at the same staging sites in central Sweden during migrations. This decreased the strength of the migratory connectivity especially during the spring migration (Figure 3). Our results therefore confirm the recent findings of Knight et al. (2021), who showed that the connectivity can vary substantially during the annual cycle. The fact that the population can be more separated in different times of the year, can complicate population size estimation (censuses should be timed correctly to cover the whole population). It also has implications for conservation (effective actions must be focused on sites and at times when the population is most likely to be limited) and population genetics (since the population can become structured as a result of the separate timing and place of pair formation, see below). However, we require further research to reveal all implications of migratory connectivity to the conservation of migratory animal populations, not least to estimate migratory connectivity comprehensively throughout the annual cycle.

As pair formation among waterfowl usually takes place during winter (Rohwer & Anderson, 1988), low migratory connectivity between breeding and wintering sites should lead to genetically mixed populations. Birds marked in Finland (breeding both in Finland and Russia) showed low connectivity (Figure 3), so our

results are coherent with the recent study by Honka et al. (2022), who found no genetic structure among the taiga bean geese sampled in Finland. The geese wintering in Denmark showed higher migratory connectivity (Figure 3), potentially leading to genetic differentiation between the birds wintering in Denmark and Sweden, although this has not been investigated to date. Genetic mixing among goose populations can also take place during summer on molting grounds (as found among greater white-fronted goose *Anser albifrons*; Kölzsch et al., 2019), and taiga bean geese from the entire breeding range of the CF population have common molting grounds in Novaya Zemlya (Piironen et al., 2021; Figure 1). Future research should concentrate on the comprehensive study of the genetic structure of taiga bean geese from different breeding origins, and on determining the timing of pair formation in taiga bean geese and its implications for the genetic structure of the population.

4.2 | Nonbreeding distribution and estimation of taiga bean goose population size

The relative size of the area including all of the tagged taiga bean geese was at its lowest from the last half of November to the beginning of January (Figure 4), implying that this is the point in the annual cycle when the population is most favorable for monitoring. The size of the area covered by the population increased slightly in the beginning of January, but remained low until mid-March, which suggests there are good reasons for continuing the current counts carried out in Sweden in mid-winter and spring. In contrast, the same results suggested that the current autumn counts (carried out in mid-October) seem vulnerable to bias caused by the fact that a part of the population remains on staging areas in Finland at that time in some years (Figure 2). The timing is also crucial with regards to the spring count, as the birds started moving northwards in February, and some birds had already arrived in Finland in early March. The correct timing will probably become even more critical in the future, especially as global warming advances the spring migration (Cotton, 2003).

Regarding the comparison between tracking data and count data, the incompleteness of the census data (the lack of comprehensive information on the areas covered by the counts), used count methods (nonsimultaneous counts) and relatively small number of satellite tracked individuals prevented us from using more advanced methods to assess the count data with the use of tracking data (Booms et al., 2021; Clausen et al., 2019; Dennhardt

et al., 2015; Ganter & Madsen, 2001). However, the available data from these counts provided a possibility to carry out the most simple comparison between tracking and count data. Our results indicate that these counts could underestimate the true population size, as some of the tracked birds were not present in any of the count sites at the time they were counted. This result is in line with the previous studies comparing satellite tracking data and total counts, which have revealed that total counts likely underestimate the true population sizes of various animals (Battaile et al., 2017; Dennhardt et al., 2015; Schummer et al., 2018). This is mainly caused by the birds moving between the count sites during the count period or migrating to known staging sites outside the overall count area (for example flying to Finland during the spring count), but not by birds being in some unknown sites outside the count sites. We also note that the birds from the staging sites in southwestern Finland (as well as the few birds still lingering at the wintering sites) are included in the final estimates of the taiga bean goose population size made from spring counts (Skjyllberg, 2015). This is done to correct the underestimation bias caused by the birds leaving to Finland before the counts. However, it also increases the possibility for double-counting, as birds that are counted once in Sweden can be included in the bird numbers monitored at Finnish staging sites (which was the case with one satellite tracked bird in our study in the spring 2021).

