Migration patterns of Swedish Greylag geese *Anser anser*—implications for flyway management in a changing world

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Abstract
Significant population growth of some European goose populations has led to initiatives to implement management at the flyway level. Understanding migration routes and spatiotemporal distribution is crucial for the successful and coordinated management of migratory species such as geese. In this study, we describe movements across the entire annual cycle in 76 Greylag geese (*Anser anser*) fitted with GPS tracking devices at five catch sites in Sweden. We show that Greylag geese breeding in Sweden still use a NE-SW migration path. However, the wintering range has undergone a northward shift during the last decades. Compared to previous studies, our data suggest a continued reduction in migration distance, being most pronounced in birds in southernmost Sweden. Greylag geese tagged in southernmost Sweden spent almost the entire annual cycle in Sweden and Denmark (97 and 100% of all GPS locations). In contrast, the flyway of Greylag geese from the northern catch sites still covers countries from Sweden to Spain, but presently, only a small fraction of the population migrates to Spain. Instead, most of the annual cycle is spent in Sweden, Denmark, the Netherlands, or Germany. The contrasting spatiotemporal distribution in geese of different geographical origin indicates that management initiatives for the NW/SW European Greylag Goose population need to consider that different migration strategies occur within previously defined management units. As a consequence, coordination of management actions (e.g. monitoring, harvest quotas, reserves) may need to consider different spatial scales, i.e. from the regional to the international scale depending on the origin of the Greylag geese.

Keywords Anatidae · Birds · GPS tracking · Movement patterns · Waterfowl

Introduction

Waterfowl management has a history dating back to the early 1900s and it is seen by many as one of the success stories in wildlife management (Nichols et al. 2007; Anderson and Padding 2015). Individual marking of birds and the possibility to study movements of individuals have been crucial for coordinated management actions over larger areas. The latter has also rested on an early recognition of the ‘flyway’ concept, i.e. that management needs to embrace the entire geographical area used by a species or a population during its annual cycle (Lincoln 1935; Crissey 1955; Boere and Stroud 2006). Accordingly, flyways comprise breeding and wintering grounds, as well as the corridors used when migrating between the two. Flyways typically overlap several countries, have a north–south outline, and comprise widely different habitats, often in more than one biome (Alerstam 1990; Boere and Stroud 2006).

Management of North American ducks and geese is a long-standing example of concerted efforts in conservation, hunting regulation, and monitoring at the flyway level (Hawkins et al. 1984; Anderson and Padding 2015; Lefebvre et al. 2017). In Europe, though, flyway level management has become adopted for geese only during the last few decades, in order to handle rapidly increasing as well as declining populations (Madsen et al. 2017). For centuries, European goose populations faced over-harvest and habitat loss, but this ‘historical debt’ has largely been reversed during the last 70 years (Fox and Madsen 2017). Present numbers of some goose species in Europe are higher than ever, due to increasing survival and reproductive success (Fox and Madsen
The increase in numbers and spatial expansion has not gone unnoticed when it comes to conflicts between human interests (Buij et al. 2017; Fox and Madsen 2017). Damage to agricultural crops, compromised airport safety, and negative impact on natural ecosystems are examples of impacts (Bradbeer et al. 2017; Bakker et al. 2018; Montrás-Janer et al. 2019) that often lead to stakeholder conflicts and subsequent calls for population reduction (Buij et al. 2017). However, not all goose populations are thriving. The Lesser White-fronted Goose and the Red-breasted Goose are two examples of populations in Europe in urgent need of reduced hunting mortality and increased conservation efforts (Jones et al. 2008; Simeonov et al. 2014).

It is thus a true challenge for European goose management to devise conservation policies for the rare and declining species, and at the same time, when other effective mitigating measures are not available, reduce the populations causing conflicts due to their high abundance. Common to both categories is, however, the need to provide decision makers with knowledge so that management and conservation actions can be applied at the appropriate spatiotemporal scale (Nichols et al. 2007; Madsen et al. 2017). To facilitate action planning, there may be a need to delineate management units within a flyway, for example, when the latter hosts migratory as well as resident birds (Madsen et al. 2017; Bacon et al. 2019).

