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ABSTRACT

Knowledge on flyway structures, year-round spatiotemporal distributions and migration strategies is a key for understanding the ecology of migratory populations and the evolution of migratory behaviours. Knowledge on these factors is also a prerequisite to reliably estimate the size and trend of migratory populations, and to successfully conserve and manage them.

In this thesis, I studied the migratory behaviour of two goose species, the bean goose (*Anser fabalis*) and the greylag goose (*Anser anser*) using high-resolution satellite tracking, traditional neckbanding and birdwatcher observations. Satellite tracked taiga bean geese belonging to the Central Flyway population revealed a comprehensive moult migration of non-breeding and unsuccessfully breeding birds to the Arctic. This behaviour increases the length of the annual migration distance and delays the autumn migration of moult migrants. The strength of migratory connectivity among the population was moderate to low between breeding and non-breeding areas, and both migratory connectivity and the spatial distribution of the population varied substantially within the non-breeding season. Additionally, satellite tracking indicated that the current population censuses might underestimate the size of the taiga bean goose population. Birdwatcher observations showed both spatial and temporal difference in occurrence of different bean goose subspecies in Finland during spring and autumn migrations, which affects the harvest management of the subspecies with different conservation statuses.

The satellite tracking data and neckband resightings of greylag geese confirmed the existence of a gradual migratory divide in the continuous breeding distribution of the species. The birds breeding at the different ends of the greylag goose breeding distribution in Finland used different flyways (Western and Central), and the birds breeding between these two extremes scattered to the two flyways. The migration strategies differed between the flyways. The overall migratory journey is longer for birds using the Western Flyway, and these birds migrate earlier in autumn and later in spring than birds on the Central Flyway. Birds using the Western Flyway also show a clear stopover of around one month during their autumn migration, whereas Central Flyway birds migrate relatively straight from their breeding grounds to their wintering sites.

The results of the thesis help to delineate the flyways of both species, provide aspects needed to understand their ecology, and supports the ongoing international management of the species. Furthermore, the results build possibilities to further study not only these two species, but also more general ecological questions related to bird migration and movement ecology.

KEYWORDS: migration, migratory behaviour, migration strategy, migratory connectivity, moult migration, movement ecology, flyway, waterfowl, gps, gaussian process

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TIIVISTELMÄ

Populaatiotason muuttoreittien, muuttostrategioiden ja koko vuodenkierron aikaisten esiintymisalueiden tunteminen on edellytys muuttavien eläinten ekologian ja muuttokäyttäytymisen evoluution ymmärtämiseksi. Se on myös ennakkoedellytys muuttavien eläinten kannan koon ja kehityksen arvioinnille sekä menestyksekkäälle kannanhoidolle ja suojelulle.

Tutkin väitöskirjassani kahden hanhilajin, metsähanhen (*Anser fabalis*) ja merihanhen (*Anser anser*) muuttokäyttäytymistä käyttäen korkean resoluution satelliittiseurantaa, perinteisiä lukurenkaita ja lintuharrastajien havaintoaineistoa. Satelliittiseuranta paljasti keskiseen osapopulaatioon kuuluvien, pesimättömien ja pesinnässään epäonnistuneiden taigametsähanhien muuttavan kesäisin säännönmukaisesti Arktikselle sulkasatoa varten. Sulkasatomuutto tundralle yli kaksinkertaistaa näiden lintujen vuotuisen muuttomatkan ja viivästyttää niiden syysmuuttoa populaation muihin yksilöihin verrattuna. Taigametsähanhipopulaation kytkeytyneisyys pesimäalueiden ja lintujen muina vuodenaikoina käyttämien alueiden välillä on kohtalaista tai heikkoa, ja populaation kytkeytyneisyys sekä sen esiintymisalueen laajuus vaihtelevat voimakkaasti vuodenkierron aikana. Satelliittiseurannan perusteella nykyiset laskennat aliarvioivan taigametsähanhien määrän. Lintuharrastajien havaintoaineisto osoittaa metsähanhien eri alalajien esiintymisen eroavan toisistaan sekä ajallisesti että maantieteellisesti syys- ja kevätmuuton aikaan Suomessa, mikä on vaikuttaa lajin optimaaliseen metsästyksen säätelyyn.

Merihanhien satelliittiseuranta ja kaularengashavainnot vahvistivat, että lajin levinneisyysalueella Suomessa on niin sanottu vaiheittainen muutonjakaja. Levinneisyysalueen ääripäissä linnut käyttävät eri muuttoreittejä (keskistä ja läntistä reittiä), ja levinneisyysalueen keskiosista linnut hajaantuvat näille kahdelle reitille. Myös merihanhien muuttostrategia eroaa muuttoreittien välillä. Läntistä reittiä käyttävien lintujen vuotuinen muuttomatka on pidempi, ja linnut muuttavat aiemmin syksyllä ja myöhemmin keväällä kuin keskistä muuttoreittiä käyttävät linnut. Läntistä muuttoreittiä käyttävät linnut pysähtyvät levähtämään noin kuukaudeksi kesken syysmuuton, kun taas keskistä muuttoreittiä käyttävät linnut muuttavat pesimäalueiltaan pysähdyksittä talvehtimisalueilleen.

Väitöskirjani tulokset auttavat molempien lajien populaatiotason muuttoreittien hahmottamisessa, niiden ekologian ymmärtämisessä ja tukevat lajien kansainvälistä kannanhoitoa. Lisäksi tulokset luovat edellytyksiä tutkia jatkossa yleisiä ekologisia kysymyksiä lintujen muuttoon ja liikkumisekologiaan liittyen.

ASIASANAT: muutto, muuttokäyttäytyminen, muuttostrategia, kytkeytyneisyys, sulkasatomuutto, liikkumisekologia, muuttotie, vesilintu, gps, gaussinen prosessi

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List of Original Publications

This dissertation is based on the following original publications, which are referred to in the text by their Roman numerals:

I 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.

II Piironen, A., Piironen, J. & Laaksonen, T. 2022. 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

III Piironen, A., Fox, A.D., Kampe-Persson, H., Skyllberg, U., Therkildsen, O. & Laaksonen, T. 2022. When and where to count? Implications of migratory connectivity and non-breeding distribution to population censuses in a migratory bird population. *Population Ecology*, early view. https://doi.org/10.1002/1438-390X.12143

IV Piironen, A. & Laaksonen, T. 2022. A gradual migratory divide determines not only the direction of migration but also migration strategy of a social migrant bird. Manuscript. Pre-print available at: https://biorxiv.org/cgi/content/short/2023.02.24.529898v1

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1 Introduction

1.1 Migration and migratory connectivity

Migration is a taxonomically widespread phenomenon comprising regular, seasonal movements of animals (Alerstam et al., 2003; Newton, 2008). Movements between several biomes and habitats allow animals to use spatially and temporally versatile resources and thus enables them to utilize areas where they cannot live over the whole annual cycle (Alerstam et al., 2003). Every year, billions of animals perform impressive long-distance movements, tracking these periodically available resources and avoiding unfavourable environmental conditions (Thorup et al., 2017). By doing so, migratory animals transport seeds, nutrients, parasites, pathogens etc. between the habitats they use during the annual cycle and thereby link ecological communities to each other, transferring changes from one community to another (Bauer & Hoye, 2014). Therefore, comprehensive understanding of the migration patterns of animals is vital to understand how environmental conditions affect their population dynamics but also how the animals affect the environment they live in.

Migratory connectivity (the co-occurrence of animals originating from different breeding sites throughout the annual cycle; Webster et al., 2002) is an essential concept when assessing which areas are connected by migratory animals and which environments migratory animals depend on during the annual cycle. Migratory connectivity is high when individuals from the 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. Therefore, migratory connectivity provides a useful measure of how separate elements of a population may remain together throughout the annual cycle (Webster et al., 2002; Cohen et al., 2017). The strength of migratory connectivity between breeding and non-breeding sites can vary between various phases of the non-breeding seasons (Knight et al., 2021). Migratory connectivity has wide-reaching impacts on the population dynamics, behaviour, and evolution of migratory species along with their conservation and management (Webster et al., 2002). Additionally, connectivity measurements help to reveal population clustering through the non-breeding season and its implications for population size assessment (i.e. when and where individuals should be counted to avoid missing any clusters).

Together with measurements of the spatial dispersion of populations, measurements of migratory connectivity over the annual cycle also help identify the most favourable periods for population size assessment.

1.2 Flyway delineation and migratory divides

To understand the ecology of migratory animals and to successfully conserve and manage them, identification of flyways is one of the most essential steps to take. Flyways of populations (or subpopulations) are formed when the annual movements of migratory birds belonging to the same population are combined together. In other words, flyways consist of all habitats used by the birds during the annual cycle (Boere & Stroud, 2006). Flyways are often separated by migratory divides, i.e. contact zones where birds of the same species orientate to different directions during the non-breeding season to reach their wintering grounds (Newton, 2008). By separating flyways, migratory divides drive intraspecific genetic differentiation and reproductive isolation (Bearhop et al., 2005; Boulet et al., 2006; Rolshausen et al., 2009). They also create geographically independent, intraspecific population entities (often called management units), which form the base units for the conservation and management of migratory species (Boulet et al., 2006; Faaborg et al., 2010). Migratory divides also affect the availability of habitats that individuals of the same species can utilize during the non-breeding season, which may facilitate intraspecific differences in migration strategies (Alerstam & Lindström, 1990) on distinct flyways.

The structure of a migratory divide (gradual vs. precipitous) is likely to affect its ecological and evolutionary implications (for example, genetic differentiation and reproductive isolation; Delmore & Irwin, 2014). Presumably, on a continuous breeding range without any geographical obstacles, the structure of a divide would differ from one existing alongside a geographical barrier (such as a sea, mountain, or desert). However, previous studies have not tracked individuals breeding both on a divide and at different distances from it, and thus the structure of the divide has usually remained unknown (e.g. Bearhop et al., 2005; Boulet et al., 2006; Delmore et al., 2012; Hobson et al., 2015; van Bemmelen et al., 2019). This has possibly led to a simplified understanding regarding the structure of the migratory divides, as only precipitous divides have been described. Additionally, conservation and management would probably benefit from knowledge regarding the location of the divides, as the precise delineation of flyways (and thus, populations) is essential for them (Madsen et al., 2014). To better understand the ecological, evolutionary, and conservation implications of migratory divides, it is important to unravel their structures and locations by studying the migratory behaviour of individuals breeding at different distances from a migratory divide.

1.3 Migration strategies and optimal bird migration

When birds move along their flyways, the core choices for them to be made regarding their migration are 1) the location and number of wintering and stopover sites, 2) duration of the wintering period and of each stopover, and 3) the timing of movement between breeding, wintering, and stopover sites. These decisions can be referred to as a migration strategy (Alerstam & Lindström, 1990), which is known to have important ecological and evolutionary consequences, along with considerable conservation and management implications (e.g. Bearhop et al., 2005; Delmore et al., 2012). Migration strategy is thought to be guided by the availability of suitable habitat (Alerstam & Lindström, 1990; Gudmundsson et al., 1991), although other factors, such as weather, are also known to play a role (e.g. Tøttrup et al., 2008; Tøttrup et al., 2012). According to the optimal migration theory (Alerstam & Lindström, 1990), birds can be expected to show a migration strategy consisting of frequent stopovers (refuelling periods) and short flights between the stopover sites to minimize the costs of flying with the fuel loads (fat reserves), if suitable habitats for stopovers are abundant along the flyway. Accordingly, if suitable habitats are far away from each other in the flyway, birds would be forced to show longer flights between them. When comparing birds using distinct flyways, similar migration strategies would be expected between populations using different flyways whenever suitable habitats are equally distributed between different flyways (and different strategies if habitats are not equally distributed). However, intraspecific comparisons of migration strategies between populations using different flyways (with different habitat characteristics) have produced contradicting results: Some studies have found differing strategies (Buehler & Piersma, 2008; Delmore et al., 2012; Alves et al., 2013, van Bemmelen et al., 2019) between flyway populations. However, also surprisingly similar strategies have been found from populations using distinct flyways with different habitat characteristics (Fraser et al., 2013; Trierweiler et al., 2014), indicating that factors other than the availability of suitable habitat can also contribute to migration strategies. As conditions faced during the non-breeding season (and thus, migration strategy) are known to affect breeding populations through survival and productivity (e.g. Marra et al., 1998; Norris et al., 2004), exploring the migration strategies of populations using distinct flyways is important for a better understanding of not only the factors guiding migration strategy, but also the drivers of population dynamics of migratory populations.

1.4 Moult migration

For birds, migration often means moving between breeding sites at higher latitudes and wintering sites at lower latitudes, with some stopover sites *en route* (Greenberg

& Marra, 2005). However, this view is sometimes complicated by other, rarer migratory behaviours (Newton, 2008). Among waterfowl species, one such behaviour is moult migration, a phenomenon where a part of the population disperses (usually) outside of the breeding range during the breeding season for wing moult (Salomonsen, 1968). Most ducks and geese moult and regrow all their flight feathers simultaneously during summer, which leaves them flightless for several weeks every year (Hohman et al., 1992). In many species, a part of the population leaves the breeding area to moult somewhere else. Moult migration can dramatically impact migratory connectivity and thus, flyways of populations (Øien et al., 2009), and it can also have important ecological (Luukkonen et al., 2008) and evolutionary (Kölzsch et al., 2019) consequences. Therefore, unravelling moult migration patterns of waterfowl populations is important for understanding the migratory behaviour and flyway structure of the populations and for further understanding the drivers of their population dynamics. Moreover, the impacts of moult migration on migratory patterns must be known to estimate the size of the populations and to successfully conserve and manage them.

1.5 Study species

In my thesis, I study migratory behaviour of two goose species, the greylag goose (*Anser anser*) and the two subspecies of bean goose (*Anser fabalis*). The Western Palearctic taiga bean goose (*Anser fabalis fabalis*, hereafter taiga bean goose) is one of the two subspecies of bean goose, which regularly occurs in Europe. The taiga bean goose population is commonly divided into four subpopulations (or management units) based on their separate flyways (Marjakangas et al., 2015; Heinicke et al., 2018). The Central Flyway is the main flyway for taiga bean geese, holding over 60 per cent of the whole subspecies (Heinicke et al., 2018). These birds breed in Fennoscandia and Northwestern Russia and migrate across Finland to winter mainly in southern Sweden (Nilsson et al. 1999), and some of them also move to Denmark and the northern parts of Germany and Poland, especially during cold winters (Nilsson et al., 1999). The movements of the non-breeding part of the population during the breeding season are poorly known, but some observations regarding the moult migration to Novaya Zemlya have been made (Nilsson et al., 2009). In addition to this, the movements of birds breeding in Northwestern Russia are completely unknown.

The Western Palearctic tundra bean goose (*Anser fabalis rossicus*, hereafter tundra bean goose) is the other subspecies of the bean goose, which regularly occurs in Europe. Its population has doubled since the late 1980s and is recently estimated at 600,000–650,000 individuals (Heinicke, 2018). Tundra bean geese breed in the tundra zone and winter in a broad area in Western and Central Europe, and hence the wintering distribution is mainly different from that of taiga bean geese (Heinicke, 2018; Heinicke et al., 2018). However, the subspecies can overlap during migrations at stop-over sites (de Jong et al., 2013; Honka et al., 2017), but the spatiotemporal distribution of both subspecies are poorly understood.

Greylag geese have increased in numbers in recent decades in Europe (Fox & Leafloor, 2018). The European population breeds on a large area around the Baltic Sea and is often divided into two flyways: The Western Flyway (or Northwest Flyway) and Central Flyway (Madsen et al., 1999; Fox & Leafloor, 2018). Birds using the Western Flyway breed in Fennoscandia and Western Europe, and winter sporadically in Western Europe (Nilsson, 2018). The breeding range of birds using the Central Flyway reaches from Southern Finland in the north to Czechia and Slovakia in the south, and the wintering sites are located sporadically around the Mediterranean Sea (Azafzaf et al., 2018). However, the movements of Finnish greylag geese have never been studied, and all information on them is based on old and scarce ring recovery data (see Andersson et al., 2001). Thereby, the existence of the presumed migratory divide has remained unverified, not to mention its location. Moreover, the migration strategy of greylag geese breeding in Finland is completely unknown.

1.6 Aims of the thesis

In this thesis, I studied several aspects regarding the migratory behaviour of bean geese and greylag geese. Previously, these aspects have been poorly known, but they are important for understanding the evolution and ecological implications of these migration patterns, and for successful management of the populations.

In chapter I, I studied the moult migration among the taiga bean goose population utilizing the Central Flyway and revealed the details regarding the moult migration. These details include exact moulting sites of birds breeding at different sites, the migratory connectivity between the breeding and moulting sites, and the impact of moult migration to the migratory performance of moult migrants compared with individuals that do not moult migrate.

In chapter II, I studied spatiotemporal differences in the occurrence of different taiga and tundra bean geese in Finland during migration periods. Additionally, the chapter introduces a general-purpose R package `gplite` (Piironen, 2021) for fitting Gaussian process (GP) models and promotes GP models for further usage in ecology.

In chapter III, I described the overall movements of the Central Flyway population of the taiga bean geese during the annual cycle (including movements of birds breeding in Western Russia) and studied the effects of migratory connectivity and spatial dispersion to the assessment of the taiga bean goose population size.

Additionally, the performance of the current population censuses is evaluated in chapter III.

In chapter IV, I studied the existence and the structure of the migratory divide among the greylag goose breeding distribution in Finland and migration strategies of birds across the divide in the light of optimal migration theory (Alerstam & Lindström, 1990).

2 Materials and Methods

2.1 Capture sites

In chapter I, III and IV, I used individual satellite tracking as a common approach to study migratory behaviour of geese. In addition, I used resightings of neckbanded geese to study the migratory divide in chapter IV and birdwatcher observation data to study spatiotemporal differences in the occurrence of bean goose subspecies in chapter II. The capture sites for geese caught for satellite tracking and neckbanding in chapters I, III and IV are shown in Figure 1. Apart from the taiga bean geese (n = 10) marked at a wintering site in Denmark (at Lille Vildmose, Jutland, 56°54’N 10°13’E) in chapter III, all taiga bean geese were caught in Finland. The capture sites in Finland were located at stopover sites at Outokumpu and Liperi (lat 62° 42ˈ lon 29° 07ˈ) in North Karelia, and at breeding grounds at Virrat in South Ostrobothnia (latitude (lat) 62° 22ˈ longitude (lon) 23° 16ˈ), Lieksa in North Karelia (lat 63° 16ˈ lon 30° 28ˈ), Pudasjärvi and Utajärvi in North Ostrobothnia (lat 65° 04ˈ lon 26° 50ˈ and lat 65° 12ˈ lon 26° 52ˈ, respectively), and Salla in Lapland (lat 66° 51ˈ lon 28° 36ˈ). The greylag geese used in chapter IV were caught at their breeding sites throughout the species’ breeding distribution in Finland (i.e. along the Baltic Sea coast in Finland).

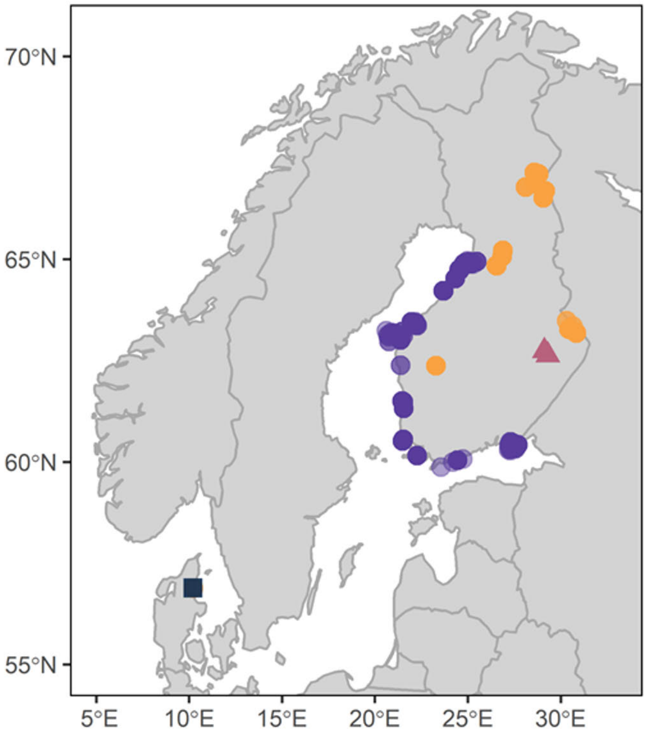


Figure 1. Capture and marking sites of geese used in the study. All greylag geese were marked at the breeding sites in Finland (blue circles), and taiga bean geese were marked at their breeding (yellow circles) and staging (burgundy triangles) sites in Finland, and at a wintering site at Lille Vildmose, Denmark (dark blue square).

2.2 Satellite tracking and neckbanding

In chapters I and III, I studied the migratory behaviour of the taiga bean geese using satellite tracking. In chapter I, all birds (n = 55) were marked in 2019–2020 at the breeding and stopover sites in Finland. In chapter III, the majority of the birds (n = 61) were marked in Finland in 2019–2021 and an additional ten birds were marked at Lille Vildmose in Denmark in 2014–2015. The birds marked in Denmark were caught using large clap nets by decoying wild birds with tame geese. They were marked with GPS-GSM transmitters (Ibis solar-powered neck-collars produced by Ecotone Telemetry) that had GPS resolutions set to two hours. The devices transmitted the data via GSM-SMS.

In Finland, all taiga bean geese were caught using cannon-nets combined with short-term artificial feeding, and the caught birds were equipped with GPS-GSM transmitters (OrniTrack-44 solar-powered neck-collars produced by Ornitela UAB). The GPS resolution was set to ten minutes at high battery level, but it was allowed to decrease with the battery level. The transmitter logs GPS positions and sends data to the server via a GSM/GPRS network either by e-mail or SMS.

In chapter IV, I studied the migratory behaviour of greylag geese also using satellite tracking. The satellite-tracked greylag geese (n = 71) were marked in 2019–2022 at different sites across their breeding distribution in Finland (see Fig. 1). The majority of the birds were caught using cannon-netting combined with short-term artificial feeding, and some birds were also caught at sea with a hand net after a short chase with a motor-driven boat when they were flightless due to remigial moult. The devices used for satellite tracking (as well as their settings) were identical to the ones used for taiga bean geese in Finland in chapters I and III (i.e. OrniTrack-44 by Ornitela UAB were used).

All caught birds (both taiga bean geese and greylag geese) were sexed with a cloacal examination and aged based on the shape of the wing coverts. GPS transmitters were deployed only onto adult birds (at least two years old) and females were preferred as they show the highest fidelity to their breeding sites (Rohwer & Anderson, 1988), and as the inference regarding the breeding time events (such as timing of incubation, hatching and brood loss etc.) is easier from movements of females than from movements of males. In chapter IV, neckband resighting data were also used to the study migratory divide in greylag geese. The neckbanded birds (altogether n = 115 birds were used in the analysis) were caught in the same capture events as those marked with GPS transmitters, and they were also aged and sexed using the same methods. Birds from all cohorts were marked with neckbands, and neckbanded birds were resighted opportunistically throughout the year by voluntary observers. Neckband resightings were received from the website www.geese.org and from the database of the Finnish Bird Ringing Centre.

2.3 Bird observation data

I received the birdwatcher observation data used in chapter II from BirdLife Finland, and they were collected during 2011–2019 via the online bird observation portal Tiira (https://www.tiira.fi/). Species, location, date, and number of observed birds are mandatory information provided in the observation. In the analysis, only observations where the subspecies was identified and where the bird's status was recorded as local (i.e. not flying) were used.