Our original intention was to compare the satellite tracking data with the mid-winter census data also. However, sufficient data from these counts were not available even from Sweden, which is why we excluded them from the analysis. We note that bird numbers on mid-winter counts are known to correlate positively with January temperature (Nilsson, 2013), and they are also known to produce lower population size estimates than spring and autumn counts (Heldbjerg et al., 2019). These are probably caused by birds moving further south (especially to Germany) during cold winters and the lack of any available count data from Germany (Heldbjerg et al., 2019). As results from the Swedish mid-winter counts are used in the integrated population model (Johnson et al., 2021) to monitor the taiga bean goose population size for the purposes of international management, it would be important to study their performance in the future. In addition, it would be vital to develop mid-winter counts also in Germany and to merge these data with the Swedish count data.

To improve the current taiga bean goose censuses in the future and to increase the accuracy and transparency of the population size estimates, we suggest three actions to carry out in the future. First, the documentation of the counts should include the areas covered by

the counts with precise timestamps. Second, it would be important to carry out each census simultaneously at all count sites, which would avoid some of the bias introduced by birds moving during the count (which seems to be currently the most important source of bias). Third, population size estimates (based on total counts) should be evaluated also in the future, preferably providing corrected population size estimates. The evaluation could be done, for example, using some of the several variants of mark-recapture-based population size estimates, or modeling the spatial distribution of the population as a density function (using tracking data), and using counts to draw samples for population size estimates from that function. These studies would, however, require a higher number of tracked animals (distributed randomly to the population).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Antti Piironen designed the study (together with Toni Laaksonen), led the field work for capturing and marking of geese in Finland, Anthony D. Fox and Ole Roland Therkildsen were responsible for the same during the earlier project in Denmark. Ulf Skjyllberg and Hakon Kampe-Persson provided the census data and participated in the writing of the manuscript. Toni Laaksonen conceived the original idea, designed the study (together with Antti Piironen), participated in the writing of the manuscript and supervised throughout the process. Antti Piironen led the manuscript writing, aided by all other coauthors, who agreed to the final version.