In Europe, the first flyway management plan for geese was implemented in 2012 for the Svalbard-breeding population of Pink-footed geese (Madsen et al. 2017). A European goose management platform has been launched, with the purpose to facilitate similar plans for other goose species (Mediated by AEWA (Agreement on the Conservation of African-Eurasian Migratory Waterbirds); Marjakangas et al. 2015; Jensen et al. 2018; Powolny et al. 2018). The Greylag goose is one of the focal species in this endeavor, as the European population has gone from rarity to being widespread and numerous in just five decades (Fox and Madsen 2017). Due to its present high abundance, wide geographical range, and continued population growth, the European Greylag goose population has become subject of management and conservation conflicts in terms of negative impact on human livelihoods and putative negative effects on natural ecosystems (Bakker et al. 2018; Montrás-Janer et al. 2019; Heldbjerg et al. 2021). As a result, the flyway management plan for this species will likely include measures to control population size and growth at the flyway scale (Powolny et al. 2018).

In the ongoing AEWA-based effort to instate a flyway management plan for European Greylag geese, re-sighting data of neck-banded individuals have been used to suggest delineation of the population into three management units (MUs) based on migration patterns and connectivity (Bacon et al. 2019). Two different units, separating the migrating (Nordic breeders, MU1) and the sedentary (Central European breeders, MU2), were later adopted in the management plan (Powolny et al. 2018). However, such analyses of movements of neck-banded individuals commonly include biases caused by uneven spatiotemporal distribution of ringing and observer effort (Korner-Nievergelt et al. 2010). Consequently, the recent emergence of GPS tracking devices suited for geese is a source of movement data of entirely different resolution and reduced bias (Bacon et al. 2019). To remotely GPS track individual birds continuously makes it possible to efficiently study variation in movement behaviour among individuals in a population, as well as between populations breeding in different areas of a management unit or flyway. Such differences, should they exist, are crucial for management to consider. For example, location data derived from GPS tracking devices can help managers to better understand the origin and likely imminent movements of geese occurring in a certain area at a given time. GPS location data may also allow for comparison with older data based on leg band recoveries and neck collar readings. Several previous studies, based on these older techniques, indicate that Greylag geese in Europe have changed their migratory behaviour significantly in recent decades, including bird breeding in southernmost Sweden (Andersson et al. 2001; Ramo et al. 2015; Podhrázský et al. 2017; Nilsson and Kampe-Persson 2018). If so, flyway delineation may change altogether, or for specific management units.

The Greylag goose breeds over most of Sweden, a country covering a long latitudinal gradient and a wide range of climatic conditions. Swedish Greylag geese are thus well suited for a study of present migratory patterns, including possible variation among individuals within a management unit. Further reasons for this claim are the availability of historical ringing data for comparison (Andersson et al. 2001; Fransson and Pettersson 2001; Nilsson and Kampe-Persson 2018), and a well-documented long-term increase in Greylag goose numbers in Sweden in all seasons, e.g. ~170,000–250,000 individuals staging in September in recent years (Haas and Nilsson 2019; Liljebäck et al. 2021).

In this paper, we describe movements over the entire annual cycle for 76 Greylag geese fitted with GPS tracking devices at five catch sites within the species’ main breeding range in Sweden. The explicit aims were to answer four questions of imminent relevance for management of this species in Europe:

1) What is the present geographical extent of the flyway of Swedish Greylag geese?
2) Where are Swedish Greylag geese at different times of annual cycle?
3) Which countries are used by Swedish Greylag geese during the annual cycle?
4) Do the patterns (1–3 above) differ among areas of origin in Sweden?