It is noteworthy that the birdwatcher observation data contain two main sources of uncertainty. First, the observation effort is not evenly distributed spatially or temporally. This not a problem in the analysis performed in chapter II, as it will only increase the uncertainty of the model predictions in regions and times with few observations (note that only the subspecies ratio was of interest in the analysis). Second, observations are made by numerous birdwatchers with unknown and variable expertise, possibly generating incorrectly identified birds into the data. However, the low percentage (c. 40%) of bean goose observations identified to subspecies level among all bean goose observations indicates that birdwatchers are somewhat prudent in difficult identification situations, and the majority report their observations only when they are confident with the identification. Additionally, temporal differences in subspecies composition in the same area indicate that no obvious or severe spatial biases exist in subspecies identification. Therefore, erroneous observations can be considered to be randomly distributed in the observation data.

2.4 Analysis of satellite tracking data

In chapters I and III, I analysed the nesting status and success of females using location revisitation metrics (Picardi et al., 2020; see chapters I and III for details). Breeding males were identified from non-breeding males when they joined the females and goslings after hatching, i.e. once they stopped flying and began moving continuously by walking before mid-June (moult period). I assessed the brood-rearing success in chapter I for both males and females using the same criteria (a bird was considered to be with a brood if at least 99 per cent of daily locations indicated movement at a speed of ≤ 20 km/h). Individuals caught and GPS-tagged during moult or right after moult were in flocks including both adults and juveniles, and thus all these adults were considered successful breeders.

In chapters I and III, I measured the strength of migratory connectivity between breeding and non-breeding sites using Mantel's correlation (r_M), a correlation between two (distance) matrices and ranging between −1 and 1, so that 1 expresses full connectivity (individuals that breed close to each other are also close to each other during the non-breeding 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 non-breeding season, Cohen et al., 2017). In chapter III, r_M was calculated between the breeding sites and the daily locations during the non-breeding season. The fact that birds used in chapter III 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, r_M was calculated not only for all birds, but also for the birds only marked near the breeding sites. In chapter I, r_M was calculated only between the breeding and moulting locations, and 1000 bootstrap samples were obtained to get an uncertainty estimate for connectivity.

In chapter III, I assessed the performance of different taiga bean goose population censuses by comparing satellite tracks of tagged geese to the positions and timing of the counts (note that all of them are so-called total counts). The count data were compared to satellite tracking data from all individuals tracked during the count (for autumn 2019 and spring 2020 n = 16, for spring 2021 n = 40). The comparison was done simply by comparing whether the locations of satellite-tracked birds matched with the locations and timestamps of the counts.

In chapter IV, I quantified the migratory behaviour of satellite-tracked greylag geese by measuring their daily displacement from the breeding site. The displacement was measured between a random location for each individual per day and the first location on 1 July in the first year the bird was tracked. All analyses of satellite tracking data were performed using packages `adehabitatHR` (Calenge, 2006), `MigConnectivity` (Cohen et al., 2017), `move` (Kranstauber et al., 2021), `Rnest` (Picardi et al., 2020), and related packages in R software (R Core Team, 2021).

2.5 Statistical methods

In chapter I, I studied the effect of moult migration on the timing of autumn migration using linear models. In chapter IV, I analysed the location and structure of the migratory divide among Finnish greylag geese by modelling the probability for individuals to migrate either of the flyways as a binomially distributed variable. The probability was then estimated separately in each area (see Fig. 4 for the areas) in a Bayesian framework by giving it a uniform prior distribution (which is equal to the distribution Beta(1, 1)), and sampling from the posterior distribution, which is also (due to conjugacy) a Beta distribution with known parameter values.

In chapters II and IV, the spatiotemporal differences in the occurrence of bean goose subspecies (chapter II) and migratory behaviour of greylag geese (chapter IV) were modelled using Gaussian processes (GP). GPs have only recently begun gaining popularity in ecological research (see chapter IV) and hence, most readers are probably not familiar with them. In short, they provide a flexible probabilistic approach for modelling non-linear data in a Bayesian framework. They offer a powerful and flexible way of incorporating prior knowledge into the model while allowing a principled way to handle uncertainties. A brief introduction in ecological context is provided in chapter II, but for an in-depth introduction, see Rasmussen and Williams (2006).

Chapter II introduces an R package `gplite` (Piironen, 2021), which is a tool for general purpose GP modelling. All statistical analyses were performed using it and related packages in the R software (R Core Team, 2021).

3 Results and discussion

3.1 Moult migration of taiga bean geese

The results of chapter I show that both non-breeding and unsuccessfully breeding taiga bean geese migrate from the breeding grounds to moult on Novaya Zemlya in the Barents Sea (Fig. 2). This means that a large proportion of the Central Flyway taiga bean goose population will annually spend the summer in the area. The birds annually spend approximately three months on the island, which is around four times longer than the duration of moult. This means that the high Arctic is as relevant an environment for the population as their boreal breeding and temperate wintering areas, and is an integral part of the birds' flyway. Moult migration also changes migratory performance for a non-random part of the population by increasing the length of the annual migration distance (by a factor of 2.18) and by delaying the autumn migration of moult migrants. Additionally, migratory connectivity between breeding and moulting sites was low (r_M = -0.001, 95% CI -0.1562–0.2897), indicating that birds from different breeding origins mix with each other at the moulting sites.

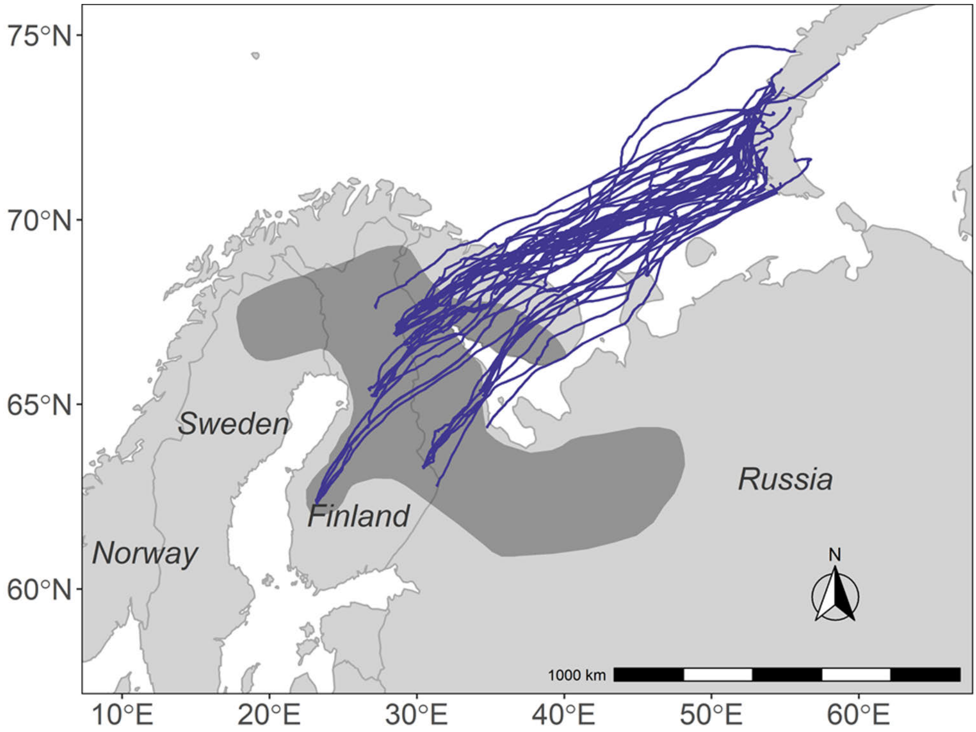


Figure 2. The moult migration routes of satellite-tracked taiga bean geese from Finland and Russia to Novaya Zemlya in 2019–2020. The green lines visualize the tracks and the shaded grey shows the breeding distribution of taiga bean goose in the Central Flyway (redrawn after Heinicke et al., 2018).

The results of chapter I reveal ubiquitous moult migration among Central Flyway population of taiga bean goose, but leaves the reasons behind moult migration unknown. Although moult migration as a phenomenon has been known for long (Salomonsen, 1968) and the behaviour has been described from various species (e.g. Jehl, 1990), the driving forces behind it are poorly understood. It may give moult migrants a possibility to exploit newly grown, nutritious vegetation, or it may help prevent intraspecific food competition between different age and/or sex classes. Moult migration outside the breeding areas may provide i) longer days for feeding (it often directs northwards), ii) the possibility of exploiting more nutritious vegetation, or iii) a way of avoiding predators. It may also help prevent intraspecific food competition or serve some social function (Salomonsen, 1968; Jehl, 1990). Although these hypotheses have been studied on some occasions (Glahder et al., 2007; Fox et al., 2014), the reasons behind moult migration remain unknown. The fact that a large part (likely a majority) of the taiga population moult migrate annually to Novaya Zemlya indicates strong selective benefit for doing so, as the moult migration also includes apparent costs (such as energetic costs caused by an increased migration distance). To understand the evolution of moult migration, it would thus be essential to reveal the fitness gains for individuals caused by moult migration in the future.

The fact that moult migration changes the timing of migration for moult migrants has direct impacts on the ongoing population monitoring activities in the Central Flyway (Jensen et al., 2022). Monitoring of the taiga bean goose breeding population on the breeding grounds during the moult period has recently been developed in Finland (Natural Resource Institute Finland, work in progress). The results of chapter I show that this monitoring scheme needs to consider that breeding success has a strong impact on taiga bean geese numbers on the breeding grounds during moult. If the goal of these counts is to monitor the size or development of the breeding population, breeding success must be carefully monitored and estimated to separate yearly changes in breeding population size from the yearly changes in breeding success. Second, the productivity of the Central Flyway population is estimated by counting juvenile ratios in autumn flocks in Sweden (Heinicke et al., 2018). Moult migrants returning from Novaya Zemlya consist exclusively of non-juvenile birds that arrive in Sweden from late September to mid-November, thereby decreasing the juvenile ratio observed in Sweden during autumn. If counts are carried out in early autumn, there is a risk of overestimating the juvenile ratio (i.e. productivity), as all sub-adults and a large proportion of the breeding adults may still be in Novaya Zemlya.

3.2 Spatiotemporal distribution of bean goose subspecies

The results of chapter II show both spatial and temporal difference in occurrence of different bean goose subspecies in Finland during migrations (see Fig. 3 for autumn migration). Tundra bean geese migrate later than taiga bean geese, both in spring and autumn. They are almost absent during the beginning of the autumn migration in late August and early September, but their proportion of all bean geese in southeastern Finland increases in the last half of September and remains high in October. During spring migration, the taiga bean goose migration begins in the first half of March, when tundra bean geese are nearly absent from Finland. Tundra bean goose numbers begin increasing in the middle of April, and the migration peak occurs approximately at the shift from April into May.

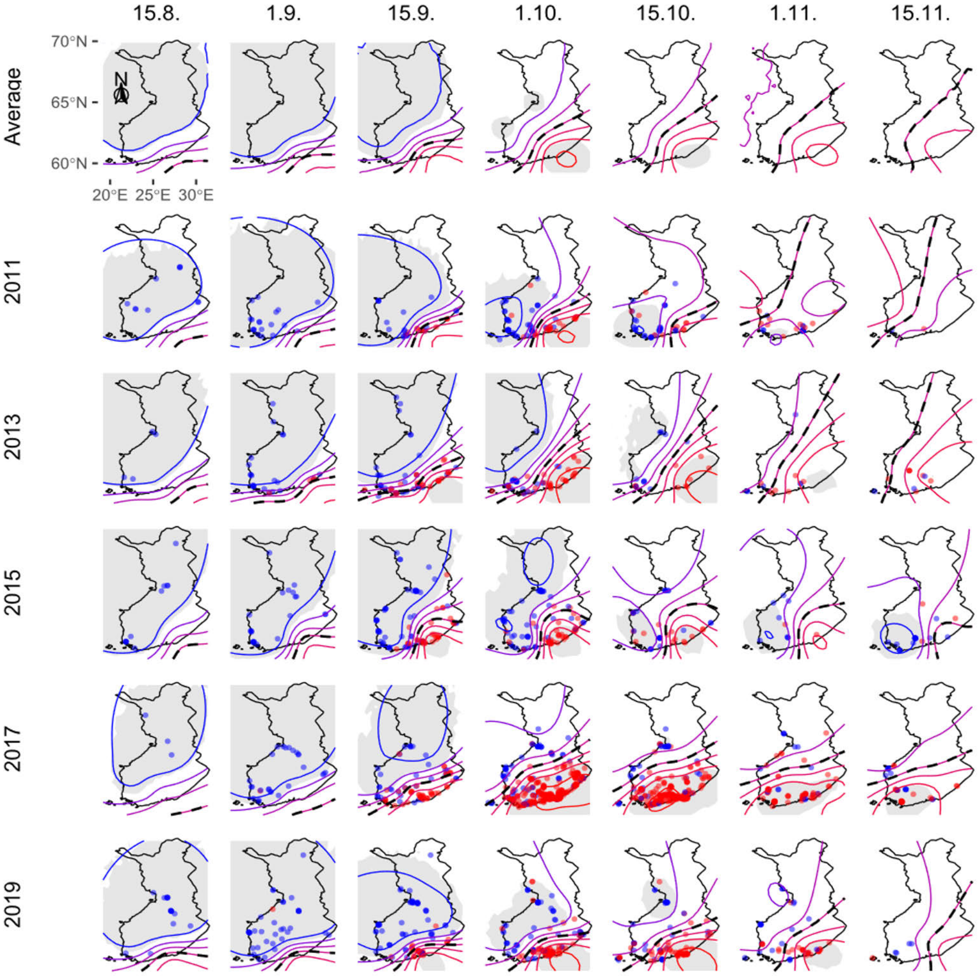


Figure 3. Spatiotemporal occurrence of bean goose subspecies in Finland at different dates and years during autumn. Due to the long time series, only average and every other year of the study period in chapter II are shown. The figure illustrates model predictions so that the contours denote the posterior mean for the probability of taiga bean goose ranging from 0.1 (red) to 0.9 (blue). The dashed black highlights the contour with a probability of 0.5 (i.e. the probability for each subspecies is the same). Shaded grey denotes areas where at least 95% of the posterior probability differs from 0.5 (i.e. where there is high statistical support that either one of the subspecies is more abundant than the other). Dots denote observations within ± 8 days from the given day; red and blue colours mark whether the majority of the observed bean geese were tundra or taiga bean geese, respectively.

3.3 Year-round migratory connectivity and spatial dispersion of taiga bean geese

The results of chapter III show moderate to low migratory connectivity between breeding and non-breeding areas among the Central Flyway taiga bean goose population. The results also show that both migratory connectivity and the spatial distribution of the population (the total area instantaneously containing members of the population) varies substantially within the non-breeding season. A comparison of satellite tracking and count data indicated that current autumn and spring count schemes for the taiga bean geese likely underestimate true population size, even though spring and autumn counts generally exceed the corresponding winter counts (Johnson et al., 2021). Large-scale movements of birds breeding in Western Russia were very similar to those breeding in Finland.

According to the results in chapter III, the relative size of the area including all of the tagged taiga bean geese remained lowest from the last half of November to the beginning of January, implying that this is the point in the annual cycle when the population is most favourable for monitoring. The size of the area covered by the population 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 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. The timing is also crucial with regards to the spring count, as the birds began 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).

The results of the simple comparison between satellite tracking and count data in chapter III indicate that the current total counts probably underestimate the true population size of the Central Flyway taiga bean geese, as some of the tracked birds were not present in any of the count sites at the time they were counted (i.e. the assumptions behind the counts were not fulfilled). As results from these censuses are used as inputs 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 increase their accuracy and transparency. To do this, three actions are recommended: 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 currently be 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. Generally, the result regarding the underestimation of the population size by the total counts are in line with previous studies comparing total counts with some other population size assessment method with various species (Ganter & Madsen, 2001; Dennhardt et al., 2015; Battaile et al., 2017; Schummer et al., 2018; Clausen et al. 2019; Booms et al. 2021). As population size estimates are desired instead of population trends in some applications (for example, the adaptive harvest management of waterfowl) and as total counts will probably remain a common tool for assessing population sizes also in the future, these observations underline the importance of evaluating the accuracy of total counts and to produce 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 by modelling 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.

3.4 Migratory divide and migration strategies of greylag geese

The results of chapter IV show a gradual migratory divide in the continuous breeding distribution of greylag geese in Finland (Fig. 4), which also divides the birds into different migration strategies. The birds breeding at the far end of the Gulf of Bothnia use the Western Flyway, the birds breeding in the Gulf of Finland use the Central Flyway, and the birds breeding between these two extremes scatter to the two flyways. The migration strategies were different between the two flyways (Fig. 5). The overall migratory journey is longer for birds using the Western Flyway, and they migrate earlier in autumn (and later in spring) than birds on the Central Flyway. Birds using the Western Flyway also show a clear stopover of around one month during their autumn migration, whereas Central Flyway birds migrate relatively straight from their breeding grounds to their wintering sites.

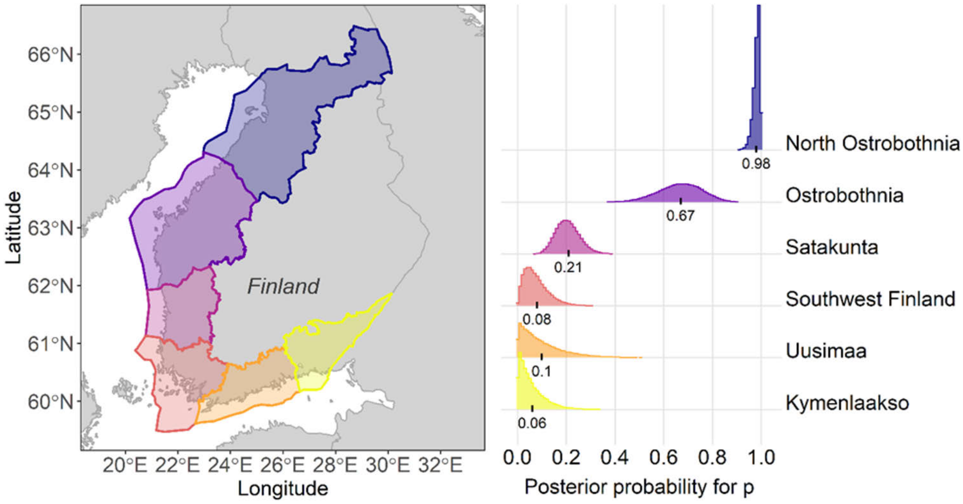
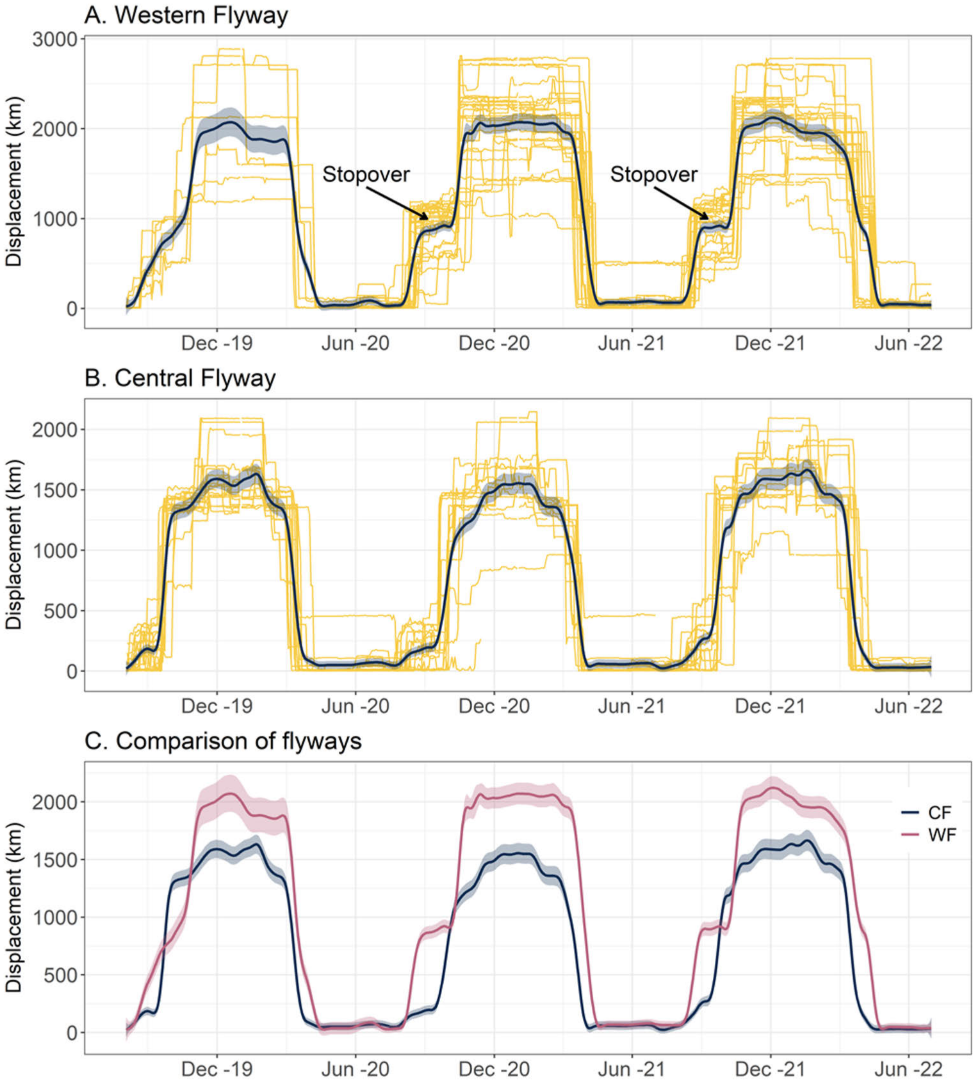


Figure 4. The posterior distribution for the probability of a Finnish greylag goose to migrate along the Western Flyway (*p*) in different coastal areas in Finland. The colour of each histogram represents the probability in the area coloured with the same colour in the map. The numbers under the histograms denote the posterior mean for p in each area.



A. Western Flyway

B. Central Flyway

C. Comparison of flyways

Figure 5. Migration strategies of greylag geese in the Western and Central Flyways. The figure illustrates the model predictions for the displacement of satellite-tracked greylag geese from their breeding sites in both flyways in 2019–2022. In subplots A and B, the beige lines denote the displacement data and the black lines and shaded grey areas denote the posterior mean and 95 % credible interval for model predictions. To facilitate easier comparison, subplot C visualises the model predictions for both flyways.

The optimal migration theory suggests that if suitable habitats for stopovers are abundant along the flyway, birds should exhibit a migration strategy consisting of frequent stopovers and short flights between the stopover sites, to minimize the costs of flying with the heavy energy stores. According to chapter IV, the migration strategies of greylag geese do not seem to follow this prediction. The greylag geese using the Central Flyway fly non-stop from southern Finland to their wintering sites in Central Europe. During their autumn migration, they fly over several sites in the Baltic countries and Poland that are known to be suitable stopover and wintering habitats for geese (for example, see Madsen et al., 1999; Fox & Leafloor, 2018). In addition, birds from both flyways migrate somewhat straight from their wintering grounds to their breeding grounds in spring. These findings indicate that greylag geese do not try to minimize the flight with low energy stores (as suggested by the optimal migration theory), but rather some other factors guide their migration strategy.

Second, birds using the Western Flyway begin their autumn migration approximately one month earlier than those using the Central Flyway by moving from their breeding sites to stopover sites in Sweden before September. Although the majority of the Western Flyway birds breed north of those using the Central Flyway, the habitats and weather conditions in the Gulf of Bothnia remain suitable for geese until October–November, as other goose species (e.g. bean geese, see chapter III) occur in the area until then. Therefore, it is unlikely that a lack of suitable habitat would force the greylag geese to depart from the Gulf of Bothnia in August, as suggested by the optimal migration theory. Last, the migration strategies of greylag geese differ between the Western and Central Flyways, although the habitat characteristics are at least roughly similar in both flyways. Greylag geese winter and stopover mainly in agricultural landscapes that also hold some wetlands (e.g. Fox & Abraham, 2017), and these habitats are more available to birds along both flyways than used by the greylag geese (Okruszko et al., 2011; Xu et al., 2019; d'Andrimont et al., 2021). As the optimal migration theory suggests similar migration strategies between flyways with similar habitats, my results do not indicate support for it in this sense. Although habitat availability and quality in each flyway were not quantified, and the differences in migration strategies were not explained with quantitative habitat factors, I consider that differences in habitat characteristics will probably not explain the observed differences in migration strategies between the flyways. To better understand bird migration and how migratory birds can respond to habitat loss and environmental changes, such as climate change, it is important to study factors guiding migration strategies in the future.