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REFERENCES

- Alisauskas, R. T., Arnold, T. W., Leafloor, J. O., Otis, D. L., & Sedinger, J. S. (2014). Lincoln estimates of mallard (*Anas platyrhynchos*) abundance in North America. *Ecology and Evolution*, 4, 132–143. <https://doi.org/10.1002/ece3.906>
- Battaile, B. C., Jay, C. V., Udevitz, M. S., & Fischbach, A. S. (2017). Evaluation of a method using survey counts and tag data to estimate the number of Pacific walrus (*Odobenus rosmarus divergens*) using a coastal haulout in northwestern Alaska. *Polar Biology*, 40, 1359–1369. <https://doi.org/10.1007/s00300-016-2060-5>
- Boer, J. (2019). *Migration routes, stopover sites and home range sizes of taiga bean geese (Anser fabalis fabalis) breeding in northern Sweden and Central Norway tracked by GPS tags* [Master's thesis, Swedish University of Agricultural Sciences]. <https://stud.epsilon.slu.se>
- Booms, T. L., Paprocki, N. A., Eisaguirre, J. M., Barger, C. P., Lewis, S. B., & Breed, G. A. (2021). Golden eagle abundance in Alaska: Migration counts and movement data generate a conservative population estimate. *Journal of Raptor Research*, 55, 496–509. <https://doi.org/doi.org/10.3356/JRR-20-81>
- Calenge, C. (2006). The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 516–519. <https://doi.org/10.1016/j.ecolmodel.2006.03.017>
- Clausen, K. K., Balsby, T. J. S., Goma, V., & Madsen, J. (2019). Using re-sighting data to estimate population size of Pink-footed Geese (*Anser brachyrhynchus*). *Ornis Fennica*, 96, 112–123.
- Cohen, E. B., Hostetler, J. A., Hallworth, M. T., Rushing, C. S., Sillet, T. S., & Marra, P. P. (2017). Quantifying the strength of migratory connectivity. *Methods in Ecology and Evolution*, 9, 513–524. <https://doi.org/10.1111/2041-210X.12916>
- Cotton, P. A. (2003). Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences*, 100, 12219–12222. <https://doi.org/10.1073/pnas.1930548100>
- Cramp, S., & Simmons, K. E. I. (1977). *The birds of the Western Palearctic 1*. Oxford University Press.
- Delany, S., & Scott, D. A. (2005). *AEWA Conservation guidelines No. 9. Guidelines for waterbirds monitoring protocol*. AEWA technical series no. 24. Wageningen.
- Dennhardt, A. J., Duerr, A. E., Brandes, D., & Katzner, T. E. (2015). Integrating citizen-science data with movement models to estimate the size of a migratory golden eagle population. *Biological Conservation*, 184, 68–78. <https://doi.org/10.1016/j.biocon.2015.01.003>
- Finger, T. A., Afton, A. D., Schummer, M. L., Petrie, S. A., Badzinski, S. S., Johnson, M. A., Szymanski, M. L., Jacobs, K. J., Olsen, G. H., & Mitchell, M. A. (2016). Environmental factors influence lesser scaup migration chronology and population monitoring. *Journal of Wildlife Management*, 80, 1437–1449. <https://doi.org/10.1002/jwmg.21131>
- Fox, A. D., & Leafloor, J. O. (2018). *A global audit of the status and trends of Arctic and Northern Hemisphere goose populations*. Conservation of Arctic Flora and Fauna International Secretariat.
- Fox, A. D., Mitchell, C., Stewart, A., Fletcher, J. D., Turner, J. V. N., Boyd, H., Shimmings, P., Salmon, D. G., Haines, W. G., & Tomlinson, C. (1994). Winter movements and site-fidelity of Pink-footed Geese *Anser brachyrhynchus* ringed in Britain, with particular emphasis on those marked in Lancashire. *Bird Study*, 41, 221–234. <https://doi.org/10.1080/00063659409477222>
- Ganter, B., & Madsen, J. (2001). An examination of methods to estimate population size in wintering geese. *Bird Study*, 48, 90–101.
- Heinicke, T., Fox, A. D., & de Jong, A. (2018). A1 western taiga bean goose *Anser fabalis fabalis*. In A. D. Fox & J. O. Leafloor (Eds.), *A global audit of the status and trends of Arctic and northern hemisphere goose populations*. Conservation of Arctic Flora and Fauna International Secretariat.
- Heldbjerg, H., Fox, A.D., Christensen, T.K., Clausen, P., Kampe-Persson, H., Koffijberg, K., Liljebäck, N., Mitchell, C., Nilsson, L., Skjallberg, U. & Alhainen, M. 2019. *Taiga bean goose population status report 2018/2019*. AEWA EGMP technical report no. 14. AEWA.
- Honka, J., Bains, S., Searle, J., Kvist, L., & Aspi, J. (2022). Genetic assessment reveals inbreeding, possible hybridization and low levels of genetic structure in a declining goose population. *Ecology and Evolution*, 12, e8547. <https://doi.org/10.1002/ece3.8547>
- Johnson, F. A., Alhainen, M., Fox, A. D., & Madsen, J. (2016). *Development of an adaptive harvest management program for taiga bean geese (Anser fabalis fabalis)*. Technical Progress Summary I. AEWA EGMP technical report no. 2. AEWA.
- Johnson, F. A., Heldbjerg, H., & Mäntyniemi, S. (2021). *An integrated population model for the central management unit of taiga bean geese*. AEWA European goose management platform report. AEWA.
- Johnson, F. A., Zimmerman, G. S., Jensen, G. H., Clausen, K. K., Frederiksen, M., & Madsen, J. (2020). Using integrated population models for insights into monitoring programs: An