Methods

Catching procedures

In June 2017–2019, breeding and moulting Greylag geese were caught when foraging in fields, pastures, or lawns near water. They were herded slowly by foot and canoe via raised nets into corrals. Caught geese were immediately put in gunny sacks to let them calm down until further handling. In addition to classical tarsal rings, geese were provided neckbands fitted with solar powered GPS tracking devices: Ornitela (OT-N35 and OT-N44) and Made-by-Theo (Theo Gerrits). Geese were aged (juvenile or adult) based on plumage and sexed by cloacal inspection. All catching and handling were done according to permits from the Animal Ethics Committee of Central Sweden (# 5.8.18–03584/2017). In total, 83 individuals from five different catch sites in Sweden (Fig. 1; Table 1) were tracked for at least one annual cycle.

Catch sites

Five catch sites were selected to represent a latitudinal range from central to southern Sweden, embracing the main part of the national breeding range of Greylag geese (55–61° N; Fig. 1).

Table 1 Number of studied individuals (females within brackets) and subsequently recorded annual cycles for Greylag geese provided with a GPS tracking device at five catch sites in Sweden in 2017–2019

| Site               | Individuals | Annual cycles |
|--------------------|-------------|---------------|
| Svedala            | 10 (5)      | 17            |
| Kristianstad       | 12 (7)      | 20            |
| Nyköping           | 14 (14)     | 22            |
| Örebro             | 30 (12)     | 50            |
| Hudiksvall         | 10 (10)     | 17            |

Hudiksvall (N 61° 43′, E 17° 6′), by the coast of the Bothnian Sea in the southern boreal biotic zone (see Hallanaro and Pylvänäinen 2002 for classification of biotic zones in the Nordic countries). The site is a wetland (24.5 hectares (ha)) in an urban park area, surrounded by intensively managed grasslands including mowed lawns. The wetland holds less than five breeding pairs of Greylag geese annually, but numerous moulting flocks.

Örebro (N 59° 10′, E 15° 23′), just south of the border between the southern boreal and the boreo-nemoral biotic zones. The catch site sits within a large nature reserve (Kvismaren, 732 ha) holding vast areas of wetlands, swamp forests, and reed-beds. Management of the reserve includes cattle grazing and mowing of fields to promote meadow birds. As large parts of the reserve are inaccessible for humans, the exact numbers of breeding and moulting Greylag geese are not known but minimum numbers of breeding pairs were estimated to 240 by the Kvismare bird observatory in 2017 and 2018.

Nyköping (N 58° 58′, E 17° 9′), in the boreo-nemoral biotic zone. The site (Öster Malma) is a wetland (8.4 ha) constructed in 1992 to promote breeding waterfowl. It is situated in a fragmented landscape with forests interspersed by patches of agricultural fields and many lakes. Deciduous forests and extensively managed grasslands surround the wetland, which annually holds 10–20 breeding pairs, and in most years about 80–110 moulting Greylag geese. Öster Malma was a focal site for a large-scale re-introduction program for Greylag geese in Sweden in 1970–1975 (Andersson et al. 2001).

Kristianstad (N 56° 5′, E 14° 21′), in the nemoral biotic zone. The catch site (Bäckaskog) is situated in two pastures on a narrow land strip between two large lakes (6200 and 1520 ha). The surrounding land comprises meadows and arable fields mixed with deciduous forests. Up to 20 pairs of breeding Greylag geese and their offspring utilize the area in June, accompanied by varying numbers of moulting non-breeding birds.

Svedala (N 55° 33′, E 13° 14′), in the nemoral biotic zone. The catch site consists of two artificial wetlands (2.8 and 0.8 ha respectively) situated within a golf course.
surrounded by beech forest and arable fields. Up to 20 families of Greylag geese utilize the area during the breeding season.