3.5 Future prospects

Geese are social migrants, which means that the migration routes are inherited through cultural transmission (i.e. young birds learn their migration routes from more experienced individuals, mainly from their parents, Mueller et al., 2013). Juvenile geese usually follow their parents during their first year and learn the migration routes to their wintering sites and back from their parents. However, the comprehensive moult migration of immature, non-breeding taiga bean geese to Novaya Zemlya (described in chapter I) raises an interesting question about the orientation of the juvenile geese to the island: At the time when the young, one-year-old birds depart to their first moult migration, their parents are already breeding. Thus, the moult migration routes cannot be learned from the parents. To better understand the inheritance mechanisms of navigation among social migrants, it would be important to study whether the young geese inherit the migration routes to their moulting sites genetically or whether they follow other sub-adult birds (and which birds do they follow).

Pair formation and thus genetic mixing in goose populations and between them is traditionally thought to take place during winter (Rohwer & Andersson, 1988). However, individuals from two populations of greater white-fronted geese (*Anser albifrons*) have recently been shown to change their flyway (population) during summer at shared moulting sites, probably through pair formation during moulting (Kölzsch et al., 2019). The comprehensive moult migration (chapter I) together with a low degree of migratory connectivity between the breeding and moulting sites (chapters I and III) can thereby contribute to the genetic mixing of Central Flyway taiga bean goose population, if at least some pair formation takes place during moulting. Thus, it can further contribute to the low genetic structure within the population (Honka et al., 2022), but it's impact on population genetics is currently unknown.

Migratory divides are known to drive intraspecific genetic differentiation and reproductive isolation (Bearhop et al., 2005; Boulet et al., 2006; Rolshausen et al., 2009). Chapter IV shows that the migratory divide among Finnish greylag geese is gradual but not precipitous (as opposed to many previously described divides), which implies that a part of the birds using different flyways breed and also moult (Piironen, A., unpublished data) sympatrically. As some genetic mixing of goose populations can take place during summer on common moulting grounds (Kölzsch et al., 2019), this can dilute the genetic differentiation between the flyways. In line with this, some of the greylag geese tracked in chapter IV changed their flyway during the study period. This interchange of birds indicates gene flow between flyways at the overlapping breeding and moulting sites, which may contribute to the low level of genetic structure among European greylag geese (Pellegrino et al., 2015). To conclude, the results of chapter I, III, and IV call for future research to study the summertime movements (such as moult migration) and the extent of pair formation among geese during summer, and to unravel their contribution to the gene flow inside and between goose populations. Moreover, based to the results of chapter IV, it is important to study the structure of the migratory divides and consider their effect on the population genetics of different species in the future.

The analysis in chapters II and IV utilized and promoted Gaussian process (GP) models. GPs have been used in the machine learning community for a few decades, but have recently begun gaining popularity also in ecology (see e.g. Ingram et al., 2020; Wright et al., 2021; Doser et al., 2022; Wiens & Thogmartin, 2022). They offer a flexible, non-parametric way to model non-linear data in the Bayesian framework, and they are an appealing tool for ecologists due to their inherent flexibility (Rasmussen & Williams, 2006) and good predictive accuracy (Ingram et al., 2020; Wright et al., 2021). In addition to these benefits, chapters II and IV show that the rich covariance structure of GPs makes them an auspicious tool for modelling phenomena, such as animal migration, with various kinds of data. In this sense, as shown in chapter II, particularly useful is the possibility to implement periodic or quasi-periodic covariance structure to the models, as this assumption is many times reasonable when modelling phenomena, such as animal migration, over multiple years (as migration patterns in different years often remind each other but are not exactly similar). As shown in chapter IV, GPs enable finding fine-scale migratory behaviours (such as stopover during migration) from the displacement data, which are impossible to model with methods traditionally used for these purposes (i.e. non-linear mixed-effect models introduced, Bunnefeld et al., 2011). However, the drawback of GPs in ecology is the mathematical degree of difficulty, poor scaling to large datasets, and lack of practical tools for model fitting in R. Also, in some applications, difficult interpretation of their hyperparameters can be non-beneficial (see chapter IV). However, GPs have proven to be a promising tool for multiple non-linear problems in ecology, and their capabilities should be better utilized in ecology. As shown in chapter IV, the R package `gplite` (Piironen, 2021), which was introduced in chapter IV, provides an easy-to-use tool to fit GP models for general purposes, and it will hopefully encourage ecologists to try GP models in the future.

3.6 Management implications

As shown in chapter I, taiga bean geese returning from the moulting sites at Novaya Zemlya have a major impact on the spatial distribution of the taiga bean goose population during autumn and thereby need to be considered in harvest management. Spatial and temporal hunting regulations have a major impact on which part of the taiga bean goose population the harvest is targeted. Harvest on breeding grounds is targeted at successful breeders and their offspring, as birds returning from Novaya Zemlya mainly fly over the breeding grounds. Harvest on the staging areas on the western coast of Finland as well as central and southern Sweden is targeted at breeding birds and their offspring at the beginning of early autumn. Later in the season, it is targeted also at sub-adults and adults that failed in breeding as they return from Novaya Zemlya.

The results of chapter II show suggest that the bean goose harvest can be targeted at tundra bean goose in Finland by geographically restricting hunting to southeastern Finland and by delaying the beginning of the hunting season from August to approximately the beginning of October. This kind of spatial and temporal hunting regulation is a common practice in harvest management in Finland, and the results provide a scientific base for adjusting the bean goose hunting season and area to meet the different management goals for both subspecies. Generally, this approach could be used to better meet the different management needs of bean goose subspecies also elsewhere in their range, and it can also be applied more broadly to similar situations with other species.

Finland is a range state in the international management of the Northwest–Southwest European population of greylag geese (which uses the Western Flyway of greylag geese; Nagy et al., 2021). However, the proportion of Finnish greylag geese belonging to this population has been unknown (Bacon et al., 2019). The results of chapter IV enable the allocation of the Finnish breeding population between the flyway populations based on their breeding grounds (see Fig. 4). However, the population size estimation in Finland is still a work in progress (Natural Resource Institute Finland, unpublished data). Although the migratory connectivity and spatiotemporal distribution of Finnish greylag geese must be studied in detail in the future to facilitate decision-making in management, the results of chapter IV show that the Finnish greylag geese belong to two different flyway populations, which must be considered both in international and national management and when monitoring the species.

4 Conclusions

In chapters I–IV, I have studied several aspects of migratory behaviour of taiga bean geese and greylag geese. The results of chapter I show that moult migration can crucially affect the flyway structure, migratory connectivity, migratory behaviour and spatiotemporal distribution of waterfowl populations. Therefore, future research should pay more attention to unravelling moult migration patterns, and moult migration should be carefully considered in the future conservation and management of migratory populations. The results of chapter II show how the spatiotemporal distributions of the bean goose subspecies differ during migrations, and how Gaussian processes can be used to model that difference. As the status and the development of the subspecies are different, the spatiotemporal differences in their occurrence should be considered in the harvest management of the species. Importantly, Gaussian processes include many features which would be advantageous in ecology, and they could be utilized more in the future research.

The results of chapter IV show that the Finnish greylag geese are divided into two different flyway populations, and describe the gradual structure of the migratory divide. To the best of my knowledge, gradual migratory divide has not been described previously and hence, it’s ecological and evolutionary impacts should be studied in the future. Knowledge regarding the location of the migratory divide also helps to delineate the flyway populations of the species, which should be considered in the management of the species. The results of chapter IV also show that migration strategies of greylag geese differ between the flyways despite the lack of apparent difference of habitat composition between the flyways. This result is not in line with the optimal migration theory, and therefore the drivers of the bird migration strategies should be studied more in the future.

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Original Publications

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Movement Ecology

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Birds of three worlds: moult migration to high Arctic expands a boreal-temperate flyway to a third biome

Antti Piironen[1*], Antti Paasivaara[2] and Toni Laaksonen[1]

Abstract

Background: Knowledge on migration patterns and flyways is a key for understanding the dynamics of migratory populations and evolution of migratory behaviour. Bird migration is usually considered to be movements between breeding and wintering areas, while less attention has been paid to other long-distance movements such as moult migration.

Methods: We use high-resolution satellite-tracking data from 58 taiga bean geese *Anser fabalis fabalis* from the years 2019–2020, to study their moult migration during breeding season. We show the moulting sites, estimate the migratory connectivity between the breeding and the moulting sites, and estimate the utilization distributions during moult. We reveal migration routes and compare the length and timing of migration between moult migrants and successful breeders.

Results: All satellite-tracked non-breeding and unsuccessfully breeding taiga bean geese migrated annually to the island of Novaya Zemlya in the high Arctic for wing moult, meaning that a large part of the population gathers at the moulting sites outside the breeding range annually for approximately three months. Migratory connectivity between breeding and moulting sites was very low ($r_m = -0.001$, 95% CI −0.1562–0.2897), indicating that individuals from different breeding grounds mix with each other on the moulting sites. Moult migrants began fall migration later in autumn than successful breeders, and their overall annual migration distance was over twofold compared to the successful breeders.

Conclusions: Regular moult migration makes the Arctic an equally relevant habitat for the taiga bean goose population as their boreal breeding and temperate wintering grounds, and links ecological communities in these biomes. Moult migration plays an important role in the movement patterns and spatio-temporal distribution of the population. Low migratory connectivity between breeding and moulting sites can potentially contribute to the gene flow within the population. Moult migration to the high Arctic exposes the population to the rapid impacts of global warming to Arctic ecosystems. Additionally, Novaya Zemlya holds radioactive contaminants from various sources, which might still pose a threat to moult migrants. Generally, these results show that moult migration may essentially contribute to the way we should consider bird migration and migratory flyways.

Keywords: Migratory connectivity, Migration ecology, Waterfowl ecology, Adaptive management, Flyway ecology, Flyway management

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Background

Migration is a taxonomically widespread phenomenon comprising regular, seasonal movement of animals [1, 2]. Movements between several habitats allow animals to use spatially and temporally versatile resources and thus enables them to utilize areas where they cannot live over the whole annual cycle [3]. The downside is that migration exposes animals to changing environmental conditions and human actions in all the locations they utilize during the annual cycle [4]. Migratory animals also link ecological communities to each other, transferring changes in one community to another, which makes it crucial to understand the migratory patterns of the populations [5].

Bird migration has typically been considered a movement between "two worlds" i.e. between breeding and non-breeding (wintering) areas, with some staging sites *en route* [4]. However, this view may be complicated by moult migration, a phenomenon where a part of the population disperses (usually) outside of the breeding range during breeding season for wing moult [6, 7]. While moult migration is recognized in several bird taxa, it is most widespread and best known among waterfowl *Anatidae* [6, 8]. Most ducks and geese moult and regrow all their flight feathers simultaneously during summer, which leaves them flightless for several weeks every year [9]. In many species, a part of the population leaves the breeding area to moult somewhere else. This may have important ecological and evolutionary consequences that should be known to understand migratory behaviour and population dynamics of the species, and to successfully conserve it.

To understand the evolution and occurrence of moult migration, we should understand the general components of this movement within the conceptual movement ecology framework [10]. First, we should examine the internal factors i.e. reasons for "why to move" [10]. The flightless period reduces feeding site choice and increases the risk of predation, which emphasizes the importance of the moult area choice as a reason to move. Moult migration outside breeding areas may provide (1) longer days for feeding (it often directs northwards), (2) a possibility of exploiting newly grown, nutritious vegetation, or (3) a way of avoiding predators [6]. It may also help prevent intraspecific food competition or serve some social function [6, 8]. These hypotheses have been studied on a few occasions [11, 12], but the reasons behind moult migration remain unknown. Second, moult migration typically concerns only a part of the population, which in many bird species appears to constitute mostly immature individuals. This is interesting regarding the navigation capacity ("where to move") of moult migrants, as it is unknown how young, inexperienced birds navigate to the moulting sites far away from their natal grounds unless they can follow some experienced birds. Before we can begin to examine factors behind the evolution of moult migration, we have to know where the birds are going, how the moult migration sites are connected with the breeding sites and the flyway of a population, and how the moult migration changes the migratory patterns compared to the individuals that do not moult migrate. Surprisingly, these characteristics are rarely known. Some of these aspects are known for a handful of populations [6, 8, 13, 14], but we are not aware of populations, for which all these basic aspects of moult migration are known.

While the reasons behind moult migration remain poorly studied, its wide-reaching impacts on migration ecology and population dynamics have begun to emerge. First, a recent study revealed that moult migration links two flyway populations that have previously been considered separate populations, forming a meta-population across the flyways [14]. This highlights the previously unknown impact of moult migration on the connections and gene flow between flyway populations. Second, moult migration may shape the entire flyway concept by linking previously unknown environments (moulting sites) that can be situated in unpredictable directions from the traditional path between breeding and wintering grounds (the "two worlds", e.g. [4, 15]). Third, moult migration may contribute substantially to the migratory connectivity of the populations, as it can change migration routes and timing of migration for a part of the population [e.g. 15]. Finally, moult migration is known to affect the demographic parameters of moult migrants and to thereby directly contribute to the dynamics and management of migratory populations [13]. To set the scene for studying the evolutionary and ecological factors behind moult migration, and to understand the impact it has on the ecology of migratory populations, it is essential to identify population-specific moult migration patterns and moulting sites.

The Western taiga bean goose *Anser fabalis fabalis* (hereafter taiga bean goose) from the Central flyway breeds in Fennoscandia and north-western Russia, and is distributed mainly in southern Sweden, Denmark and northern Germany during the non-breeding season [16, 17]. It was discovered decades ago that a part of the population disappears from the breeding grounds in early summer [18]. An earlier list of potential moulting sites included northern Fennoscandia and continental Russia, but not Novaya Zemlya [17]. A previous satellite-tracking study found that three birds migrated from Sweden to Novaya Zemlya, which suggested the possibility that moult migration to the high Arctic could take place [19]. Based on this knowledge, the latest population review on the species noted that moult migration to

Russia, potentially mainly to Novaya Zemlya, occurs [16]. However, the taiga bean goose moulting sites, the extent of moult migration in the population and the impact of moult migration to the migration patterns of the population have remained unknown.

Here, we examine via satellite-tracking (1) how commonly the taiga bean geese from several different breeding areas moult migrate outside the breeding areas; (2) where they moult; and (3) whether there is connectivity between breeding and moulting areas. We further examine (4) how this behavior changes the length, timing and route of their migration compared to the individuals that do not moult migrate. Finally, we discuss the evolution of moult migration and the importance it has for the flyway concept, individual migratory behaviour, migratory populations and their conservation.

Material and methods

Field methods

Taiga bean geese were caught for global positioning system (GPS) transmitter deployment during spring and summer 2019 and spring 2020 on five sites in Finland (Fig. 1). The catching sites on the Finnish breeding grounds are located at Virrat in South Ostrobothnia (latitude (lat) 62° 22′ longitude (lon) 23° 16′), Lieksa in North Karelia (lat 63° 16′ lon 30° 28′), Pudasjärvi and Utajärvi in North Ostrobothnia (lat 65° 04′ lon 26° 50′ and lat 65° 12′ lon 26° 52′, respectively), and Salla in Lapland (lat 66° 51′ lon 28° 36′). Birds breeding in Russia were caught on staging sites at Outokumpu and Liperi (lat 62° 42′ lon 29° 07′) in North Karelia. We caught birds in breeding areas using cannon-nets combined with short-term artificial feeding. Catching sites were located on small fields, mires, or at the edge of ponds and they were prepared prior to catching events by feeding geese with grain from several days up to three weeks. To mark breeding pairs on their specific breeding sites in Finland, geese were caught in pairs immediately after the first geese had arrived at the breeding grounds in spring. On staging sites at Outokumpu, birds were caught using cannon-netting on agricultural fields.

All caught birds were sexed with a cloacal examination and aged based on the shape of the wing coverts. GPS transmitters were deployed only onto birds of age + 2 cy (calendar year) (see Additional file 2: Table 1 for individual data on marked birds). We used OrniTrack-44 solar-powered GPS-GSM (global system for mobile communication) neckcollars produced by Ornitela UAB. The collar weighs appr. 45 g, which is under 3% of the weight of an adult female taiga bean goose (Piironen A., unpublished). The transmitter logs GPS positions and sends data to the server via a GSM/GPRS (general packet packet radio service) network either by e-mail or SMS (short message service).

Individuals with only limited data sets were used for analysis when data allowed. For example, data from birds that moult migrated, but did not send any data after departure, were used to calculate the beginning of moult migration even if they could not be included in other analyses. Seven individuals were tracked over both years, and their data are probably non-independent between the two years. To avoid pseudoreplication, we only used data from one year for these individuals when we merged the data from both years for analysis. Likewise, our data

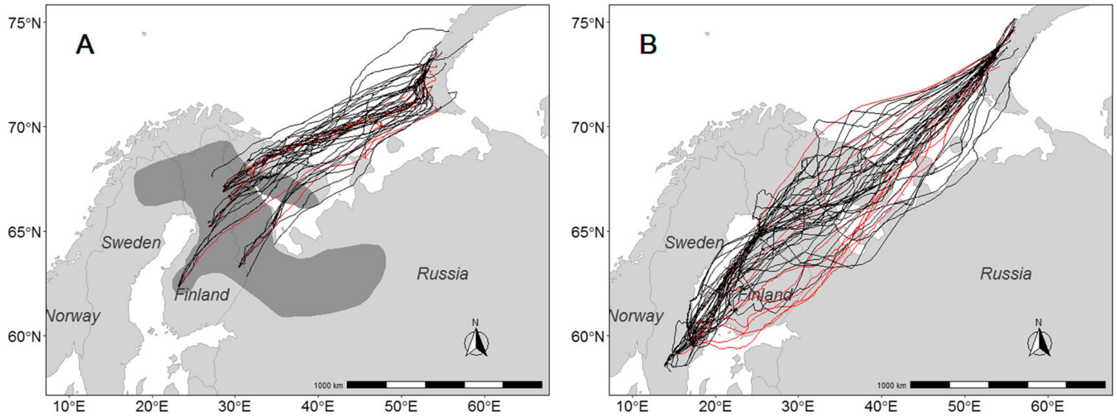

Fig. 1 The moult migration routes of satellite-tracked taiga bean geese from Finland and Russia to Novaya Zemlya (map A) and breeding distribution of taiga bean goose in the Central Flyway (shaded area in map A). Map B represents the autumn migration routes of the same birds from Novaya Zemlya to Sweden after moult. Red lines denote routes in 2019 and black lines routes in 2020. The breeding distribution is redrawn after [16]

included two pairs, which produce non-independent data as paired individuals usually move tightly together. Therefore, we used data from one member of a pair when it was more appropriate than to use both individuals (see Additional file 3: Table 2 for sample sizes used in different analyses).

Data and analysis

GPS resolution was set to one position per ten minutes, except for three birds in 2019, whose GPS resolution were set to one hour. Before the analyses, we excluded GPS noise from the data (i.e. locations with lat 00° 00′ lon 00° 00′). To ensure the best possible quality of the locations, we only used locations with hdop (horizontal dilution of precision of the GPS fix) values ≤ 2. We assessed the nesting status and success for females using location revisitation metrics following [20]. We identified possible nest sites from the period 15th April–30th June 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 [21]) must be visited in at least six consecutive days (corresponding to average clutch size and laying approximately one egg per day [22]), (2) it must be visited in at least 50% of days between first and last visit, and (3) at least 50 locations must be from the site. We note that the last two criteria are subjective, but necessary to exclude other often visited sites such as feeding and roosting sites and thereby to reduce the amount of candidate nest sites. However, we think that any true nest site should fill these criteria. If the bird's track included at least one site filling these criteria, we considered that the bird attempted to nest in that year. Vice versa, we considered any bird that did not fill the criteria as a non-breeder. 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 [18]). We assessed nesting success for females by comparing incubation duration to the previously known incubation duration for the species (27–29 days [22]). We considered that the bird started incubation when the daily nest site attendance was at least 70%. If the amount of consecutive incubation days was at least 28, we considered nesting successful (i.e. at least one egg hatched). We note that these quantitative assessment rules include some subjective threshold values. However, the conclusions about nesting on these bases are in accordance with what could be evaluated from it when following the tracks of individual birds from the (high resolution) satellite-tracking data.

We identified breeding males from non-breeding males when they joined the females and goslings after hatching i.e. stopped flying and started to move continuously by walking before the mid-June (moult period). We considered that a male was with brood, if at least 99 percent of daily locations indicated movement at a speed ≤ 20 km/hour (km/h) (i.e. the distance covered between two locations indicated movement at a speed ≤ 20 km/h). We note that this assumption carries a risk of a misjudgement. According to our observations, taiga bean goose males usually do not indicate nest location with their movements (the male does not visit the nest often or guard it intensively). Thereby, a breeding male may be judged to be a non-breeder if the nest is lost before hatching.

We assessed brood rearing success for both males and females using the same criteria (bird is with a brood if at least 99% of daily locations indicated movement at a speed ≤ 20 km/h). We judged that a brood was lost when parents with a brood suddenly began flying after a non-flight period following hatching and before moult or moult migration. Individuals caught and GPS-tagged during moult or right after moult were in flocks including both adults and juveniles, and we thereby considered all these adults to be successful breeders.

The natal origin of non-breeding birds often remains unclear, and it is therefore uncertain where spring migration ends and moult migration begins. This was particularly the case with four birds (two pairs) marked at staging areas in North Karelia in 2020. They flew to the Kola Peninsula on 4th May, staged there for over a month, and moult migrated to Novaya Zemlya on 14th June. Due to a very long staging period in the Kola Peninsula, we considered it more likely that these birds originated from Russia rather than Finland, and their moult migration is thus considered to begin from the Kola Peninsula instead of Finland.

We performed a phenology analysis separately for years 2019 and 2020 whenever the nature of the event suggested considerable variation between years. We considered the moulting period for each bird to be the longest period during which its speed at locations did not exceed 20 km/h or the distance between two points did not require a speed of ≥ 20 km/h. With these criteria, moulting period length obtains biologically reasonable values, although variation is probably larger than the true variation in moulting period length. This is probably due to inaccuracy in speed sensor values and location precision (too high speed during the moulting period resulting in overly short moulting periods) or to a time lag between re-gaining the ability to fly and recording the first flight observation (resulting in excessively long moulting periods).

Low GPS resolution increases the uncertainty of bird movements between locations, which leads to larger estimates for utilization distributions compared to individuals with short location intervals. Increasing location intervals also decrease the ability to accurately determine the moult period. For accurate and comparable estimates for moult timing and utilization distributions during moult, three birds with location intervals of 1 h in 2019 were removed from these analyses. Utilization distributions during moult were estimated using dynamic Brownian Bridge Movement Models [23] with a window size of 29 locations and a margin size of 11 locations. We estimated the strength of migratory connectivity between breeding and moulting locations by calculating Mantel's correlation (r_M, correlation between two matrices) with 1000 bootstrap runs for distances between individuals on breeding grounds and moulting sites. Mantel's test is commonly used to calculate correlation between two matrices and in this case, we used it to test whether the birds breeding in separate areas also moult in separate areas. We tested the effect of moult migration to the timing of autumn migration by fitting a linear model with the log-transformed arrival time in Sweden as a response variable and year and moult migration status (moult migrated or stayed at the breeding grounds) as categorical explanatory variables. All analyses were performed using packages Rnest [20], move and MigConnectivity [24] and related packages in R software version 4.0.3 [25].