- application using pink-footed geese. *Ecological Modelling*, 415, 108869. <https://doi.org/10.1016/j.ecolmodel.2019.108869>
- Kampe-Persson, H. (2017). Höstinventering. *Vår Fågelvärld*, 76, 38–40 [In Swedish].
- Knight, E. C., Harrison, A. L., Scarpignato, A. L., Van Wilgenburg, S. L., Bayne, E. M., Ng, J. W., Angell, E., Bowman, R., Brigham, R. M., Drolet, B., Easton, W. E., Forrester, T. R., Foster, J. T., Hache, S., Hannah, K. C., Hick, K. G., Ibarzabal, J., Imlay, T. L., Mackenzie, S. A., ... Marra, P. P. (2021). Comprehensive estimation of spatial and temporal migratory connectivity across the annual cycle to direct conservation efforts. *Ecography*, 44, 665–679. <https://doi.org/10.1111/ecog.05111>
- Kölzsch, A., Müskens, G. J., Szinai, P., Moonen, S., Glazov, P., Kruckenberg, H., Wikelski, M., & Nolet, B. A. (2019). Flyway connectivity and exchange primarily driven by moult migration in geese. *Movement Ecology*, 7, 1–11. <https://doi.org/10.1186/s40462-019-0148-6>
- Madsen, J., Williams, J. H., Johnson, F. A., Tombre, I. M., Dereliev, S., & 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>
- Maes, D., Isaac, N. J. B., Harrower, C. A., Collen, B., van Strien, A. J., & Roy, D. B. (2015). The use of opportunistic data for IUCN Red List assessments. *Biological Journal of the Linnean Society*, 115, 690–706. <https://doi.org/10.1111/bij.12530>
- Marjakangas, A., Alhainen, M., Fox, A. D., Heinicke, T., Madsen, J., Nilsson, L., & Rozenfeld, S. (2015). *International single species action plan for the conservation of the taiga bean goose Anser fabalis fabalis*. AEWA Technical Series No. 56. AEWA.
- Mitchell, C., Griffin, L., Maciver, A., Minshull, B., & Makan, N. (2016). Use of GPS tags to describe the home ranges, migration routes, stop-over locations and breeding area of taiga bean geese *Anser fabalis fabalis* wintering in central Scotland. *Bird Study*, 63, 437–446. <https://doi.org/10.1080/00063657.2016.1236779>
- Mohr, C. O. (1947). Table of equivalent populations of North American small mammals. *American Midland Naturalist*, 37, 223–249.
- Nilsson, L. (2011). The migrations of Finnish bean geese *Anser fabalis* in 1978–2011. *Ornis Svecica*, 21, 157–166.
- Nilsson, L. (2013). Censuses of autumn staging and wintering goose populations in Sweden 1977/1978–2011/2012. *Ornis Svecica*, 23, 3–45.
- Nilsson, L., & Kampe-Persson, H. (2020). Changes in numbers of staging and wintering geese in Sweden: 1977/78–2019/20. *Wild*, 70, 107–126.
- Nilsson, L., van den Bergh, L., & Madsen, J. (1999). Taiga bean goose *Anser fabalis fabalis*. In J. Madsen, A. D. Fox, & G. Cracknell (Eds.), *Goose populations of the Western Palearctic. A review of status and distribution* (1st ed.). Wetlands International.
- Picardi, S., Smith, B. J., Boone, M. E., Frederick, P. C., Cecere, J. G., Rubolini, D., Serra, L., Pirrello, S., Borkhataria, R. R., & Basille, M. (2020). Analysis of movement recursions to detect reproductive events and estimate their fate in central place foragers. *Movement Ecology*, 8, 24. <https://doi.org/10.1186/s40462-020-00201-1>
- Piironen, A., Paasivaara, A., & Laaksonen, T. (2021). Birds of three worlds: Moulting migration expands a boreal-temperate flyway to a third biome. *Movement Ecology*, 9, 47. <https://doi.org/10.1186/s40462-021-00284-4>
- Pirkola, M. K., & Kalinainen, P. (1994). The status, habitats and productivity of breeding populations of bean goose, *Anser fabalis fabalis*. *Swedish Wildlife Research*, 13, 9–48.
- R Core Team. (2020). *A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.r-project.org/>
- Rohwer, F. C., & Anderson, M. G. (1988). Female-biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. In R. F. Johnston (Ed.), *Current ornithology*, 5. Springer.
- Schummer, M. L., Afton, A. D., Badzinski, S. S., Petrie, S. A., Olsen, G. H., & Mitchell, M. A. (2018). Evaluating the waterfowl breeding population and habitat survey for scaup. *Journal of Wildlife Management*, 82, 1252–1262. <https://doi.org/10.1002/jwmg.21478>
- Skyllberg, U. (2015). Numbers of taiga bean geese *Anser f. fabalis* utilizing the western and central flyways through Sweden during springtime 2007–2015. *Ornis Svecica*, 5, 153–165. <https://doi.org/10.34080/os.v25.22542>
- Skyllberg, U., & Tjernberg, M. (2008). Spring staging of taiga bean goose (*Anser f. fabalis*) in southern Sweden 2007—Estimate of the size of populations using the western and central flyway. *Ornis Svecica*, 18, 45–51. <https://doi.org/10.34080/os.v18.22677>
- Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S., & Holmes, R. T. (2002). Links between worlds: Unraveling migratory connectivity. *Trends in Ecology and Evolution*, 17, 76–83. [https://doi.org/10.1016/S0169-5347\(01\)02380-1](https://doi.org/10.1016/S0169-5347(01)02380-1)
- Wilson, H. J., Norriss, D. W., Walsh, A., Fox, A. D., & Stroud, D. A. (1991). Winter site fidelity in Greenland white-fronted geese *Anser albifrons flavirostris*: Implications for conservation and management. *Ardea*, 79, 287–294.

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