**Data treatment**

Movement data from 83 individuals carrying GPS tracking devices were manually inspected for possible inter-dependence bias, i.e., if any bird was consistently moving together with other GPS tagged individuals. When this was the case, only one individual from pairs or family groups was retained in the study. Accordingly, 7 individuals were removed from the data set, leaving 76 individual geese in which the number of complete annual cycles ranged from one to three (Table 1; Supplemental Information 1). We only included an annual cycle if data could be retrieved from >90% of the days within it (i.e., GPS locations in at least 329 out of 365 days). July 1st was set as the start of the annual cycle, as this is a time when all birds were positively at the breeding or moulting site (i.e., being flightless for 3–4 weeks). As geese migrate in pairs and family groups (Black et al. 2014; Kölzsch et al. 2020), we did not separate between the sexes when compiling the data.

The GPS positioning rate was first set to a default of one location per 15 min, but later came to vary over the annual cycle, mainly due to solar panel recharging problems in mid-winter (less frequent positioning) and some periods of individual behavioural studies (more frequent positioning). We used all data available independent of positioning rate for all complete annual cycles to create migration paths for each individual (Fig. 2). Consequently, up to three complete annual cycles were obtained for some individuals.

When calculating mean coordinates and the proportion of locations in different countries within the flyway, we standardized data to only include one location per 24 h, and we used the location closest in time to 12:00 AM UTC (Coordinated Universal Time; i.e. noon) to avoid possible bias due to different positioning rates along the migration path. Before calculating mean coordinates by catch site, we calculated a mean value for individuals with more than one annual cycle, and then the grand mean for all individuals. Maps were created in ArcMap (version 10.7).

**Results**

The studied Swedish Greylag geese show a cohesive south-westerly autumn migration corridor and a northeasterly return direction in spring, with very few individuals deviating from this pattern (Fig. 2). The combined paths and thus the flyway outline suggested by the locations in the entire sample ranges from the coastal areas of the Bothnian Sea in the northeast, to southern Spain in the southwest (Fig. 2). However, only one individual migrated to Spain and two individuals to France. One of the latter paths passed the southeast corner of Great Britain, deviating slightly to the west from the general migration corridor. Another individual showed a somewhat deviating path by passing the southeast corner of Norway during one spring migration. To the east, only one individual crossed the Baltic Sea, to reach the archipelagoes of SW Finland in summer.

For the standardized data set (one location per 24 h), we obtained locations from eight countries in total; the majority were within Sweden (on average 74% for all individuals), followed by lower proportions in the Netherlands (9%), Denmark (8%), and Germany (8%) (Fig. 3). The migration paths passing Norway and Great Britain were not covered by the standardized data (i.e. one location per 24 h) as the time spent within these countries was too short and did not coincide with the noon locations.

Geese tagged at the southernmost site Svedala showed very limited movements overall, some birds appearing to be more or less resident and only making local movements (82% of the locations within Sweden; Figs. 2 and 3). The individuals from Svedala that left Sweden migrated no farther than across Öresund to nearby Denmark. Birds from the second site in southernmost Sweden (Kristianstad) were also mainly resident and non-migratory (96% of the locations within Sweden), although two out of twelve individuals migrated to the Netherlands and three other individuals made a summer flight to moulting sites ~ 250 km to the north (Figs. 2 and 3). Note though that despite a large share of resident birds at both these southern sites, the general axis of movement was SW-NE, conforming to the general flyway outline. In contrast, geese tagged at the three northerly sites left Sweden for the winter (62–66% of the locations per individual within Sweden) (Figs. 2 and 3), except for one goose that remained in the southeast of the country. Only a few individuals from the two northernmost catch sites reached as far as France and Spain (Fig. 2). In addition to the variation found among catch sites, it is evident that individuals may change migration pattern between years, e.g. one goose migrated to France in one year but spent the winter in the Netherlands the other two years.