Results

Moult migration routes and timing of moult migration

All satellite-tracked non-breeders (7 individuals in 2019 and 28 in 2020) and failed breeders from Finland and Russia moult migrated to Novaya Zemlya for wing moult (4 individuals in 2019 and 13 in 2020). Four out of ten (40%) and six out of 20 (30%) birds that started breeding were successful in breeding in 2019 and 2020, respectively. We note that stress caused by capturing and marking (especially close to breeding season) might negatively affect the breeding success of the birds. Thereby, these breeding successes should be treated as minimums in years 2019–2020. Four birds that bred in 2019 skipped breeding in 2020 and were considered non-breeders. Altogether, the majority of birds alive thus moult migrated in these two years, as we documented 10 successful breeding events, 17 failed breeding events and 35 non-breeding events, of which the latter two always lead to moult migration.

On average, non-breeders began their moult migrations on 8th June ± 3.4 (s. d.) days in 2019 ($n = 7$) and 14th June ± 5.1 days in 2020 ($n = 26$). Failed breeders began moult migration on average 18.8 ± 7.2 days after losing the nest or brood ($n = 16$), which means 24th June ± 14.9 and 8th June ± 8.6 days in 2019 and 2020, respectively.

Moult migrants from Finland and Russia flew straight to southern Novaya Zemlya (Fig. 1). Most individuals flew almost continuously (stopped for less than one day) from the breeding sites to Novaya Zemlya, while some birds staged shortly (5.5 ± 4.9 days) on the way. The birds arrived at Novaya Zemlya on 20th June ± 11.1 days in 2019 ($n = 10$) and 15th June ± 7.2 days in 2020 ($n = 39$, see Fig. 2). After arriving on the island, most birds headed straight to the moulting sites in the central parts of Novaya Zemlya, whereas some individuals staged shortly before reaching the moulting sites. Moult began 18.69 ± 8.7 days after arrival at Novaya Zemlya ($n = 42$).

Moulting sites, timing of moult and connectivity between breeding and moulting sites

Moulting began 13th July ± 11.1 days and ended 8th August ± 15.4 in 2019 ($n = 10$). In 2020, moulting began 2nd July ± 7.7 days and ended 23rd July ± 8.1 ($n = 41$). In merged data from both years, moulting began 5th July ± 9.8 days and ended 27th July ± 12.3 days ($n = 44$). Thereby, the moult period took on average 21 days (Fig. 2).

The taiga bean goose moulting sites in Novaya Zemlya are located in the middle part of the island, between 72° and 76° latitudes (Fig. 3). Many of the birds were moulting in the area of the most active nuclear testing in the archipelago (Fig. 2). Seven individuals were tracked to Novaya Zemlya in both years of the study. Four of these birds moulted on the same site in both years, whereas three individuals changed moulting sites between years (Fig. 3). All birds spent their moult periods close to water on the seacoast, on tundra lakes, or in river valleys. Examples of utilization distributions during moult are shown in Fig. 4 and utilization distributions for all individuals are in the Additional file 1.

We estimated connectivity between breeding sites and moulting sites in Novaya Zemlya only for failed breeders, as the non-breeders obviously lacked a breeding area. Mean estimate for Mantel's correlation r_m with 1000 bootstrap samples for distances between individuals on breeding and moulting sites was -0.001 (95% CI -0.1562–0.2897), indicating low connectivity between breeding and moulting sites (Fig. 5).

Autumn migration

We define the onset of autumn migration here as the time when birds leave from Novaya Zemlya, but we note that some birds had small-scale movements within the island before leaving it. As these movements can appear in any direction (and be back and forth movements), they are not considered to be part of autumn migration here. The satellite-tracked taiga bean geese left Novaya Zemlya in late September or early October. Average departure date was 19th September in 2019 (± 3.4 days; $n = 10$) and 20th September in 2020 (± 7.7 days; $n = 39$). Average

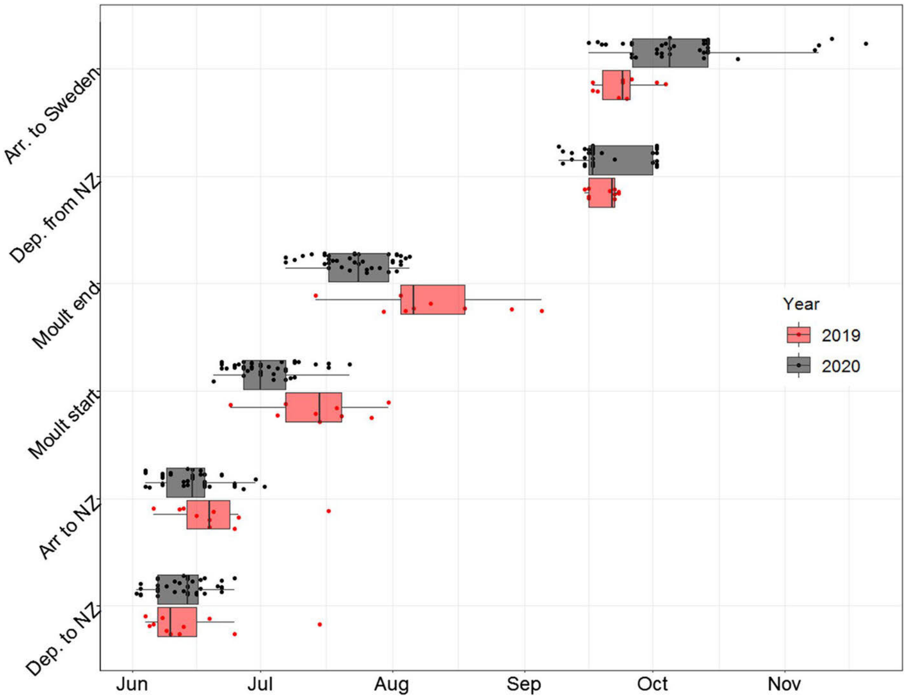

Fig. 2 Timing of moult migration, moult, and autumn migration of satellite-tracked taiga bean geese moulting in Novaya Zemlya in 2019–2020. Boxes represent the interquartile range (IQR), vertical bars the median, and the whiskers the 25th percentile − 1.5*IQR and 75th percentile + 1.5*IQR

time lag between the end of moult and departure was 41.8. ± 16.6 days in 2019 (n = 10) and 58.9 ± 11.1 days in 2020 (n = 39). Six out of ten birds (60%) and 15 out of 41 birds (37%) stayed on their moulting sites until leaving the island in 2019 and 2020, respectively. The rest of the birds had small-scale movements within the island before crossing the Barents Sea.

Migration routes from Novaya Zemlya to the staging areas in Sweden are presented in Fig. 1b. The migration corridor was wide, reaching from the south coast of the White Sea to the northwest corner of the Kola Peninsula. The main route followed the west coast of Finland and crossed the Baltic Sea north of Åland islands. During autumn migration, the birds that staged for at least one day did so only in Finland (not in the Kola peninsula or elsewhere in Russia). In 2020, 24 birds (62%, n = 39) staged in Finland, and the duration varied between 1 and 54 days (median 21 days, n = 30). In 2019, only two birds (20%, n = 10) stopped in Finland during autumn migration, with duration times of 7 and 17 days.

The main destinations in Sweden were located in Enköping and Örebro, where the birds arrived from late September to mid-November. Mean arrival date was 24th September ± 5.8 days (n = 10) in 2019 and 8th October ± 15.3 days in 2020 (n = 38). In comparison, successfully breeding birds from Finland arrived in Sweden on 19th September ± 6.9 days (n = 7) and 25th September ± 18.2 days (n = 6) in 2019 and 2020, respectively (note that sample size of successful breeders in 2019 increased from four to seven because three additional birds were tagged while rearing broods). Despite the fact that both groups migrated later in 2020 than in 2019 (year: $t_{1,60} = 2.91$, $p = 0.005$), moult migrants arrive in Sweden earlier in autumn than successful breeders (migratory status: $t_{1,60} = -2.31$, $p = 0.024$, Fig. 6).

Moult migration increased the individual annual migration distance (compared to migration only between breeding and wintering grounds) by 6140 ± 758 km (n = 51). The overall annual migration distance was 2.18 times longer for moult migrants than successful breeders moulting at the breeding grounds (Additional file 4: Table 3).

Discussion

Our results show that both non-breeding and unsuccessfully breeding taiga bean geese migrate from their boreal breeding grounds to moult on Novaya Zemlya in the Arctic Ocean. This means that a large proportion of the

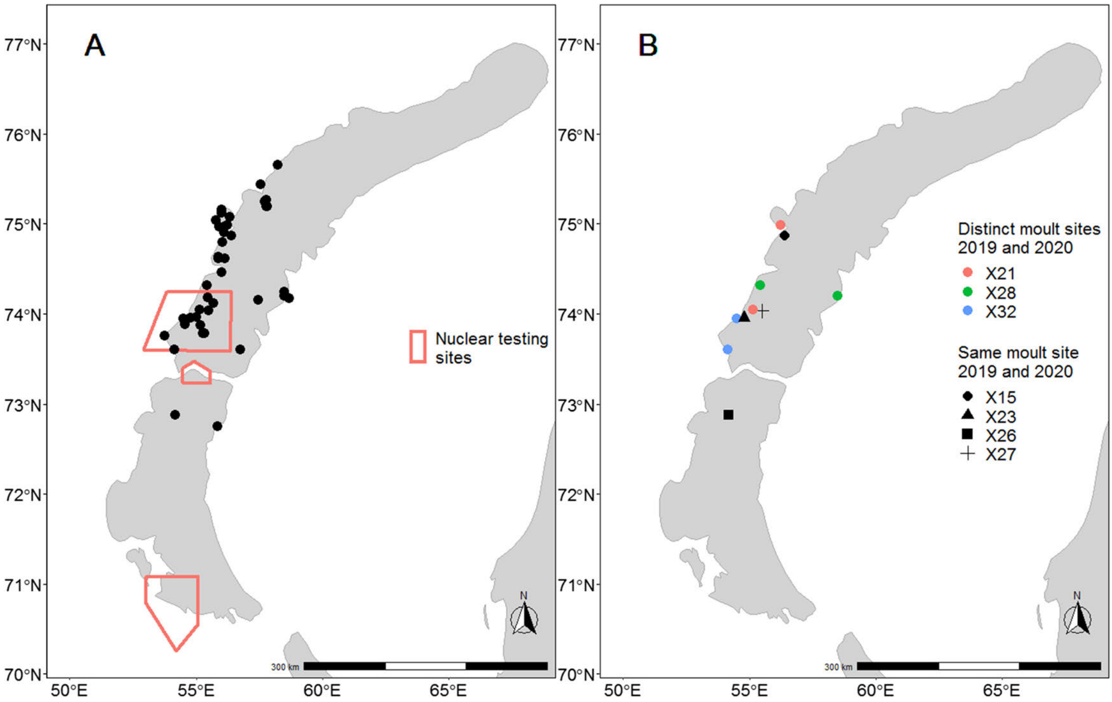

Fig. 3 Moulting site locations of satellite-tracked taiga bean geese in 2019–2020. Map A shows all recorded moulting sites and former nuclear testing sites. Map B shows the moulting locations of individuals tracked to Novaya Zemlya over both years. Nuclear testing sites are redrawn after [25]

Central Flyway taiga bean goose population is concentrated in this relatively small area every year. Bean geese spend approximately three months on the island, around four times longer than the typical duration of moult. This shows that the high Arctic is as relevant an environment for them as the boreal breeding and temperate wintering areas. The observed moult migration changes migratory performance of the population by increasing the length of the annual migration distance and delaying the autumn migration for a non-random part of the population. An alarming finding is that the moulting area is close to the most active historical nuclear testing sites in the world in a biome that is facing rapid climate change. Altogether, the inclusion of the high Arctic to the migration system that has mainly been considered boreal-temperate links the three ecological communities to each other, raises interesting questions on the potential evolution of the flyway and has important implications for population censuses and management.

Impacts of moult migration on individual behaviour

The observed moult migration behaviour means that breeding success and breeding status have a major impact on individual migratory behaviour of the taiga bean geese. By spending the summer in Novaya Zemlya, moult migrants more than double the length of their annual migration route and delay their autumn migration in comparison to successful breeders. Migratory connectivity between breeding and moulting sites have not been previously studied as a previously unknown portion of the population participates in moult migrations, and the specific moulting sites on Novaya Zemlya, or other destinations, have been generally unknown. As shown in Fig. 5, migratory connectivity between breeding and moulting sites in Novaya Zemlya is very low, meaning that individuals from different origins mix with each other during the moulting season. Although the pair formation in goose populations is traditionally thought to take place during winter, it has recently been shown that individuals from two populations of greater white-fronted geese *Anser albifrons* changed their flyway (population) in shared moulting sites, probably through pair formation during moulting [14]. In a similar manner, it is possible that low connectivity between breeding and moulting sites could contribute to the gene flow inside the Central Flyway taiga bean goose population, if at least

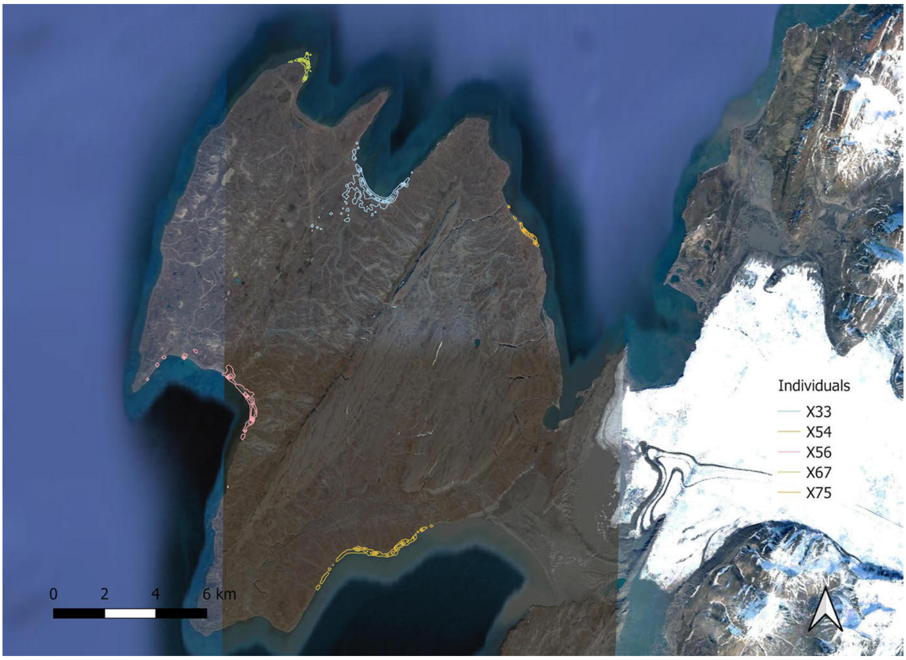

Fig. 4 Estimated utilization distributions of five taiga bean geese during moult at Novaya Zemlya in 2020. The outermost contour is a 0.95 probability contour for each individual. Background map: Google© 2021 Terrametrics, Maxar Technologies

some pair formation takes place during the moulting. However, this should be investigated in future studies. In general, more attention should be paid to migratory connectivity between breeding and moulting sites, and its consequences to the gene flow inside and between moult migrating populations.

Population consequences of moult migration

All satellite-tracked non-breeding and unsuccessfully breeding taiga bean geese in this study (from Finland and Russia) and a previous study (from Sweden [19]) have moult migrated to Novaya Zemlya. This indicates that a large part of the population is there in the late summer, which was previously unknown. This can be concluded because the bean geese typically only start breeding in their third year (the largest cohorts being non-breeders) and a large proportion of breeding-age individuals fail to breed successfully. That clearly a minority of adult birds are successful breeders can be seen in the counts of birds in Sweden, in which the proportion of first-year birds has been 7.7–14.2% of the whole population [16]. With a conservative average brood size estimate of two individuals (each successful pair having two offspring), this would mean that 15.2–28.4% of the population are successful breeders and their offspring, while all the rest are non-breeders and unsuccessful breeders. In concert with this, we found that 40 and 29% of the breeding attempts of the tagged birds were successful in 2019 and 2020, respectively. Late snowmelt in northern Finland in 2020 probably contributed to low breeding success, but also to the fact that four individuals which bred in 2019, skipped breeding in 2020. However, our results show that moult migration can strongly contribute to the spatio-temporal distribution of the population and that it can be an integral part of the migratory flyway of a population. Therefore, more attention should be paid to moult migration in future research on migratory birds with synchronous wing moult and potential moult migration (see [8] for relevant taxonomic groups).

Evolution of the moult migration behaviour

The extensive moult migration far outside of the breeding range raises two interesting questions regarding the evolution of the behaviour: How does it develop in individuals and which selective factors are behind it? The evolutionary history behind the moult migration is interesting regarding the question on how the birds navigate to the moulting sites (“where to move” [10]), as the history might reveal whether the navigation to the island is more likely to be based on genetics or social learning.

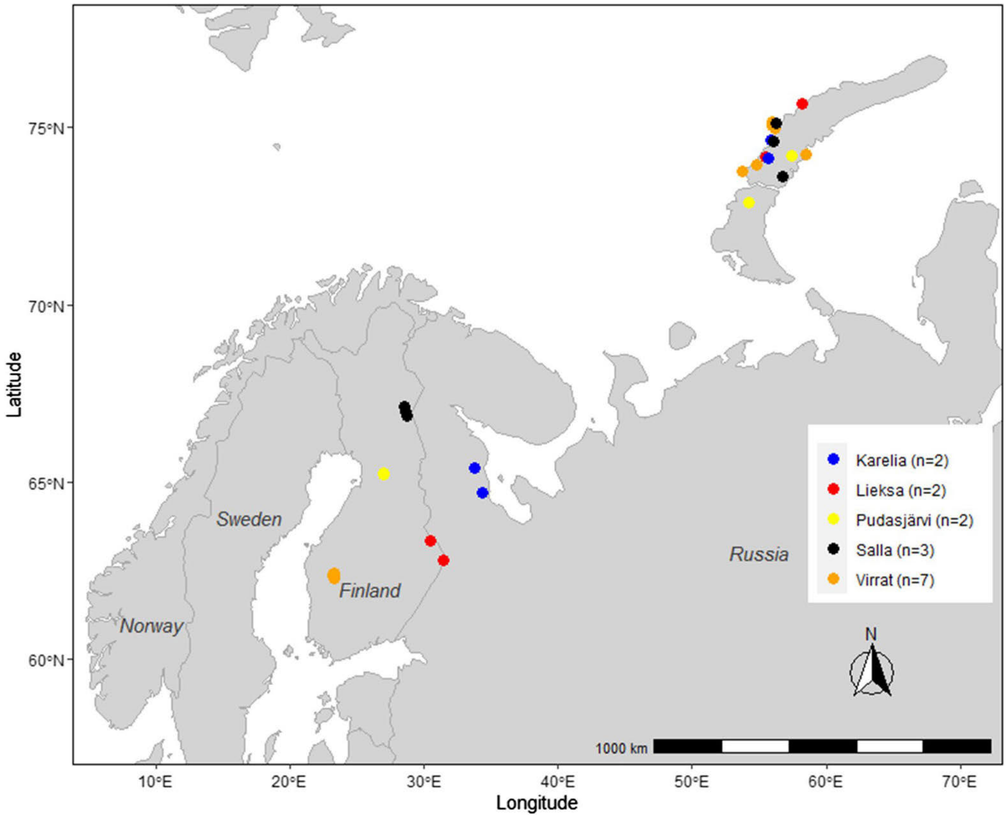

Fig. 5 Connectivity between breeding sites and moulting sites in Novaya Zemlya. Birds breeding in the same area are denoted with the same colour. Mean estimate for Mantel's correlation r_M for distances between individuals on breeding and moulting sites is – 0.001 (95% CI – 0.1562–0.2897)

Currently, we can only speculate about the evolutionary history of the behaviour, and we are not aware of any other populations for which it would be known either. This would be an important topic for future studies, to better understand the development of current flyway structures. However, that a large part of the population is now known to undertake moult migration would in this case seem to suggest strong selective benefit for doing so. The selective factors behind moult migration should be studied to understand the birds internal factors for this movement ("why to move"). Avoidance of predators, food supply or temperature (niche tracking) are plausible candidates, but whether and which of these factors play a role remains to be examined. This is also relevant because all of these factors may be changing, which may change the scene of selection for moult migration. It is apparent that moult migration to the high Arctic includes at least energetic costs of flying for moult migrating individuals, which must be outweighed by one or several fitness benefits. To understand the evolution of moult migration and the flyways related to moult migrating populations, it would thus be essential to reveal the fitness gains for individuals caused by moult migration.

Conservation concerns of moulting in a high Arctic nuclear testing site

Novaya Zemlya has been one of the most active nuclear testing sites in the world [26], and the taiga bean goose moulting sites are located in the close proximity of the testing areas (Fig. 3). Besides nuclear tests, various types of nuclear waste have been buried in soil and shores of Novaya Zemlya [27, 28]. Data on soil radioactive contamination in Novaya Zemlya is scarce [29], but contaminated areas are reported at least near nuclear waste dumping sites [28]. A large part of the taiga bean goose population thus gathers annually to an area that has exposed the population to the direct effects of detonations, nuclear fallouts and leaks of nuclear waste. The

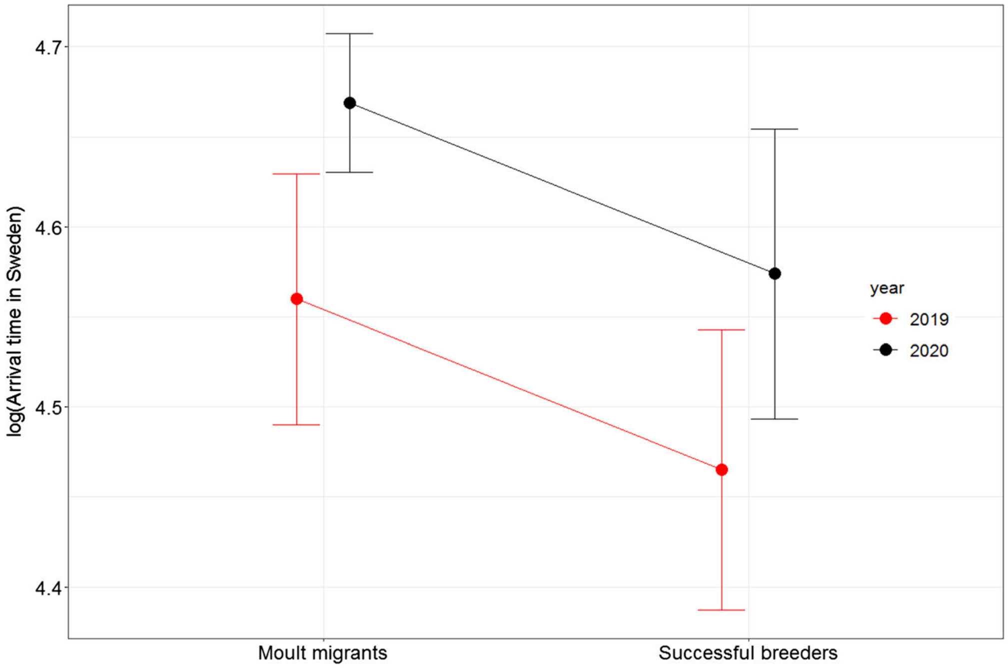

Fig. 6 Impact of moult migration to the timing of taiga bean geese autumn migration. Figure shows model predictions with 95% confidence intervals for moult migrant and successfully breeding (moulting at breeding grounds) in years 2019–2020

extent of which the taiga bean goose population has been exposed and is currently exposed to radiation is unknown, but several dozen cohorts have at least fed on radioactive-contaminated food in Novaya Zemlya over many years. While the potential historical impacts of the radioactive exposure on the population are unknown, they have clearly been possible, and the potential current and future exposure should be investigated.

Additionally, moult migration to the high Arctic exposes the taiga bean goose population also to the rapid impacts of climate change to the arctic ecosystem [30]. The frequency of extreme weather conditions increase due to global warming, along with impacts on arctic vegetation, such as shrub expansion [31]. Regular gathering of the taiga bean geese annually in a small area in the high Arctic thus makes the population vulnerable to extreme weather conditions [32] and to unfavourable changes in vegetation.

Research and management implications

Moult migration to Novaya Zemlya has direct impacts on the on-going population monitoring activities in the Central Flyway [33]. Monitoring of the taiga bean goose breeding population on the breeding grounds during the moult period has recently been developed in Finland (Paasivaara & Laaksonen, work in progress). Our results show that this monitoring scheme needs to take into account that breeding success has a strong impact on taiga bean geese numbers on the breeding grounds during moult. If the goal of these counts is to monitor the size or development of the breeding population, breeding success must be carefully monitored to separate yearly changes in breeding population size from the yearly changes in breeding success. Second, the productivity of the Central Flyway population is estimated by counting juvenile ratios in autumn flocks in Sweden [16]. Moult migrants returning from Novaya Zemlya consist exclusively of non-juvenile birds that arrive in Sweden from late September to mid-November, thereby decreasing the juvenile ratio observed in Sweden during autumn. If counts are carried out early in autumn, there is a risk of overestimating the juvenile ratio (productivity), as all sub-adults and a large proportion of the breeding adults may still be in Novaya Zemlya. Additionally, our results indicate that the arrival date of moult migrants to Sweden can have substantial variation between years.

Conclusions

Our results show that moult migration can have a major impact on migratory behaviour of birds, linking both breeding status and success to individual migratory performance and spatio-temporal occurrence of the populations. It can create unexpected connections between ecological communities in different biomes, such as the connection between boreal forests and high Arctic presented in this study. Revealing these connections and examining their consequences to both moult migratory populations and the ecological communities connected by the moult migrants are exciting questions for future research. As shown in this and other studies, moult migration can also expose populations to several anthropogenic pressures, potentially decreasing the survival of individuals [13]. On the other hand, factors behind the evolution of moult migration are rarely studied. To understand the evolution of moult migration and its current impact on bird populations, the impact of moult migration to survival rates and future breeding success would be essential to investigate in future studies.

Abbreviations

GPS: Global positioning system; GSM: Global system for mobile communications; GPRS: General packet radio service; SMS: Short message service; km/h: Kilometres/hour; lat: Latitude; lon: Longitude.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40462-021-00284-4.

Additional file 1. Utilization distributions in Novaya Zemlya during moult for all birds tracked in this study.

Additional file 2. Table 1. Individual data on taiga bean geese marked with GPS-transmitters during 2019–2020.

Additional file 3. Table 2. Length of migration routes, duration of migration and yearly additional journey caused by moult migration.

Additional file 4. Table 3. Explanation of sample sizes used in the analysis.

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Authors' contributions

A.PI. and T.L. conceived the idea. A.PI. carried out most of the field work, analysed the data and led the manuscript writing. T.L. participated in the field work, manuscript writing and supervised throughout the process. All authors gave final approval for the publication.

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Availability of data and materials

The datasets generated and analyzed during the current study are available in the Movebank Data Repository, https://doi.org/10.5441/001/1.22kk5126 (Piironen et al., 2021). Sensitive data (locations showing nest locations) are excluded from the publicly available data.

Declarations

Ethics approval

Capturing and marking of birds was done by the approval of Finnish Wildlife Agency (License Number 2019-5-600-01158-8).

Consent for publication

Not applicable.

Competing interest

The authors declare no competing interests.

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RESEARCH ARTICLE

Predicting spatio-temporal distributions of migratory populations using Gaussian process modelling

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Abstract

1. Knowledge concerning spatio-temporal distributions of populations is a prerequisite for successful conservation and management of migratory animals. Achieving cost-effective monitoring of large-scale movements is often difficult due to lack of effective and inexpensive methods.
2. Taiga bean goose *Anser fabalis fabalis* and tundra bean goose *A. f. rossicus* offer an excellent example of a challenging management situation with harvested migratory populations. The subspecies have different conservation statuses and population trends. However, their distribution overlaps during migration to an unknown extent, which, together with their similar appearance, has created a conservation–management dilemma.
3. Gaussian process (GP) models are widely adopted in the field of statistics and machine learning, but have seldom been applied in ecology so far. We introduce the R package `gplite` for GP modelling and use it in our case study together with birdwatcher observation data to study spatio-temporal differences between bean goose subspecies during migration in Finland in 2011–2019.
4. We demonstrate that GP modelling offers a flexible and effective tool for analysing heterogeneous data collected by citizens. The analysis reveals spatial and temporal distribution differences between the two bean goose subspecies in Finland. Taiga bean goose migrates through the entire country, whereas tundra bean goose occurs only in a small area in south-eastern Finland and migrates later than taiga bean goose.
5. *Synthesis and applications*. Within the studied bean goose populations, harvest can be targeted at abundant tundra bean goose by restricting hunting to south-eastern Finland and to the end of the migration period. In general, our approach combining citizen science data with GP modelling can be applied to study spatio-temporal distributions of various populations and thus help in solving challenging management situations. The introduced R package `gplite` can be applied

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Antti Piironen and Juho Piironen contributed equally.

not only to ecological modelling, but to a wide range of analyses in other fields of science.

KEYWORDS
adaptive management, citizen science, distribution modelling, ecological modelling, flyway management, migration ecology, waterfowl ecology, wildlife management

1 | INTRODUCTION

Human population growth and the intensifying use of natural resources pose increasing challenges to the conservation and management of wildlife populations (e.g. Halpern et al., 2008). Consequently, national and international activities have been proposed and initiated to safeguard the sustainable use and preservation of wildlife populations (e.g. Hawkins et al., 1984). Decision-making in conservation and management requires reliable data on population dynamics and ecosystem processes, but relevant information is often scarce, emphasizing the importance of using all available data with suitable statistical tools (Johnson et al., 2018).

Knowledge of distribution over the annual cycle is a prerequisite for the successful conservation and management of migratory animals, as it plays a vital role in habitat safeguarding, population monitoring and targeting management actions. Understanding spatio-temporal dispersion is particularly important in cases where multiple populations with different conservation statuses occur in the same area and are affected by the same human actions. Birds are probably the best-known migratory animals, but despite their movements having been intensively studied since bird ringing began in the late 1800s, the spatio-temporal occurrences of many species and populations are still poorly understood. Traditional methods, such as bird ringing, are usually ineffective and slow (Anderson & Green, 2009), whereas modern tracking technologies suffer from expensiveness, the large size of tracking devices or short life span of small devices (Tomkiewicz et al., 2010).

Citizen science may offer valuable tools for nature conservation and management (McKinley et al., 2017), but the data often suffer from weaknesses caused by spatial and temporal observation biases or the insufficient expertise of observers (Callaghan et al., 2019). Producing scientific knowledge from these large yet heterogeneous datasets often requires applying modern statistical methods in the analyses. Unfortunately, commonly used methods often have many weaknesses with heterogeneous data collected by citizens (Bird et al., 2014). Gaussian processes (GPs) offer a flexible probabilistic approach for modelling such data. The basic theory has been known for decades (e.g. O'Hagan, 1978), and the machine learning community became aware of GPs in the 1990 (e.g. Williams & Rasmussen, 1996), and nowadays they are commonplace in the field (for an excellent introduction, see Rasmussen & Williams, 2006). Previous applications in ecology, however, are relatively sparse. GPs have been used to study optimization in fisheries and predator–prey interactions (Patil, 2007), species distribution modelling (SDM; Vanhatalo et al., 2012; Golding & Purse, 2016; Ingram et al., 2020; Vanhatalo et al., 2020; Wright et al., 2021), modelling individual fish growth (Sigourney et al., 2012) and decision-making in fisheries (Boettiger et al., 2015). The GP models' flexibility and capability to account for uncertainties due to geographically and temporally uneven observation pressure enable wider usage in ecology. So far, their applicability has undoubtedly been limited by the absence of user-friendly tools for the R language, which is the de facto programming language in the field. Many R packages that provide some GP regression functionalities are limited in features, and do not support functionalities necessary for general-purpose modelling (e.g. packages `gptk`, `mlegp` and `GPfit` all implement only Gaussian noise model).

Migratory waterfowl are excellent examples of difficult conservation–management situations, as they are important quarry species but many of their populations have declined in recent decades (Madsen et al., 2015). Simultaneously, other populations, even sympatric ones, are so abundant that they require population control (Fox & Madsen, 2017). Species with different population trends can be affected by the same management actions (e.g. hunting, habitat management). For example, various waterfowl species are often similar in appearance and thus difficult to identify in a hunting situation, which complicates their harvest management. Difficult management situations with two sympatric, look-a-like birds with opposite conservation statuses have been recognized in North America (e.g. Sheaffer et al., 2004), where diverse management challenges have been dealt with by applying an adaptive harvest management framework since the 1990s (Nichols et al., 2007). In Europe, adaptive management approaches for waterfowl have been introduced more recently (e.g. Madsen et al., 2017).

The two Western Palearctic subspecies of bean goose, the taiga bean goose *Anser fabalis fabalis* and the tundra bean goose *Anser fabalis rossicus* provide an excellent example of a within-species conservation–management dilemma. The tundra bean goose population has doubled since the late 1980s and is recently estimated at 600,000–650,000 individuals (Heinicke, 2018). In contrast to that, taiga bean goose numbers have decreased in recent decades, with latest population estimates reaching 70,000–80,000 individuals (Heldbjerg et al., 2019). Both bean goose subspecies are legal quarry in many countries within their range, but due to their different population statuses and trends, their conservation and management needs are clearly different. Unfortunately, they are very similar in appearance and therefore impossible to identify in a hunting situation. This leads to considerable difficulties when aiming to target the harvest towards the abundant tundra bean goose without hampering taiga bean goose conservation goals. Taiga bean geese breed in the boreal zone of Fennoscandia and north-western Russia, and winter mainly in southern Sweden, northern Germany and Poland. Tundra bean geese breed in the tundra zone and winter in a broad area in western and central Europe (see Figure 1). However, the subspecies can overlap in their migration stop-over areas. The movements of taiga bean geese breeding in Finland are fairly well known (e.g. Nilsson, 2011), but tundra bean geese occurring alongside taiga bean geese on their migration through Finland is poorly understood. Honka et al. (2017) showed, using molecular genetic methods, that bean geese harvested in south-eastern Finland were mainly tundra bean geese, whereas birds from western and northern Finland were mainly taiga bean geese. Nonetheless, this information is coarse due to the small sample size (*N* = 103). Additionally, Honka et al.'s (2017) study was lacking the temporal component, meaning that the study did not account for yearly variation in subspecies occurrence.

Knowledge concerning spatio-temporal differences of bean goose subspecies occurrences may enable geographical and seasonal hunting regulations and thus prevent overharvesting of taiga bean geese. Despite the look-alike problem that makes bean goose subspecies identification impossible in a hunting situation, taiga and tundra bean geese have certain characteristics that differentiate the appearance of their heads and bills (Heinicke, 2010). These characteristics allow subspecies identification for most individuals in the field with a spotting scope, and thus enable birdwatchers to collect bean goose observations on a subspecies level.

The aim of this paper is to introduce and promote GP modelling as a tool for utilizing citizen science data for studying the spatio-temporal occurrence of migratory populations. In a case study, we apply GP modelling with birdwatcher observation data to predict differences in taiga and tundra bean goose spatio-temporal distributions in Finland during migration. As a result, we provide a general-purpose R package `gplite` (Piironen, 2021b) for future GP analyses along with management recommendations for the bean goose management–conservation issue.

2 | MATERIALS AND METHODS

2.1 | Bird observation data

We received birdwatcher observation data collected during 2011–2019 from BirdLife Finland. Observations were collected via the online bird observation portal Tiira (https://www.tiira.fi/). Species, location, date and number of observed birds are mandatory information to the observation. Additionally, observers can save a variety of information such as age, status etc. to the observation. A bean goose observation can be entered into the system as a taiga or a tundra bean goose, or as a bean goose if the subspecies was not identified. In our analysis, we only used observations where the subspecies was identified and where the bird's status was recorded as local (i.e. not flying), as subspecies identification from a flying bean goose is unreliable. We sorted observations from 1.3. to 31.5. for spring migration and from 1.8. to 30.11. for autumn migration annually. In the end, we had *c*. 19,500 observations that met the above-mentioned criteria (See Table S3 in the Supplementary Information). In each observation, 1–12,500 individuals were observed, with a mean of 148. Any ethical approvals for collection of birdwatcher observations were not required.

Our data contain two main sources of uncertainty, both typical to citizen science data. First, the observation effort is not evenly distributed spatially or temporally. This is not a problem, as it will only increase the uncertainty of the model predictions in regions and times with few observations (note that we are interested only in the subspecies ratio, see below). Second, observations are made by numerous birdwatchers with unknown and variable expertise, possibly generating incorrectly identified birds into the data. Nonetheless, the low percentage (*c*. 40%) of bean goose observations identified to subspecies level among all bean goose observations indicate that birdwatchers are somewhat prudent in difficult identification situations, and the majority report their observations only when they are confident with the identification. Additionally, temporal differences in subspecies composition in the same area indicate that no obvious or severe spatial biases

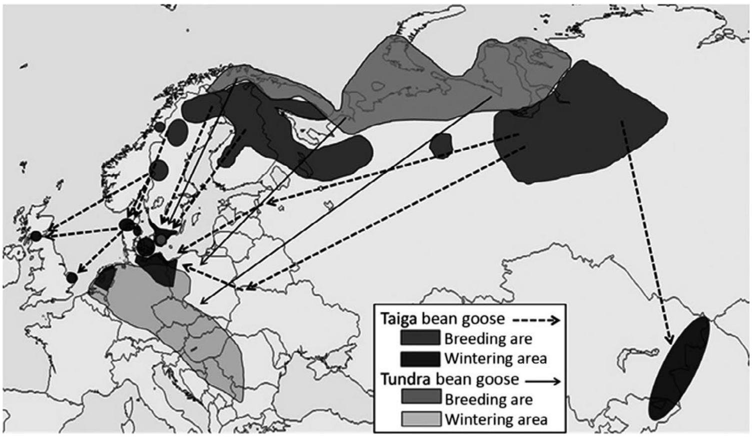

FIGURE 1 Breeding and wintering ranges and approximate migration routes of taiga and tundra bean goose in the Western Palaearctic and western parts of the Eastern Palaearctic according to Marjakangas et al. (2015)

exist in subspecies identification. Therefore, we consider erroneous observations to be randomly distributed in the data (see also Bradter et al. (2018) for a comparison between birdwatcher and systematically collected data).

Instead of modelling the occurrence of either one of the subspecies alone, we modelled the ratio of the two subspecies, as it is advantageous for statistical reasons and for producing better management recommendations. From a statistical viewpoint, modelling the ratio (presence–absence data) is considerably less vulnerable to possible biases originating from the spatially and temporally varying observation effort than modelling the distribution of each subspecies alone (presence-only data). A lack of observations does not introduce bias into estimating the ratio, as it only affects the model's uncertainty concerning the estimate. On the other hand, when modelling the distribution of one subspecies alone, you cannot ignore the bias coming from uneven observation effort, which would complicate the analysis considerably. Regarding management recommendations, our goal is to find a management solution that provides an optimal compromise between taiga bean goose conservation and avoiding unnecessary harvest regulations for tundra bean geese. Thereby, it is vital to recognize times and areas where the proportion of tundra bean geese out of all bean geese is large, as these are the times and areas where harvest is targeted at tundra bean geese while taiga bean geese are spared. Nevertheless, when modelling the ratio, we need to assume that reporting rates between the two subspecies do not differ when they are detected and identified. We are not aware of any reasons why this assumption could not be made.

2.2 | Model

Gaussian processes offer a powerful and flexible way of incorporating prior knowledge into the model while allowing a principled way to handle uncertainties. For a thorough introduction to GPs, we highly recommend the book by Rasmussen and Williams (2006). For a reader new to GPs, we provide some more details in the Supporting Information. Here we shall only give a brief description of the model. For motivation, discussion and comparison to other potential modelling choices, see the Supporting Information.

As discussed in Section 2.1, our data consist of approximately $N = 19{,}500$ observations collected during 2011–2019. The relevant information for our spatio-temporal model from each observation is as follows: coordinates $\mathbf{x} = (x_1, x_2)$, time stamp t (date) and the number of taiga and tundra bean geese observed. We use the symbol $\mathbf{z}$ to denote all the predictor features, $\mathbf{z} = (\mathbf{x}, t) = (x_1, x_2, t)$. For notational convenience, we denote the number of subspecies taiga bean goose in each observation with y, and the total number of birds in the corresponding observation with n. So, for example, $y = 90$ and $n = 100$ mean that 90 taiga and 10 tundra bean geese were observed in that particular event. We note that the data are considered presence–absence in the sense that we assume that both subspecies to be recorded, if either one of them is observed (i.e. an observation of 50 tundra bean geese means that 50 tundra bean geese were observed, but no taiga bean geese). Total absence observations are not assumed to be made.

The data have very obvious overdispersion due to the flocking behaviour of the geese. In fact, only one of the two subspecies was present in *c*. 90% of the observations. To account for this, we assume each observation y_i follows a beta-binomial distribution, which can be written as

$$\begin{aligned} y_i \mid p_i &\sim \text{Binomial}(p_i, n_i), \\ p_i \mid \mu_i &\sim \text{Beta}(a_i, b_i), \\ a_i = \frac{\mu_i}{\phi}, &\; b_i = \frac{1-\mu_i}{\phi}. \end{aligned} \tag{1}$$

Here parameter $\mu_i \in (0,1)$ is of the central interest, as it determines the expected value of y_i: $\text{E}(y_i) = n_i \text{E}(p_i) = \mu_i n_i$. What makes this model different from the binomial distribution is the overdispersion parameter ϕ, which increases the variance of y_i compared to the binomial model whenever $\phi > 0$. As $\phi \to 0$, the model approaches $y_i \sim \text{Binomial}(\mu_i, n_i)$.

We model $\mu = \mu(\mathbf{z}) \in (0,1)$ by introducing a latent function $f = f(\mathbf{z}) \in (-\infty, \infty)$ for which we give a zero mean GP prior, and then transform that through a logistic sigmoid to get μ:

$$\mu(\mathbf{z}) = \frac{1}{1 + \exp(-f(\mathbf{z}))}, \quad f(\mathbf{z}) \sim GP(0, k(\mathbf{z}, \mathbf{z}')). \tag{2}$$

The heart of a GP model is the covariance function (or kernel) $k(\mathbf{z}, \mathbf{z}')$, which specifies the properties of the model. We use the following structure

$$k(\mathbf{z}, \mathbf{z}') \propto k_s(\mathbf{x}, \mathbf{x}')\, k_t(t, t'). \tag{3}$$

In other words, the covariance factors into spatial and temporal components, which makes it easy to specify both components separately. The multiplicative covariance introduces an interaction between the spatial and temporal variation, meaning that the model allows the latent function to have spatial variation dependent on time. Recall that covariance of the form $k_s(\mathbf{x}, \mathbf{x}')\, k_t(t, t')$ corresponds to the functional form $f(\mathbf{x}, t) = f_s(\mathbf{x}) f_t(t)$ for the latent function (see Rasmussen & Williams, 2006, Section 4.2.4). An additive covariance structure $k_s(\mathbf{x}, \mathbf{x}') + k_t(t, t')$ (which corresponds to the form $f(\mathbf{x}, t) = f_s(\mathbf{x}) + f_t(t)$) could also be considered so that the latent function would look spatially the same at every time t, but this turned out be a clearly inferior choice in terms of data fit (see Supporting Information for model assessment).

For the spatial component, we use the so-called neural network covariance function (Williams, 1998)

$$k_s(\mathbf{x}, \mathbf{x}') = k_{\text{nn}}(\mathbf{x}, \mathbf{x}'). \tag{4}$$

The actual functional form is given in the Supporting Information. The neural network covariance function produces smooth nonstationary functions and has a reasonably good extrapolation ability.

Recall that covariance function $k\left(\mathbf{x}, \mathbf{x}'\right)$ is said to be stationary if it depends on $\mathbf{x} - \mathbf{x}'$ only, meaning that the latent function f is assumed to vary at the same speed everywhere (see Rasmussen & Williams, 2006, Section 4.2.1). In contrast, the non-stationary neural network kernel allows the latent function to vary more rapidly in the middle and more slowly on the boundaries of the input space $\mathbf{x}$, which matches nicely with our prior beliefs concerning the spatial behaviour of f. The covariance function has two hyperparameters, namely τ_0 and τ, which determine how rapidly f varies, and the wideness of the region where f varies substantially.

As we expect different years to be at least roughly similar, we include a periodic kernel k_{periodic} with period $T = 365$ days in the temporal component. This is achieved using a transformation $\tilde{\mathbf{t}} = \left(\sin\frac{2\pi t}{T}, \cos\frac{2\pi t}{T}\right)$ and then feeding this into some base kernel. As a base kernel, we again use the neural network covariance function, so the periodic component can be written as

$$k_{\text{periodic}}\left(t, t'\right) = k_{\text{nn}}\left(\tilde{\mathbf{t}}, \tilde{\mathbf{t}}'\right). \tag{5}$$

To allow for some inter-annual variability (i.e. deviation from exact periodicity), we modulate the above kernel by a squared exponential kernel, $k_{\text{se}}\left(t, t'\right)$ (see Supporting Information for the functional form), whose length–scale hyperparameter ℓ will determine how quasi-periodic the temporal variation is ($\ell \to \infty$ indicating exact periodicity). The magnitude hyperparameter σ_f^2 on the other hand will determine the overall magnitude of variation in the latent function. Thus, the temporal covariance function becomes

$$k_{\text{t}}\left(t, t'\right) = k_{\text{se}}\left(t, t'\right) k_{\text{periodic}}\left(t, t'\right). \tag{6}$$

Combining all the pieces together, we can write the full covariance function as

$$k\left(\mathbf{z}, \mathbf{z}\right) = k_{\text{s}}\left(\mathbf{x}, \mathbf{x}'\right) k_{\text{t}}\left(t, t'\right) \tag{7}$$

$$= k_{\text{nn}}^{(1)}\left(\mathbf{x}, \mathbf{x}'\right) k_{\text{se}}\left(t, t'\right) k_{\text{nn}}^{(2)}\left(\tilde{\mathbf{t}}, \tilde{\mathbf{t}}'\right), \tag{8}$$

The superscripts in the two neural network kernels indicate that there are two separate kernels with similar functional form but separate hyperparameters (and inputs). In total, there are six kernel hyperparameters $\left(\tau_0^{(1)}, \tau^{(1)}, \tau_0^{(2)}, \tau^{(2)}, \ell, \sigma_f\right)$ and one likelihood hyperparameter ϕ in the model. For $\tau_0^{(1)}, \tau_0^{(2)}, \tau^{(1)}$ and $\tau^{(2)}$, we use half-Cauchy priors with unit scale. Other hyperparameters are given log-uniform priors.

For fitting the models, we use the R package `gplite`. The installation instructions and a quick-start tutorial for the package are available at https://github.com/jpiironen/gplite. An example code used for the case study of the present paper is available at https://github.com/jpiironen/anser_fabalis. We fit models separately for spring and autumn, which have approximately 15,700 and 3,800 observations respectively. Both models are identical in design but are fitted separately to the two datasets. The number of observations prohibits the use of a full GP, and we use the fully independent training and test conditional (FITC) approximation with 200 inducing points (Quiñonero-Candela & Rasmussen, 2005; Snelson & Ghahramani, 2006). Due to the non-Gaussian likelihood, approximate inference for the latent values must also be used, and we employ Laplace approximation. Hyperparameters are estimated by optimizing them to their marginal maximum a posteriori values.