Monthly mean coordinates show that geese were in or near their respective catch site from March to September (Fig. 4). In October, geese from the three northerly catch sites started to migrate (Fig. 2), a month when also birds from the largely resident two southernmost catch sites displayed a minor SW shift of the mean coordinates (Fig. 4). Geese from four of the catch sites have their southernmost mean coordinates in November–December (Fig. 4), whereas geese tagged at Kristianstad reached the farthest SW later, in December–January (Fig. 4). Mean coordinates for the three northerly populations started shifting NE already in January, indicating a start of the return migration.
Fig. 2  Migration paths by GPS tracks for 76 Greylag geese caught at five sites in Sweden
Discussion

A more detailed picture of the migration patterns of Greylag geese breeding in Sweden has been provided by the results from this study, with similarities as well as dissimilarities compared with previous studies. Although the general flyway outline has not changed, thus corresponding well to patterns described earlier (Fransson and Pettersson 2001), a much smaller fraction nowadays continues southwest to historical wintering areas in France and southern Spain. The main wintering area has shifted far to the northeast, to the Netherlands and Denmark. A sizeable proportion of the geese now winter in Sweden, where wintering Greylag geese were unknown 30–40 years ago (Andersson et al. 2001).

Moreover, our study demonstrates geographical differences, i.e., that Greylag geese originating from different regions show not only different migration strategies but also a different degree of change.

Previous studies have described population growth and changes in distribution and migration patterns of Greylag geese in Europe (Fox and Madsen 2017; Nilsson and Kampe-Persson 2018; Boos et al. 2019). The present study, embracing much of the Swedish breeding range, implies that the change in migration patterns has continued and that it has been more pronounced in geese in the southernmost part of the country (cf. Andersson et al. 2001; Ramo et al. 2015; Nilsson and Kampe-Persson 2018). When comparing mean coordinates in winter (Dec–Jan) between earlier studies (based on tarsus rings and neck collars) and our recent GPS data, we did not find any profound difference in geese from our northernmost catch area, Hudiksvall, while there was a difference for geese tagged at Nyköping (Fig. 5; Andersson et al. 2001; Fransson and Pettersson 2001). The difference between “then” and “now” is even more pronounced for geese from our southernmost catch site (Svedala; Fig. 5). However, as earlier studies were based on tarsus ringed and neck collared birds, thus not on GPS locations, we cannot say for sure whether the differences are due to a true geographical shift, or to the methods used. Nevertheless, given that a general decrease in migration distance to more northerly wintering sites has been demonstrated also in earlier studies based solely on resightings of neck collars (Nilsson and Kampe-Persson 2018), and the profound differences in mean winter coordinates shown in Fig. 5, we are confident that our results show a continued northward shift, at least for Greylag geese originating from more southerly parts of Sweden. Future studies need to address to what extent spatiotemporal patterns obtained from neck collar readings are congruent with those from GPS data in the same species. The present study confirms the previously documented general SW-NE migration corridor, but based on GPS locations, we have found comparatively fewer individuals obviously deviating from the main corridor (cf. Andersson et al. 2001; Fransson and Pettersson 2001). We suggest that the higher variation in spatial distribution found in earlier studies can be explained, at least in part, by much larger samples than our 76 individuals. On the other hand, GPS tracking devices provide continuous data on a daily basis for all movements, and as a consequence, deviating patterns should be easier to detect in such data than in those derived from resightings.
Fig. 4 Monthly mean coordinates based on GPS tracks from Greylag geese originating from five sites in Sweden. See Fig. 1 for catch site locations.
of neck-banded birds (e.g. the two individuals in our study which swiftly passed Norway and Great Britain during migration would probably not have been detected by the neckband resighting technique).