3 | RESULTS

Figures 2 and 3 show the model fit and data for the autumn and spring migrations, respectively, on average and across several years. The contours show how the probability for an observed bean goose to be a taiga bean goose (i.e. posterior mean of μ) varies over time at different spatial locations (see caption for more details). As shown in Figure 2, the probability of a bean goose being a taiga bean goose is high throughout Finland at the beginning of migration. Later in autumn, the probability for tundra bean goose increases, especially in south-eastern Finland. However, between-year variation exists in the proportion of tundra bean geese.

Analogous to autumn, our model predicts a high probability for a bean goose to be a taiga bean goose at the beginning of spring migration (Figure 3), whereas the probability of tundra bean goose increases during spring in southern Finland. It is noteworthy that in spring, the main division between subspecies occurrences is in the south–north direction, while being mainly in a south-easterly to north-westerly direction in autumn.

The number of bean geese decreases at the end of both migration periods, which decreases the number of observations. This can be seen as increasing uncertainty in the model predictions (i.e. smaller coverage of shaded grey area in Figures 2 and 3).

4 | DISCUSSION

The aim of our study was to introduce and promote GP modelling as a tool for predicting the spatio-temporal distribution of migratory populations using heterogeneous citizen science data. For these purposes, we introduced the R package `gplite` and demonstrated its use with a case study that analysed spatial and temporal differences in the occurrence of taiga and tundra bean goose in Finland. In the case study, the model predicts significant tundra bean goose occurrence only in south-eastern Finland for both spring and autumn. The width of the area where tundra bean goose occurs varies between years, possibly caused by wind conditions and available food supplies on the fields during migration. Tundra bean goose occurrence is also restricted to a smaller zone during autumn than during spring. These results are compatible with results of molecular genetic study by Honka et al. (2017), who showed that the bean goose hunting bag in eastern Finland contains more tundra than taiga bean geese and vice versa in western Finland. The temporal component was absent in previous work by

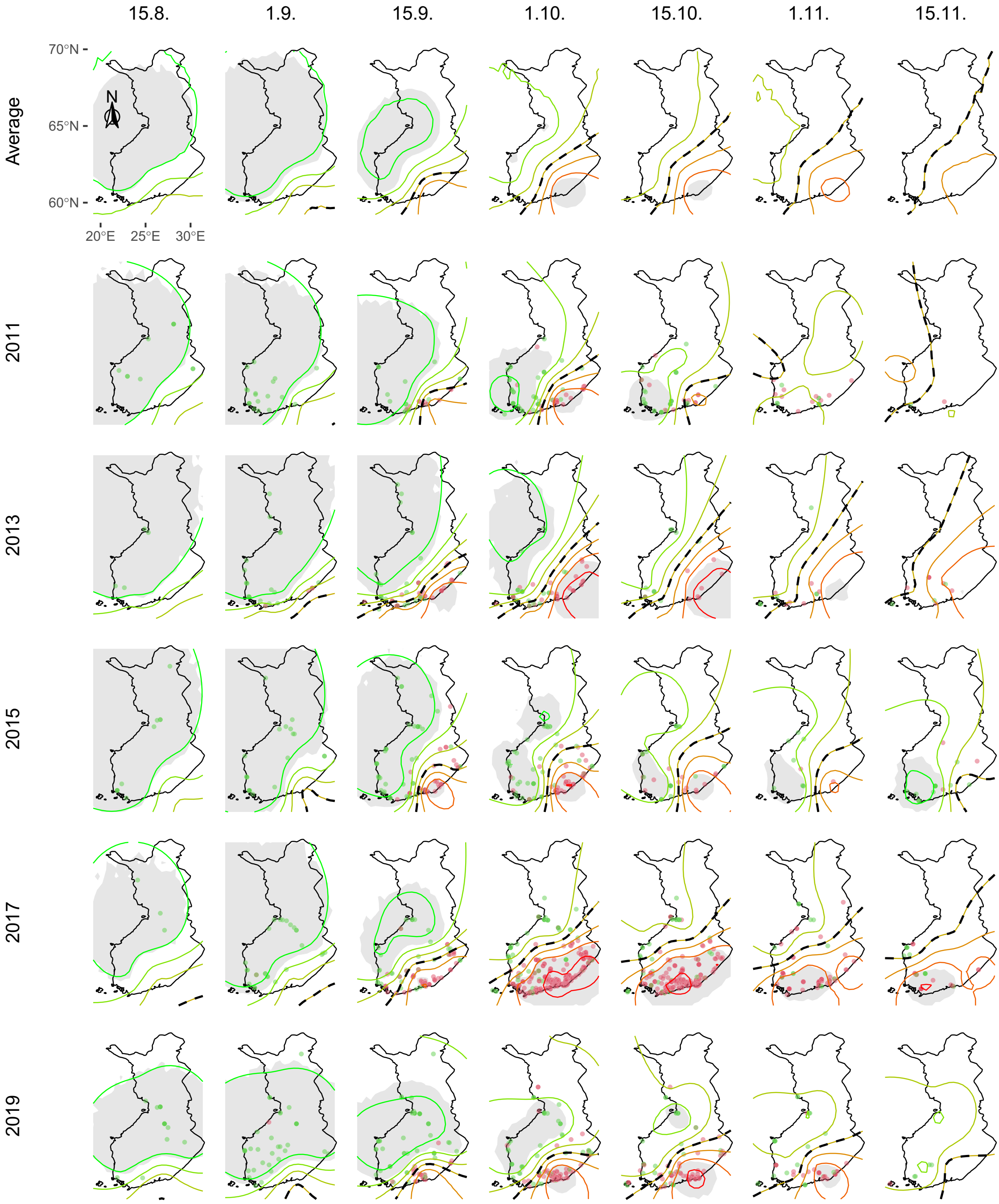

FIGURE 2 Model predictions during the autumn migration at different dates across different years. Due to long time series, only average and every other year is shown in the picture (for full time series, please see Supporting Information). The contours denote the posterior mean for μ (i.e. probability of taiga bean goose) ranging from 0.1 (red) to 0.9 (green) with approximate contour interval 0.114. Dashed black highlights contour $\mu = 0.5$. The same colour denotes the same value for μ throughout the picture. Shaded grey denotes areas where μ is different from 0.5, with posterior probability at least 95%. Dots denote observations within ± 8 days from the given day; red and green colours mark whether the majority of the observed bean geese were tundra or taiga bean geese respectively

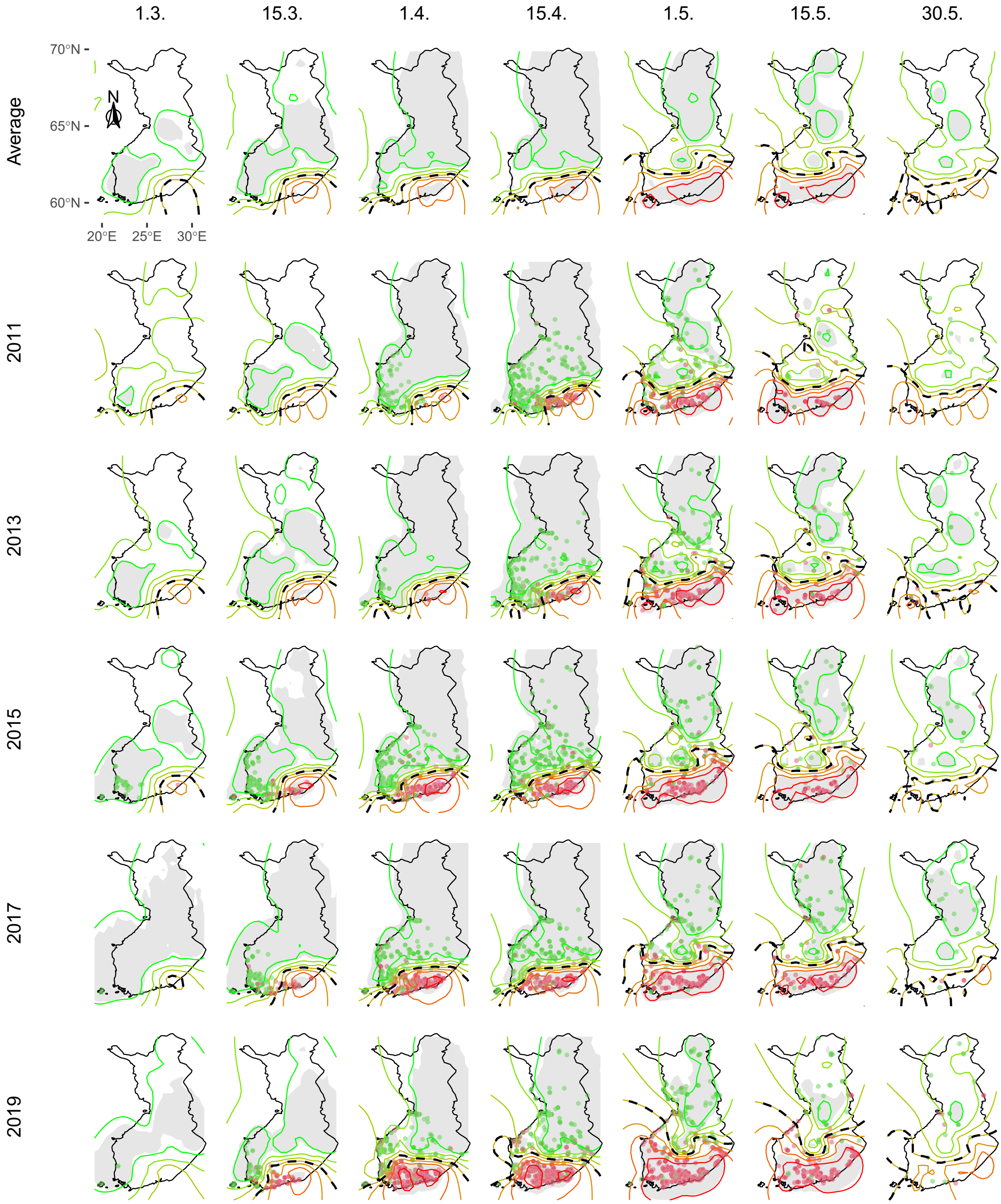

FIGURE 3 Same as in Figure 2, but for the spring migration

Honka et al. (2017). Our approach is the first detailed description of the pattern including both spatial and temporal differences in subspecies occurrence. Our study is also the first one that can be directly applied to the harvest management of these spatially overlapping populations with different population statuses and trends.

4.1 | Differences in bean goose subspecies occurrence

Tundra bean geese migrate later than taiga bean geese, both in spring and autumn. They are almost absent during the beginning of autumn migration in late August and early September, but their proportion of all bean geese in south-eastern Finland increases in the last half of September and remains high in October. Bean goose numbers and consequently the number of bean goose observations decrease in late October, also reducing our model's capability to predict subspecies occurrence (see Figure 2). During spring migration, the taiga bean goose migration begins in the first half of March, when tundra bean geese are nearly absent in Finland. Tundra bean goose numbers begin increasing in the middle of April, and the migration peak occurs approximately at the shift from April into May. Bean goose numbers decrease in the middle of May in Finland (see Figure 3). As discussed earlier in Section 3, the geographical distributions of both subspecies in Finland differ between spring and autumn migration. This is surprising, as it shows that tundra bean goose migration routes and staging areas differ between spring and autumn migration.

4.2 | Advantages of Gaussian process modelling

Previously, a variety of methods have been used to analyse species' spatial and/or temporal distributions with citizen science data. These methods include GLMs (Cheng et al., 2019), occupancy models (Altwegg & Nichols, 2019), maximum entropy models (Phillips et al., 2006) and generalized additive models (GAMs) typically using splines as basis functions (Bird et al., 2014). Tree-based models have also been used, in particular random forests (Prasad et al., 2006) and gradient boosted trees (Elith et al., 2008). Compared to these more conventional approaches, GPs have performed better in terms of predictive accuracy in comparative studies (Golding & Purse, 2016; Ingram et al., 2020; Wright et al., 2021). Additionally, GPs offer a richer (compared to GAMs and GLMs) and more flexible (compared to maximum entropy models) class of models. This includes enhanced ways of incorporating prior knowledge into the model structure and a well-calibrated uncertainty estimation (compared to tree-based models, Hastie et al., 2009, Ch. 9–10).

When comparing GPs to GLMs and GAMs technically, it is well known that GAMs include GLMs as a special case (Hastie & Tibrishanhi, 1990). Analogously, many GAMs, including some based on splines, can be seen as a special case of GPs with a specific covariance function (Rasmussen & Williams, 2006, ch. 6.3 and references therein). Therefore, GPs are inherently a richer class of models, which allow for more flexible model construction through covariance function specification. For low-dimensional data with simple covariance functions such as the squared exponential, the differences between a spline GAM and a GP can be small in interpolation (see, e.g. Riutort-Mayol et al., 2020). However, the ability to add much richer structure to the covariance function (such as quasi-periodicity, non-stationarity, etc.) that affects the model predictions (both in interpolation and extrapolation) is one of the key benefits of GP modelling over spline models. In practical applications, this allows for more complex interactions between features through a more diverse covariance function specification, which can be advantageous in terms of predictive accuracy in various modelling tasks. For practical examples in ecology (in these cases, SDM), see Golding and Purse (2016), Ingram et al. (2020) and Wright et al. (2021).

In a technical comparison to maximum entropy models and tree-based models, GPs differ more fundamentally. Maximum entropy models are designed for SDM under the assumption of presence-only data (Elith et al., 2010), and are therefore inapplicable in studies such as ours. Tree-based models, although as powerful as off-the-shelf models for prediction, suffer from difficulties in incorporating certain types of prior assumptions into the model structure. For example, the model presented in Section 2.2 factors as $f\left(x_1, x_2, t\right) = f_s\left(x_1, x_2\right) f_t(t)$ with the further assumption that $f_t(t)$ is quasi-periodic. To the best of our knowledge, encoding such structure into a tree-based model is not possible (Hastie et al., 2009, Ch. 9–10). In practical applications, various kinds of prior knowledge often exist, and the ability to utilize it in the analysis would improve the results. Therefore, GPs' ability to flexibly incorporate prior assumptions into the model structure makes them preferable to tree-based models in many cases. Additionally, as tree-based models are piecewise constant functions by definition, there is no way to control their smoothness (i.e. they are non-differentiable). Consequently, their fit is also typically jagged (see e.g. Elith et al., 2008) which is often undesirable, as species distributions are usually smooth in nature. GPs' ability to control the smoothness of the model fit thus makes them appealing in comparison to tree-based models when modelling species spatial or temporal (or spatio-temporal) distributions. Representing prediction uncertainty is also more challenging with tree-based models, although some estimates can be obtained with techniques such as bootstrapping (Hastie et al., 2009, Ch. 8). In science-based decision-making, a decision-maker often desires to know how confident one can be with the background information. Hence, GPs' well-calibrated uncertainty estimates make them an appealing choice in comparison to tree-based models in case studies such as ours, where the results will be used in political decision-making or management (see Section 4.4 for practical examples for suitable case studies).

4.3 | Future usage of Gaussian processes and the R package `gplite` in ecology

Our aim was to introduce and promote GP modelling as a powerful tool for analysing heterogeneous data and for revealing differences in the migration patterns of bean goose subspecies. Thereby, we only used time and location to predict the occurrence probability of taiga and tundra bean geese. For future reference, we emphasize that it is possible to include various environmental variables as covariates together with the model presented in this paper, and in that way study the biological factors behind the phenomenon of interest. We also note that it is possible to apply GPs to model presence-only data with the point process modelling approach, for example using the log-Gaussian Cox process model (e.g. Diggle et al., 2013).

We also emphasize that GPs are not specifically designed for modelling data collected by citizens, but can also be implemented for other types of data (satellite tracking, geologging etc.). However, data collected by citizens from various taxa offer long and cost-efficient time series for ecological research from many parts of the world. These data provide under-utilized possibilities to study the spatio-temporal occurrence of animals. This study shows the feasibility of GP models for modelling citizen science data, and their capability to produce scientific knowledge for decision-making in management. In addition to this study, the management of the greylag goose *Anser anser* population in Europe is an example case where GP models could be used to improve management. An essential problem in the greylag goose case is to recognize when and where the migratory and sedentary parts of the population overlap (Bacon et al., 2019). The currently used method for distribution modelling (kernel density estimation, Bacon et al., 2019) does not provide any uncertainty estimation to the distributions, which would be achieved using GPs. Additionally, GPs would enable the construction of a quasi-periodic time component for modelling the distributions, which is an obvious assumption for distribution changes between years for most migratory birds. Together, these advances would make the results more transparent and, presumably, more accurate (see Section 4.4 for additional examples).

Furthermore, our study provides practical tools for implementing a variety of GP models (R package `gplite`). We point out that our software provides several additional features compared to the implementation in Golding and Purse (2016), which only allows for a Bernoulli observation model and a squared exponential kernel. The extra features in our R package `gplite` include several different covariance functions (e.g. neural network, Matérn, periodic) and a possibility to combine them, multiple observation models (Gaussian, binomial, beta-binomial, Poisson), sparse approximations for facilitating larger datasets and methods for model assessment and comparison.

4.4 | Management implications

Our results can be implemented not only to bean goose management at national and flyway levels, but also to the conservation and management of animals on a global scale. In the bean goose, the conservation of subspecies taiga bean goose is carried out at a flyway level, and harvest is managed internationally by applying an adaptive harvest management framework (Marjakangas et al., 2015). The hunting bag probably consists of both subspecies in many countries, but subspecies composition in the hunting bag is largely unknown (Heldbjerg et al., 2019). The legal hunting season for bean geese in Finland begins on 20 August and ends on 31 December, but the season can be shortened and the hunting area can be restricted geographically by the Ministry of Agriculture and Forestry of Finland. This kind of regulation is a common practice in harvest management in Finland, and our results provide a scientific base for adjusting the bean goose hunting season and area to meet the different management goals for both subspecies. The results from our case study show that bean goose harvest can be targeted at tundra bean goose in Finland by geographically restricting hunting to south-eastern Finland and by delaying the beginning of the hunting season from August to approximately the beginning of October. Naturally, our approach can also be used to predict the spatio-temporal distribution of bean goose subspecies also elsewhere in their range.

On a global scale, our approach combining citizen science data with GP modelling offers useful and cost-efficient predictions on spatio-temporal distributions of populations, which can be used to solve various management problems with animals from diverse taxa. For example, the ability of ticks to spread multiple zoonotic tick-borne diseases is known to vary between species, and sample collections by citizens have already been organized (Laaksonen et al., 2018). A combination of such data and GP modelling could enable finding spatio-temporal differences in the occurrences of various tick species, which could help to address vaccination campaigns more accurately. Similarly, our approach has obvious applications in fisheries: fishing is often targeted to multiple species or populations simultaneously, which makes the spatio-temporal regulation of fishing an important tool in sustainable fish stock management (Cooke et al., 2016). A great example of such a situation is the management of various river populations of Atlantic Salmon *Salmo salar* at the Baltic Sea. These populations return to their natal rivers annually for spawning, but spend the winters at sea. Targeting fishing at sea to the desired population is one of the key actions in the successful management of these salmon populations (Torniainen et al., 2014), and thus management would benefit from the knowledge of spatio-temporal differences in the occurrence of different river populations during winter. These differences could be studied using GP modelling together with citizen science data (such as stable isotopes of scales) or with professionally collected data (radiotracking, tag recovery). Finally, our approach could be used in the management of invasive species, where the management goal is to control or eradicate harmful populations while conserving other species. An excellent example of such a case is the introduced population of northern pike *Esox lucius* in south-central Alaska that is spreading and threatening the native salmonid populations (Dunker et al., 2020). As the pikes are controlled using extreme methods, such as poisoning the water systems, knowledge of the spatio-temporal occurrence of the pike population and other species exposed to the same management actions (salmonids, piscivorous birds, macroinvertebrates) is needed to minimize the negative effects of pike management. These patterns can be studied by combining GP modelling with suitable data from various populations.

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CONFLICT OF INTERESTS

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

A.P. conceived the original idea for the study, led the writing of the manuscript and obtained the data; J.P. designed and implemented the R package, carried out the analysis and wrote the methodological parts of the article; T.L. participated to the writing of the manuscript and supervised throughout the process. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and example codes are available via GitHub https://github.com/jpiironen/anser_fabalis. For permanent link to the data and codes, see https://doi.org/10.5281/zenodo.5713729 (Piironen, 2021a). The publicly available data have been manipulated by adding a little bit of noise to the locations of all the observations. This will not affect the analyses, but was done according to the demand of the data owner (BirdLife Finland) to avoid any misuse of the data.

Installation instructions and a quick-start tutorial for the R package `gplite` can be found at https://github.com/jpiironen/gplite.

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SUPPORTING INFORMATION

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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 Skyllberg, 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

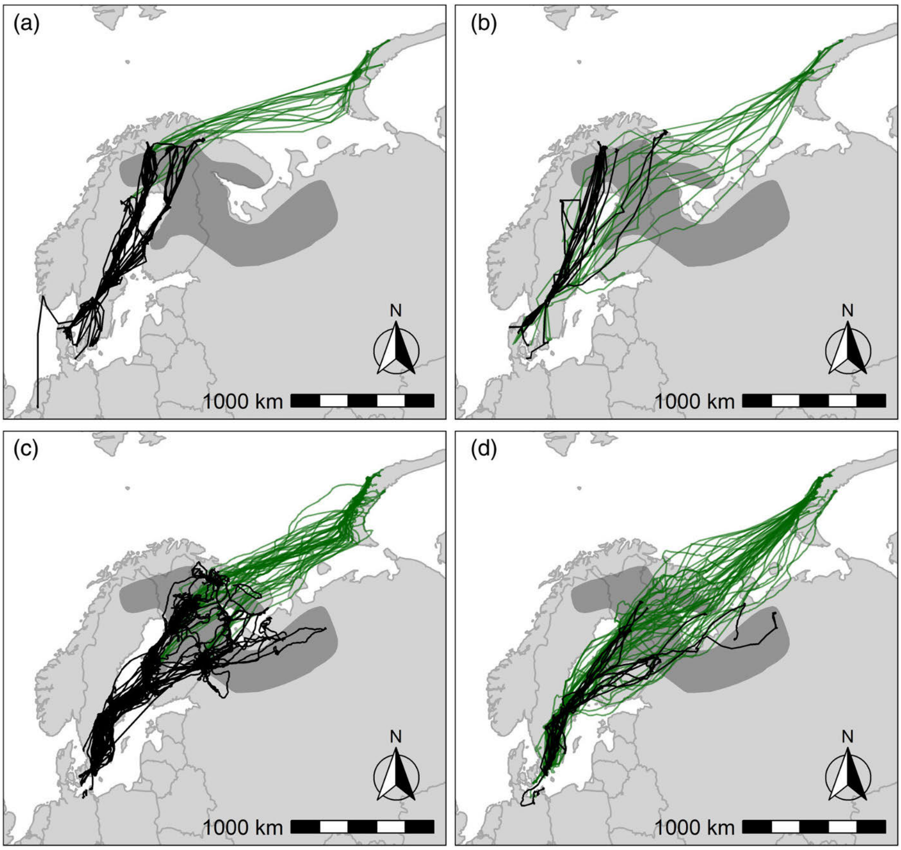

FIGURE 1 Migration routes of taiga bean geese marked for satellite tracking. Map (a) shows individuals marked in Denmark (spring migration), (b) individuals marked in Denmark (autumn migration), (c) individuals marked in Finland (spring migration) and (d) individuals marked in Finland (autumn migration). 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]

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 (Piironen 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 Skyllberg 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

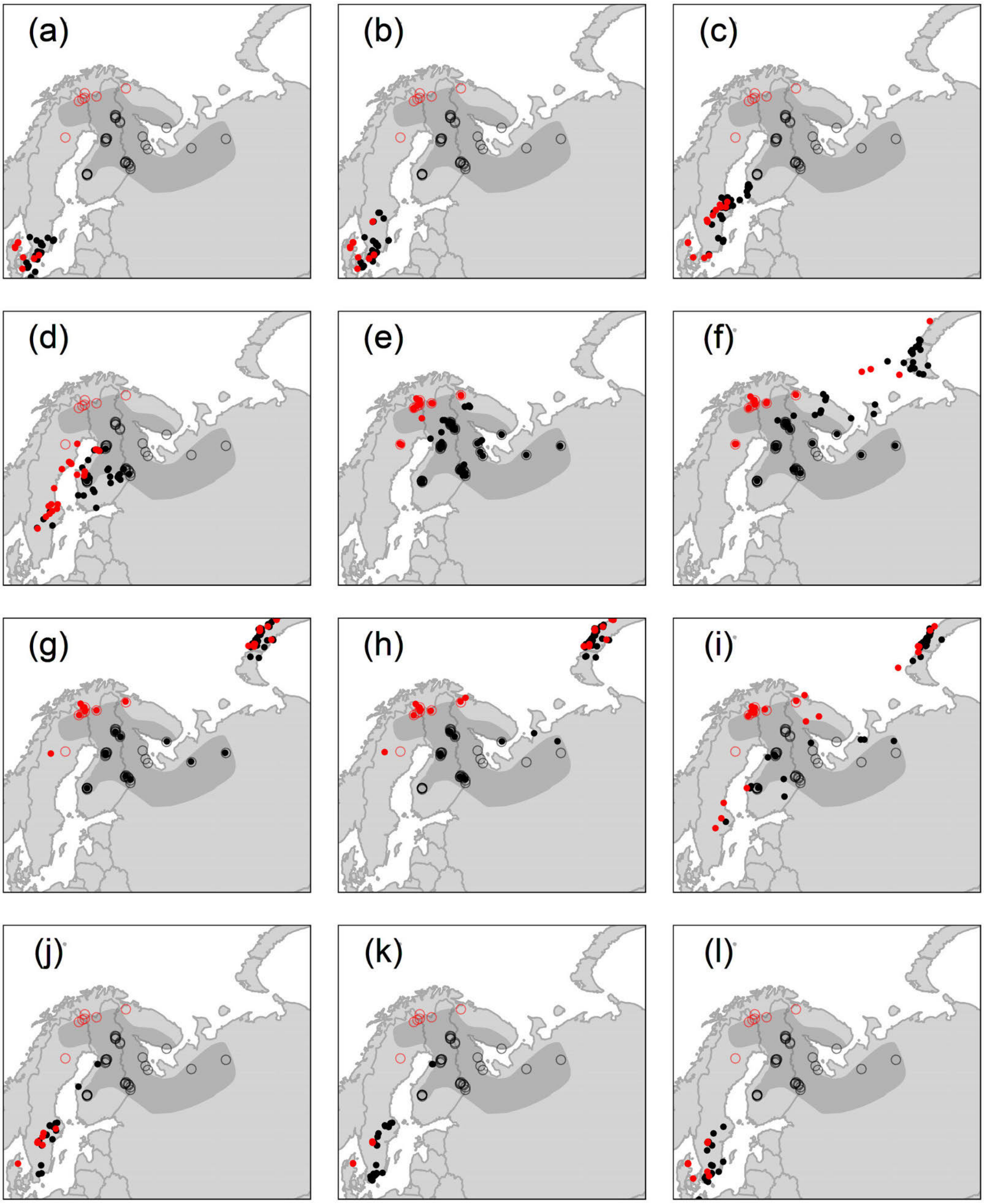

FIGURE 2 Nonbreeding distribution and breeding sites of satellite-tracked taiga bean geese in 2014–2021. The nonbreeding distribution is illustrated as the mid-month positions of individual birds (dots). Figures (a)–(l) denote months from January to December so that (a) = January, (b) = February, and 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]

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.

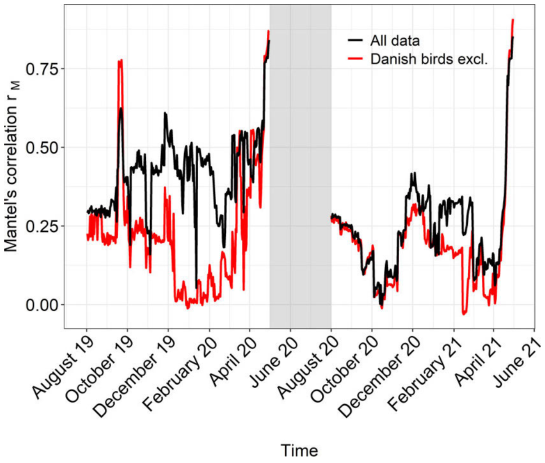

FIGURE 3 Migratory connectivity of the satellite tracked taiga bean geese during the nonbreeding season from August 1, 2019 to April 30, 2021, expressed as Mantel's correlation (r_M). The shaded gray column denotes the breeding season. [Color figure can be viewed at wileyonlinelibrary.com]

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,

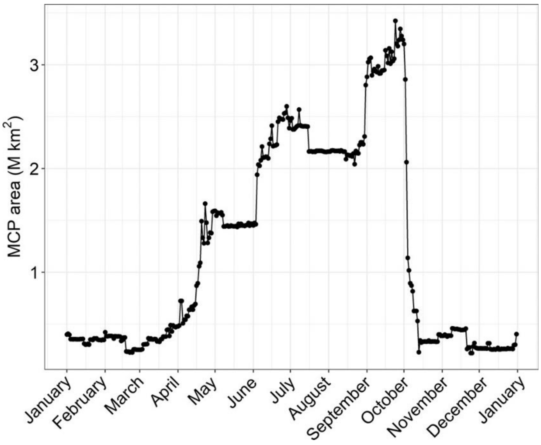

FIGURE 4 The size of the area covered by satellite tracked taiga bean geese during the nonbreeding season, calculated as minimum convex polygon (MCP). For the calculation of the daily MCPs, data have been merged from the years 2014 to 2021.

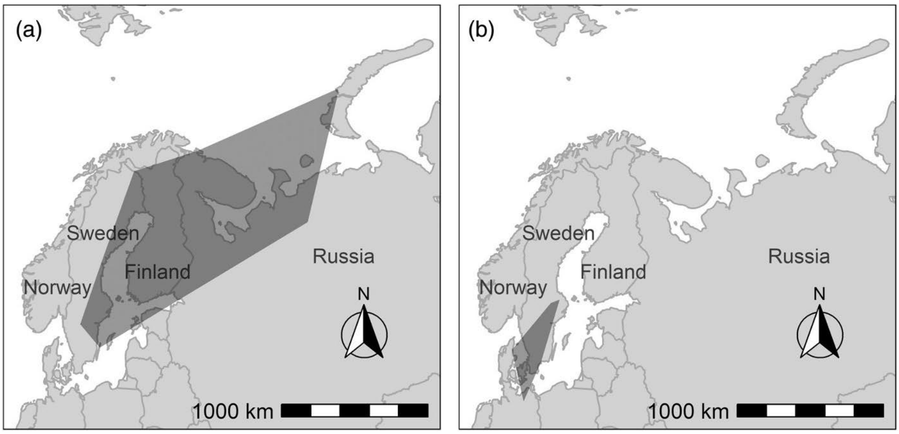

FIGURE 5 The maximum and minimum area covered by satellite tracked taiga bean geese during the nonbreeding season, expressed as a minimum convex polygon (MCP). Map (a) shows the day when MCP is at its maximum (September 24), and map (b) the day when MCP is at its minimum (November 24). For the calculation 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 (Skyllberg, 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 Skyllberg 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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A gradual migratory divide determines not only the direction of migration but also migration strategy of a social migrant bird.
Manuscript

IV

A gradual migratory divide determines not only the direction of migration but also migration strategy of a social migrant bird

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ABSTRACT

Migratory divides separate populations of migratory animals, facilitating the evolution of intraspecific differences in migration strategies. According to the optimal migration theory, differing migration strategies are expected for birds using flyways crossing different kinds of habitats. However, intraspecific differences on migration strategies between different flyways are rarely studied.

We used a combination of satellite tracking and neckband resightings from greylag geese *(Anser anser)* in years 2019–2022 to reveal 1) whether birds of different origin along the Baltic coast in Finland use different flyways (Western and Central), 2) the structure and the location of the migratory divide, and 3) to study the migration strategies of birds using the two flyways. We modelled the data using Gaussian processes, which have not been used in such analyses before, but which has been proved to be useful tools for various research questions in ecology.

The mean posterior probability for an individual to migrate along the Western Flyway decreased gradually from 0.98 at the coast of Bothnian Bay in the north to 0.06 at the eastern parts of Gulf of Finland, showing the existence of a gradual migratory divide along the Finnish coast. The steepest divide exists in the coast of the Bothnian Sea, where the mean posterior probabilities declined from 0.67 to 0.21 between adjacent counties. Migration strategies clearly differed between the flyways. The birds using Western Flyway migrated earlier in autumn, performed longer annual migration and made a clear stopover during migration compared to the birds using the Central Flyway that flew directly to their wintering sites.

The observed gradual migratory divide that also divided migration strategies provides exciting possibilities for studying ecological and evolutionary factors behind migratory divides. In the European greylag geese it furthermore affects the flyway delineation for the international management of the species. Gaussian processes enabled modelling migration strategies that would have been impossible to model using traditional methods, encouraging their future usage in ecology.

Keywords: movement ecology, optimal migration, resource tracking, waterfowl management, migratory behaviour, ecological modelling

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1. BACKGROUND

Migration allows animals to use spatially and temporally versatile resources, enabling them to utilise habitats where they cannot live over the whole annual cycle (Newton, 2008). Every year billions of animals perform impressive long-distance movements tracking these periodically available resources and avoiding unfavourable environmental conditions (Thorup et al., 2017). For birds, migration often means moving between breeding sites at higher latitudes and wintering sites at lower latitudes, with some stopover sites *en route* (Newton, 2008). When the annual movements of individuals belonging to the same species are combined together, they form flyways of populations, which consist of all habitats used by the population during the annual cycle. Hence, the flyway level forms the basis for conservation and management of migratory species (e.g. Faaborg et al., 2010).

Flyways of birds are separated by more or less precipitous migratory divides, contact zones on sides of which birds of the same species orientate to different directions during the non-breeding season to reach their wintering grounds (Newton, 2008). By separating flyways, migratory divides have wide-reaching evolutionary impacts. They drive intraspecific genetic differentiation and reproductive isolation (Bearhop et al., 2005; Boulet et al., 2006; Rolshausen et al., 2009) and create geographically independent, intraspecific population entities (often called management units, Boulet et al., 2006; Faaborg et al., 2010). Importantly, migratory divides affect the availability of habitats that individuals of the same species can utilise during the non-breeding season, which can facilitate intraspecific differences in migration strategies (Alerstam & Lindström, 1990) on distinct flyways.

The structure of a migratory divide (gradual vs. precipitous) is likely to affect its ecological and evolutionary implications (for example, genetic differentiation and reproductive isolation; Delmore & Irwin, 2014). One would assume that on a continuous breeding range without any geographical obstacles, the structure of a divide would differ from a one existing alongside with a geographical barrier (such as sea, mountain or desert). However, previous studies have not tracked individuals breeding at different distances from the divide, and thus the structure of the divide has usually remained unknown (e.g. Bearhop et al., 2005; Boulet et al., 2006; Delmore et al., 2012; Hobson et al., 2015; van Bemmelen et al., 2019). This has possibly led to a simplified understanding regarding the structure of the migratory divides as only precipitous divides have been described. To better understand the ecological, evolutionary and conservation implications of migratory divides, it is vital to unravel their structures by studying migratory behaviour of individuals breeding at different distances and on a migratory divide.

While the potential importance of migratory divides on evolution of migratory behaviour has been long acknowledged, few studies have examined differences in the year-round migratory behaviours in the different flyways. The core choices for birds to be made regarding their migration are 1) the location and number of wintering and stopover sites, 2) duration of wintering period and of each stopover, and 3) timing of movement between breeding, wintering and stopover sites. These decisions can be referred to as a migration strategy (Alerstam & Lindström, 1990), which is known to have important ecological and evolutionary consequences, as well as considerable conservation and management implications (e.g. Bearhop et al., 2005; Delmore et al., 2012). Migration strategy is thought to be guided by the availability of suitable habitat (Alerstam & Lindström, 1990; Gudmundsson et al., 1991), although other factors such as weather are also known to play a role (e.g. Tøttrup et al., 2008; Tøttrup et al., 2012). According to the optimal migration theory (Alerstam & Lindström, 1990), frequent stopovers (refuelling periods) and short flights between the stopover sites, to minimise the costs of carrying energy stores (fat reserves), should be expected if suitable habitats are abundant along the migration route. When comparing birds using distinct flyways, one would expect similar migration strategies between populations using different flyways whenever suitable habitats are equally distributed between different flyways (and different strategies if habitats are not equally distributed). Intraspecific comparisons of migration strategies between populations using different flyways (with different habitat characteristics) have produced contradicting results: Some studies have found, as expected, differing strategies (Buehler & Piersma, 2008; Delmore et al., 2012; Alves et al., 2013, van Bemmelen et al., 2019) between flyway populations. However, also surprisingly similar strategies have been found from populations using distinct flyways with different habitat characteristics (Fraser et al., 2013; Trierweiler et al., 2014), indicating that factors other than availability of suitable habitat can also contribute to migration strategies. The conditions faced during the non-breeding season (and thus, migration strategy) are known to affect breeding populations through survival and productivity (e.g. Marra et al., 1998; Norris et al., 2004). Thus, exploring the migration strategies of populations using distinct flyways is important for a better understanding of not only the factors guiding migration strategy, but also the drivers of population dynamics of migratory populations.

Migration strategies of tracked animals are often described by measuring their displacement from the breeding site throughout the year (e.g. Turchin, 1998). These data are traditionally analysed with non-linear mixed-effect models (Bunnefeld et al., 2011). These models have many obvious advantages (such as easily interpretable parameters), but they suffer from non-flexibility to model complex migration strategies. Recent development of satellite tracking devices has made it possible to track more individuals with higher spatial resolution than ever before, allowing the exploration of new and more complex behaviours and thus, calling for novel analytical approaches (Nathan et al., 2022). Gaussian processes (GP) offer a flexible, non-parametric way to model non-linear data in the Bayesian framework, and they have been used in the machine learning community for a few decades. Earlier GPs were seldom used in ecological studies, but in recent year they have started to increase popularity (see e.g. Ingram et al., 2020; Wright et al., 2021; Doser et al., 2022; Piironen et al., 2022a; Wiens & Thogmartin, 2022). This is most likely due to their inherent flexibility (Rasmussen & Williams, 2006), good predictive accuracy (Ingram et al., 2020; Wright et al., 2021) and rich covariance structure that makes them an auspicious tool to model complex phenomena such as animal migration (Piironen et al., 2022a).

The greylag geese (*Anser anser*) breeding in the northern Baltic Sea coast provide an excellent system to study the migration strategies of birds breeding in different distances from a migratory divide in a landscape without geographical barriers. These birds breed on a narrow zone along the Finnish coast (Valkama et al., 2011), and they have been hypothesized to use two different flyways during the non-breeding period: The Western Flyway (or Northwest Flyway, hereafter WF) and Central Flyway (hereafter CF, Madsen et al., 1999; Fox & Leafloor, 2018). The birds using WF breed in Fennoscandia and Western Europe, and winter sporadically in Western Europe (Nilsson, 2018). The breeding range of the birds using CF reaches from Southern Finland in the north to Czechia and Slovakia in the south, and the wintering sites are located around the Mediterranean Sea (Azafzaf et al., 2018). Despite the preliminary suggestions by Madsen et al. (1999) and Fox & Leafloor (2018), the movements of Finnish greylag geese have never been studied. Thereby, the existence of the presumed migratory divide has remained to be verified, not to mention its location. Moreover, the migration strategy of greylag geese breeding in Finland is completely unknown.

Here, we use data from satellite tracked and neckbanded individuals marked throughout the greylag goose breeding range along the Finnish Baltic Sea coast, to confirm the existence and to reveal the structure of the migratory divide. In addition, we analyse the daily displacements of satellite tracked individuals with Gaussian process models to compare migration strategies of birds using different flyways. In detail, we study 1) where the migratory divide is located, 2) which flyway is used by birds breeding in different sites (i.e. the structure of the divide), and 3) differences in migration strategy between birds using the different flyways.

2. MATERIAL AND METHODS

2.1. Field methods for satellite tracking

We caught greylag geese for satellite tracking and neckbanding throughout their breeding range in Finland in the years 2018–2022 (see Fig. I in supplemental information). The majority of the birds were caught in May and June using cannon-netting combined with short-term baiting. Catching sites were located on sea shores and they were prepared prior to catching events by feeding geese with grain from several days up to some weeks. All birds marked with GPS transmitters were adults (at least two years old) and the majority of them were caught with their broods. Caught birds that were not marked with GPS transmitter were neckbanded. Additionally, we caught some birds in late June and early July, when they were flightless due to remigial moult. These birds were caught at sea with a hand-net after a short chase with a motor-driven boat. All birds were sexed using cloacal examination, aged based on the shape of wing coverts and marked also with traditional metal ring.

For satellite-tracking, we used OrniTrack-44 solar-powered GPS-GSM (Global Positioning System-Global System for Mobile communications) neckcollars produced by Ornitela UAB. The devices weigh 45 grams, 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. locations where lat 00° 00' lon 00° 00') and locations with hdop (horizontal dilution of precision of the GPS fix) values ≤ 2. Altogether, we marked 71 birds with GPS transmitters (61 females and 10 males).

We used neckbands which were made of blue, laminated and UV resistant plastic, and had white, individual three-digit field-readable codes on them. Neckbanded birds were resighted opportunistically throughout the year by voluntary observers along their flyways. We received neckband resightings from the website www.geese.org and from the database of Finnish Bird Ringing Centre.

2.2. *Analysis of the migratory divide*

To ensure the independence of observations, we excluded all birds that were known to be paired with another marked individual (e.g. birds caught as pairs as well as birds observed together with a marked individual at any point of their encounter history). As goose families move together for the first year, we also excluded all observations from birds marked as juveniles and observed during their first annual cycle. Additionally, we excluded five individuals from the migratory divide analysis (one satellite tracked and four neckbanded), who changed their flyway during the study period (see Discussion).

To associate the individuals to one of the two flyways (Western or Central, hereafter WF and CF, respectively), used the flyway range descriptions provided by Azafzaf et al. (2018) and Nilsson (2018) as following: If a neckbanded bird was resighted at least once in Denmark, northern Germany, the Netherlands, Belgium or northern France or northwest Poland, it was labelled as a WF bird. Accordingly, if a neckbanded bird was resighted east from these countries (excluding resightings from Finland), it was labelled as a CF bird. Satellite tracked birds were associated to different flyways based on their migration routes and wintering areas following the same ranges as for neckbanded birds. We note that, based on satellite tracking data, some birds are known to use an intermediate flyway by migrating from Finnish breeding sites to stopover sites in Sweden (along the WF), and then migrating from there to the wintering sites of CF in Central Europe. Therefore, for the neckbanded birds resighted only in Sweden ($n = 10$), we considered their flyway unknown and hence excluded them from the analysis. We categorised birds visiting both Sweden and the wintering sites of CF as CF birds (neckbanded birds $n = 7$, satellite tracked bird $n = 2$). For locations of satellite tracked individuals and their association into two flyways, see Figure 1. For the geographical distribution of all neckband resightings and their association into two flyways, see Figure II in supplemental information. In the end, we had 64 satellite tracked (55 females, 9 males) and 115 neckbanded (56 females, 59 males, resighted 665 times outside Finland) individuals with sufficient data for the analysis.

Following the above-mentioned allocation into two flyways, we gave the flyway status z_i a value 1, if a bird was allocated to WF and a value 0, if it was allocated to the CF. We treated z_i as a binomially distributed variable, i.e. $z_i \sim \text{Binomial}(n, p)$, where p denotes the probability for a random individual to migrate along the WF. We estimated p by combining binomial likelihood with uniform prior distribution $p \sim \text{Unif}(0, 1)$, which is equivalent to $p \sim \text{Beta}(1, 1)$. Due to conjugacy, the combination of binomial observation model and beta prior will lead to a posterior distribution $p|y,n \sim \text{Beta}(y+1, n\text{-}y\text{-}1)$, where y denotes the number of individuals allocated to the WF and n denotes the sample size. We sampled 100,000 posterior samples for p in each of six coastal areas in Finland (see Results) to get the posterior distributions for p in each area. We analysed the data for the areas rather than as a continuous gradient to allow some clustering of marked individuals.

2.3. Analysis of migration strategies

We analysed the migratory strategies of satellite tracked birds ($n = 64$) on different flyways by measuring their daily displacement from the breeding site. We assigned each bird to either one of the flyways as described in Section 2.2. One bird changed its flyway during the study period, and hence it was assigned to different flyways in different years. We modelled the displacement data using Gaussian processes (GP), which we chose because of their flexibility (no assumptions on the form of dependence between variables are needed), because their predictive accuracy has been good in comparative studies (Ingram et al., 2020; Wright et al., 2021) and because they have appeared promising tools for modelling animal migration (Piironen et al., 2022a). For a reader new to GPs, a brief introduction in ecological context is provided in Piironen et al. (2022a), but for an in-depth introduction, see Rasmussen and Williams (2006).

In the analysis, we used satellite tracking data from the period 1.7.2019–30.6.2022 (one random location from each individual per day), and measured the displacement (y) for each tracked individual between the first location on 1 July in the first year the bird was tracked and every day until the tracking of the given bird ended. Due to heteroscedasticity of the data, we scaled the values y before the analysis so that

$$y' = \log(1 + \frac{y}{1000})$$

We assumed the scaled displacements y_i' to follow the gaussian observation model, i.e. $y_i' | \mu_i, \sigma \sim \mathrm{N}(\mu_i, \sigma^2)$. We note that, even after the scaling of y', the assumption regarding the homoscedasticity of the data was not completely fulfilled. However, as the model seems to fit well to the data (see Fig. 3), we believe that this will not crucially affect the results and their interpretation. We modelled the expected value (μ_i) for y_i' as a function of time (t) by introducing a latent function $\mu(t)$, to which we gave a zero-mean GP prior, so that $\mu(t) \sim GP(0, k(t, t'))$. The core part of the model is the covariance function $k(t, t')$, which specifies the covariance between any t and t'. Here, we use the so-called neural network covariance function (Williams, 1998), which produces non-stationary (i.e. values of $\mu(t)$ can vary at different speeds at different values of t) functions and thus matches our prior expectations regarding the behaviour of $\mu(t)$. The covariance function can be written as

$$k_{nn}(t, t') =$$

$$\frac{2}{\pi} \sin^{-1} \left(\frac{k_{lin}(t,t')}{\sqrt{1 + 2k_{lin}(t,t)}\,\sqrt{1 + 2k_{lin}(t',t')}} \right),$$

where

$$k_{lin}(t, t') = \tau^2(\tau_0^2 + t^T t')$$

We also fitted models with quasi-periodic (see Piironen et al., 2022a) and squared-exponential (see Rasmussen & Williams, 2006) covariance functions. We assessed the performance of different models using leave-one-out (LOO) cross-validation, and the model presented here performed best (see Table 1 in supplemental information for model assessment).

For model fitting, we have two hyperparameters for the covariance function (τ and τ_0) and one hyperparameter (σ) for the likelihood to be estimated. We gave half-student-t prior distributions for τ and τ_0 and a log-uniform prior to σ. To reduce computation time in hyperparameter estimation, we used the fully independent training and test conditional (FITC) approximation with 200 inducing points (Quiñonero-Candela & Rasmussen, 2005; Snelson & Ghahramani, 2006). We estimated hyperparameters by optimising them to their marginal maximum a posteriori values. We performed the analysis using packages adehabitatHR (displacement measurements; Calenge, 2006), gplite (fitting the GP model; Piironen, 2021) and related packages in R software version 4.1.1 (R Core Team, 2021). We included the script used in the analysis to the supplemental information.

3. RESULTS

3.1. *Migratory divide*

The satellite tracked greylag geese were clearly part of the two different flyways as shown by their migration routes (Figure 1). A clear gradual migratory divide is apparent and the probabilities of using the WF or CF varied in different coastal areas (Figure 2). In North Ostrobothnia (at the far end of the Bothnian Bay), there is a strong statistical support that basically all birds will migrate along the WF. The probability to migrate along the WF is also high in Ostrobothnia, but decreases substantially in Satakunta (at the coast of Bothnian Sea), Uusimaa and Kymenlaakso (at the Gulf of Finland), meaning that the majority of the birds from these areas will use the CF. We note that neckband resighting data might include some misread neckbands, which can potentially bias the posterior probabilities for p, if the misread neckband belongs to a bird using a different flyway. However, the neckband resighting data is well in line with satellite tracking data (compare Fig. 1 and Fig. II in the supplemental information) and hence, we do not have reasons to suspect that the possible bias caused by misread neckbands would be noticeable.

3.2. *Migration strategies*

Migration strategies of satellite-tracked greylag geese in the two flyways is presented in Figure 3. The overall length of the annual migration (maximum displacement between breeding and wintering

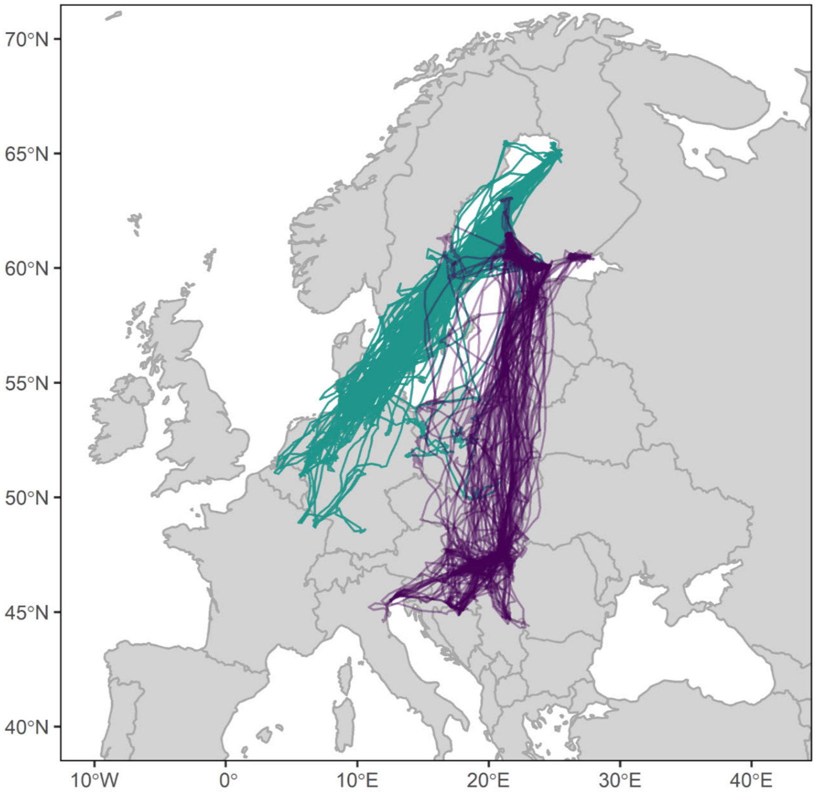

Figure 1. Migration routes of satellite tracked Finnish greylag geese in 2019–2022. Yearly migration routes are allocated to Western Flyway (turquoise lines) or to Central Flyway (purple lines) on their migration routes and wintering sites, following flyway range descriptions by Azafzaf et al. (2018) and Nilsson (2018). The allocation to flyways for birds that show intermediate migration routes between flyways (particularly birds that use stopover sites in Sweden (on WF) and winter in the wintering sites of CF in Central Europe) are allocated based on their wintering sites.

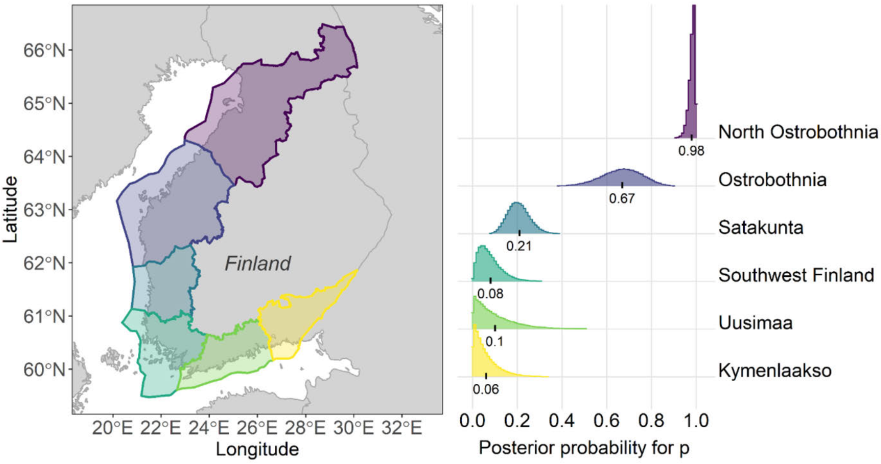

Figure 2. The posterior distribution for *p* (the probability for an individual to migrate along the Western Flyway) in different coastal areas in Finland. The colour of each histogram represents the probability in the area coloured with the same colour in the map. The numbers under the histograms denote the posterior mean for *p* in each county. The sample sizes for each county were $n_{\text{North Ostrobothnia}} = 98$, $n_{\text{Ostrobothnia}} = 25$, $n_{\text{Satakunta}} = 66$, $n_{\text{Southwest Finland}} = 24$, $n_{\text{Uusimaa}} = 8$ and $n_{\text{Kymenlaakso}} = 15$.

grounds) is more than 500 km longer among birds using WF than among birds using CF. Birds using WF have a stopover of 1–2 months during the autumn migration, whereas birds using CF migrate relatively non-stop from their breeding sites to the wintering sites, except some small-scale movement around breeding sites. Additionally, WF birds start their autumn migration approximately one month earlier than those using CF, whereas CF birds migrate earlier in the autumn.

4. DISCUSSION

Our results show that there is a gradual migratory divide in the continuous breeding distribution of greylag geese breeding at the Baltic Sea coast in Finland. Birds using different flyways also show different migration strategies. The birds breeding at the far end of the Gulf of Bothnia use the Western Flyway, the birds breeding in the Gulf of Finland use the Central Flyway and the birds breeding between these two extremes scatter to the two flyways. The overall migratory journey is longer for birds using WF and they migrate earlier in the autumn (and later in the spring) than birds on CF. Birds using WF also show a clear stopover of around one month during their autumn migration, whereas CF birds migrate relatively straight from their breeding grounds to their wintering sites. These findings provide important perspectives to be considered regarding migratory divides, drivers of the migration strategy and optimal bird migration. Importantly, our study shows that GP models have features that enable modelling migratory behaviours that could not be detected with previously used modelling techniques. Our results also provide insights for the purposes of the ongoing international management of greylag geese.

4.1. *Evolutionary implications of the gradual migratory divide*

Migratory divides are known to drive intraspecific genetic differentiation and reproductive isolation (Bearhop et al., 2005; Boulet et al., 2006; Rolshausen et al., 2009). Although pair formation among geese mainly takes place at the wintering sites (Rohwer & Anderson, 1988), some genetic mixing of goose populations is known to take place during summer (probably via pair formation) on common moulting grounds (Kölzsch et al., 2019). The fact that the migratory divide among Finnish greylag geese is gradual means that a part of the birds using different flyways breed (Fig. 1) and moult (Piironen, A., unpublished data) sympatrically. Within the birds tracked in this study, one satellite tracked individual changed its flyway during the study period (in summer) and four neckbanded birds have been re-

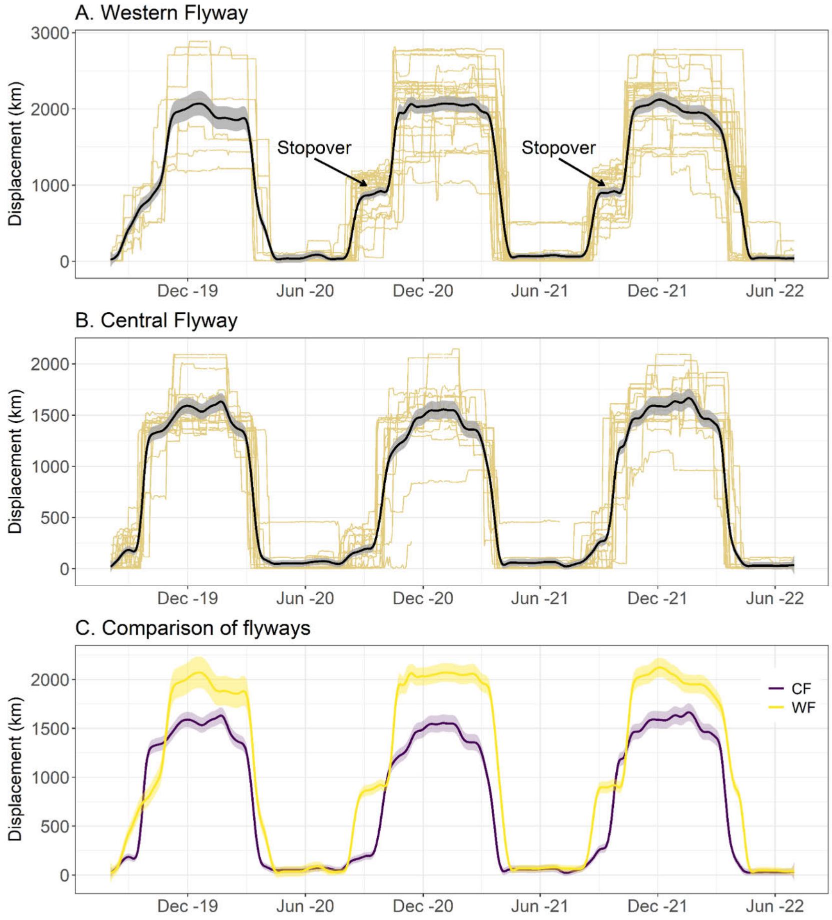

Figure 3. Model predictions for the displacement of satellite tracked greylag geese from their breeding sites in the Central and Western Flyways in 1.7.2019–30.6.2022. In the subplots A and B, the beige lines denote the data (i.e. displacement of each satellite tracked individual from the breeding site), and the black lines and shaded grey areas denote the posterior mean and 95 % credible interval for $\mu(t)$, respectively, all scaled to the original scale of y (daily displacement in kilometres from the breeding site). To facilitate easier comparison of migration strategies between flyways, subplot C visualises the above-mentioned model predictions for both flyways. Note that in all plots, the credible intervals describe the uncertainty related to the underlying function $\mu(t)$, but do not include the observation noise. Also note that the data from the Western Flyway is scarce in the year 2019, which makes the model fit also different from the subsequent years.

sighted along both flyways, most probably indicating the change of flyway (see Fig. III and IV in supplemental information). This indicates gene flow between flyways at the overlapping breeding and moulting sites, which might dilute genetic differentiation between the flyways, and contribute to the low level of genetic structure among European greylag geese (Pellegrino et al., 2015). The dilutive effect of a gradual migratory divide on genetic differentiation would probably be highlighted among species which form pairs mainly at the breeding sites (such as many passerines). Therefore, it is important to study the structure of the migratory divides and consider their effect on the population genetics in different species in the future.

4.2. *Migratory behaviour of greylag geese in light of optimal migration theory*

The optimal migration theory suggests that if suitable habitats for stopovers are abundant along the flyway, birds should exhibit a migration strategy consisting of frequent stopovers and short flights between the stopover sites, to minimise the costs of carrying the energy stores. The migration strategies of greylag geese do not seem to follow this prediction. The greylag geese using CF fly non-stop from southern Finland to their wintering sites in Central Europe (Fig. 3). During their autumn migration, they fly over several sites in the Baltic countries and Poland that are known to be suitable stopover and wintering habitats for geese (for example, see Madsen et al., 1999; Fox & Leafloor, 2018). In addition to that, birds from both flyways migrate somewhat straight from their wintering sites to their breeding sites in spring (Fig. 3). These findings indicate that greylag geese do not try to minimise the flight with energy stores, but some other factors guide their migration strategy. Second, the birds using WF start their autumn migration approximately one month earlier than those using CF by moving from their breeding sites to stopover sites in Sweden before September (Fig. 3). Although the majority of the WF birds breed north from those using CF, the habitats (including sufficient food sources) and weather conditions at the Gulf of Bothnia remain suitable for geese until October-November, since other goose species (e.g. bean geese, see Piironen et al., 2022b) occur in the area until that. Therefore, we consider it unlikely that the greylag geese would be forced to depart from the Gulf of Bothnia in August by the lack of suitable habitat as suggested by the optimal migration theory. The satellite-tracked birds indicate that hunting mortality of greylag geese is high among the birds breeding at the far end of the Gulf of Bothnia (Piironen, A., unpublished data), and thus hunting disturbance might contribute to the advanced migration schedule in the region. This, however, remains to be studied in the future. Last, the migration strategies of greylag geese differ between the WF and CF, although the habitat characteristics are at least roughly similar in both flyways. Greylag geese winter and stopover mainly in agricultural landscape holding also some wetlands (e.g. Fox & Abraham, 2017). There are more of these habitats available to birds along both flyways than used by the greylag geese (see e.g. Xu et al., 2019; d'Andrimont et al., 2021). As the optimal migration theory suggests similar migration strategies between flyways with similar habitats, our results do not indicate support for it in this sense. Although we have not quantified the availability and quality of habitat in each flyway or explained the differences in migration strategies with quantitative habitat factors, we assume that differences in habitat characteristics won't probably explain the observed differences in migration strategies between the flyways. To better understand bird migration and how migratory birds can respond to habitat loss and environmental changes, factors guiding migration strategies should be unravelled in future studies.

4.3. Gaussian processes in modelling animal movement using displacement data

We modelled migratory behaviour using Gaussian processes (GP) instead of non-linear mixed-effect model (Bunnefeld et al., 2011), which has been the most common choice for this kind of analysis. The flexibility of GPs appeared beneficial in finding fine-scale migratory behaviour such as stopover during migration, which would have been impossible to model with commonly used methods (i.e. non-linear mixed-effect models) as their fit is a double sigmoid curve. In addition to that, the possibility to implement periodic (or quasi-periodic, see Piironen et al., 2022a) covariance structure to the model is many times beneficial when modelling phenomena such as animal migration over multiple years (as migration patterns in different years often remind each other, but are not exactly similar). However, the drawback of GPs in this context is the interpretation of the parameters as their hyperparameters are very difficult to interpret in an ecologically meaningful way (as opposed to the model presented by Bunnefeld et al., (2011), which provides easily interpretable parameters). However, GPs have proven to be a promising tool for multiple non-linear problems in ecology, and their capabilities should be better explored and utilised in the expanding field of movement ecology. As satellite tracking will most likely continue to increase its popularity among movement ecologists in the future, it would be useful to conduct comparative studies of different techniques in modelling displacement data to unravel the best methods to analyse animal migration.

4.4. Implications for population delineation and international management

Finland is a range state in the international management of the Northwest-Southwest European population of greylag geese (which uses the WF), but the proportion of Finnish greylag geese belonging to this population has been unknown (Bacon et al., 2019). Our results enable the allocation of Finnish breeding population between the flyway populations based on their breeding grounds (Fig. 2). Additionally, Finnish greylag geese have formerly been observed to winter as far south as in Spain (along WF) or in North Africa (along CF, Andersson et al., 2001). Although the exploration of spatiotemporal distribution of the population is beyond the scope of this study, our data indicates that wintering sites of Finnish greylag geese might have shifted northwards in recent decedes (Fig. 1). Similar northward shift of wintering sites has recently been described greylag geese breeding in Sweden (Månsson et al., 2022), and is most likely mainly caused by climate change. As the climate will probably continue warming also in the future and greylag geese have shown their ability to rapidly adapt to the changing environmental conditions, it will remain important to track the changing migration patterns also in the future.

ETHICS STATEMENT

Capturing and marking of birds was done by the approval of Finnish Wildlife Agency (licence number 2019-5-600-01158-8).

CONFLICT OF INTEREST STATEMENT

None declared.

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AUTHOR'S CONTRIBUTIONS

AP conceived the original idea for the study, acquired funding, designed the study, led the field work, analysed the data and led the manuscript writing. TL supervised structural decisions and participated in the manuscript writing. Both authors agreed to the final version of the manuscript.

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SUPPLEMENTAL INFORMATION

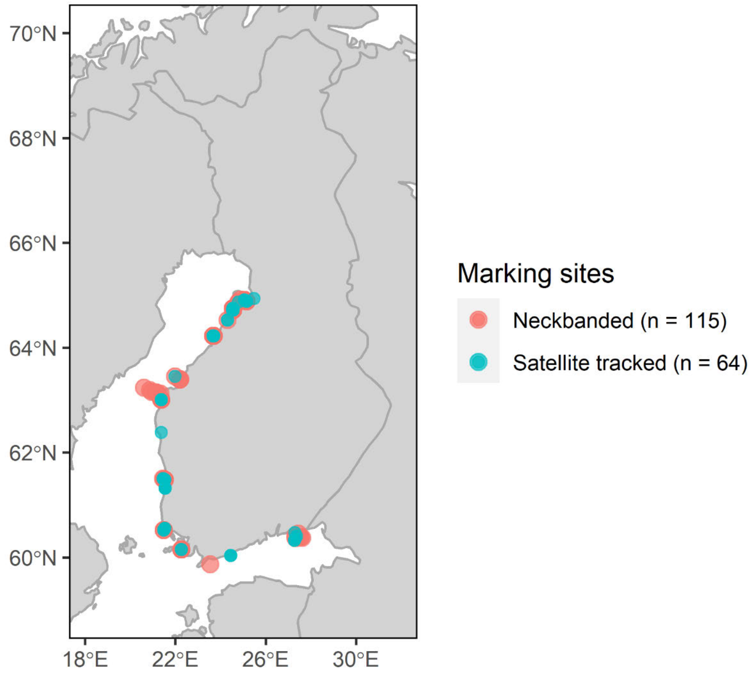

Figure I. Marking sites for greylag geese marked in Finland 2018–2022 and used in this study.

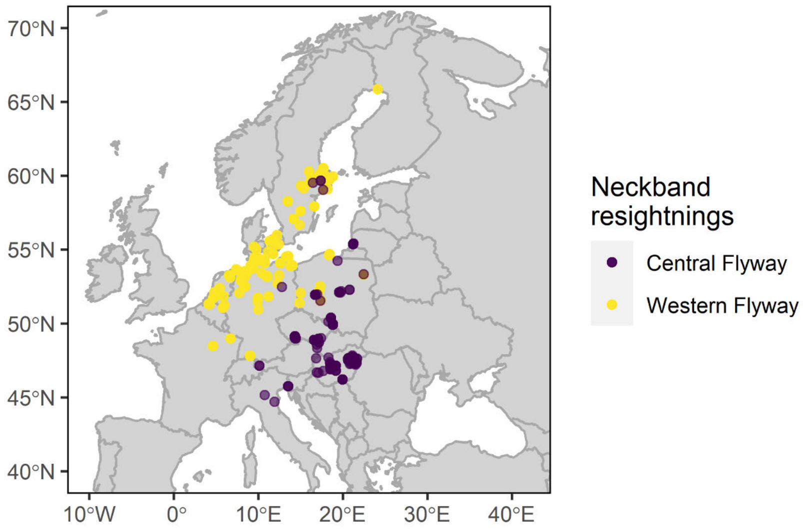

Figure II. Distribution of neckband resightings outside Finland for birds allocated to WF (yellow dots) and CF (green dots) following flyway range descriptions provided by Azafzaf et al. (2018), and Nilsson (2018). Purple dots in Sweden represent birds that have been observed on stopover sites in Sweden (on WF) and in the wintering grounds in Central Europe (on CF, see also Figure 1 in the article).

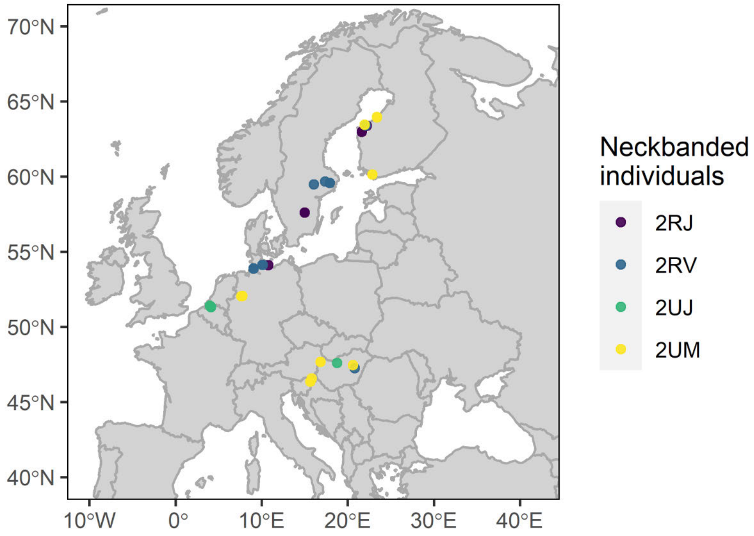

Figure III. Neckband resightings from birds which were resighted on both flyways during the study period 2018–2022.

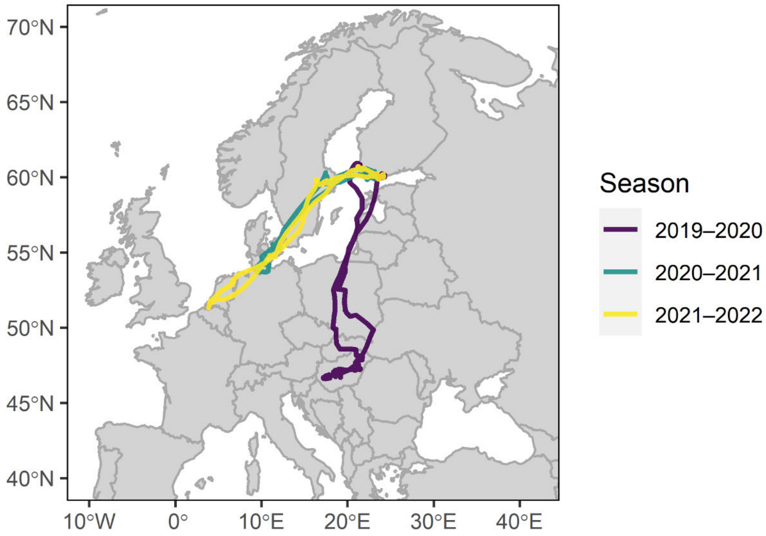

Figure IV. Seasonal tracks of the satellite tracked individual which changed its flyway during the study period in summer 2020. Each track with a unique colour represents a track between 1 July and 30 June in given years, i.e. one migration from the breeding sites to wintering sites and back.

Table 1. Model assessment. First column shows the different models i.e. the models with different covariance functions (kernels), the second column shows the difference in the sum of leave-one-out (LOO) cross-validation log-predictive densities (with the standard error in the third column) for pairwise comparison to chosen (best) model. Positive values indicate better and negative values worse performance than the chosen model.

Model	**LOO difference**	**SD**
Western Flyway		
Model with squared-exponential kernel	-21.555589	7.075035
Model with quasi-periodic kernel	-3.288889	2.976757
Model with neural network kernel	0.000000	0.000000
Central Flyway		
Model with squared-exponential kernel	-37.358402	8.616063
Model with quasi-periodic kernel	-9.210113	4.547915
Model with neural network kernel	0.000000	0.000000

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