Earlier studies show that Greylag geese from southernmost Sweden in general reached more southerly wintering sites compared to those ringed further north in the country (Andersson et al. 2001; Fransson and Pettersson 2001). In other words, it seems migration distance was previously rather equal in geese from different parts of the Swedish breeding range (Fig. 5), producing a classic ‘chain migration’ pattern (Berthold 2001). However, our results indicate a different pattern, as birds from southern sites in Sweden generally have abandoned former wintering sites and turned from being long-distance migrants to become residents or having a very short winter migration distance. This new pattern, in which migration distance increases with breeding latitude, instead recalls a ‘leapfrog migration’ pattern (Salomonsen 1955; Berthold 2001). Interestingly, Greylag geese breeding in the Netherlands have shifted from being migratory to being resident during the early 1990s, a change in accord with our results for birds in southernmost Sweden. This means that they, too, have been overflown by long-distance migrating Nordic Greylag geese to become part of an emerging ‘leapfrog migration’ pattern (Voslamber et al. 2010; Bacon et al. 2019). Our present results thus imply that Swedish Greylag geese now have migration strategies collectively creating a ‘leap-frog migration’ pattern rather than a chain migration pattern (Salomonsen 1955; Berthold 2001), but a more rigorous analysis is needed to draw such a conclusion. Specifically, the possible differences in distance and timing of migration among individuals from different breeding areas must be analyzed in a more formal and objective way. Regardless, with a continuous and expected climate change trajectory (Sorte et al. 2019) and an intensification of agriculture in Europe (Simoncini et al. 2019), we find it likely that our study gives a mere glimpse of an ongoing change in migration patterns in this population.

When the climate is changing, capacity to adapt to new conditions is key. Earlier studies have shown that some bird species have a limited capacity to adapt to new conditions, whereas others show swift changes such as range shifts in response to climate change (Böhning-Gaese and Lemoine 2004; Sekercioglu et al. 2008). Greylag geese seem to have a high degree of plasticity, be it phenotypic adaptation or evolutionary adaptation, or both. Obviously, in the era of the Anthropocene, they respond to widespread and significant human impact, for example, milder winters and increased availability of high-quality food due to changes in agricultural practices. This obviously includes the altered migration patterns of Greylag geese breeding in Sweden. When comparing our results to earlier findings, including data from 1984 to 1995, Swedish Greylag geese have radically changed their migration pattern on the population level in a mere 30–40 year period. This rapid change suggests altered behaviour within generations at the individual, family group, or flock level, rather than classical Darwinian adaptation across generations. Since we show that individuals may change migration strategies between years, the view of a phenotypic adaptation of the migration patterns of Greylag geese is to some extent supported by our study. Similar patterns of individual plasticity have been found in other studies of Nordic geese (Nilsson and Kampe-Persson 2018; Boos et al. 2019). Nilsson and Kampe-Persson (2018) also found that a higher proportion of Greylag geese ringed in southern Sweden changed wintering sites between years, compared to birds from more northern sites.
We acknowledge that a minor portion of the Swedish population of Greylag geese breeds north of our northernmost catch site Hudiksvall (61° 43’), but our study embraces the geographic area hosting the vast majority of the Swedish breeding population (Ottosson et al. 2012; Nilsson and Haas 2015). We nevertheless advocate complementary GPS tagging of Greylag geese breeding farther north, to challenge or confirm the patterns in the present study. For example, it has been shown in other waterbirds, breeding in the far north of Sweden, that at least a part of the population crosses the Gulf of Bothnia for a more easterly migration route southwards (e.g., Common crane: Skyllberg et al. 2014). Judging from the individual GPS data, the present study found little support for migration paths linking Swedish birds to Norway and Finland. However, it is known that bird breeding in northeastern Norway use stop-over sites in Sweden (Powolny et al. 2018; Boos et al. 2019). In addition, recent studies based on GPS tracking and neck collar readings show that Greylag geese breeding in Northeast Norway and Finland visit stop-over sites in certain regions of Sweden in September (Follestad and Piironen pers comm.). Moreover, Greylag geese originating from Denmark and eastern continental Europe (e.g, Poland) have been shown to perform a northbound moult migration to Sweden in summer (Nilsson and Hermansson 2019).

Management implications

Our study implies that Greylag geese breeding in Sweden have progressively abandoned former wintering sites in the southwest (Spain, France) and that individual birds may change migration strategy during their lifetime. The present study also shows that two radically different types of migration strategy occur within the Swedish population, depending on geographic origin. Such long-term change and plasticity in migration, and variation among regions create general challenges for management and conservation and thus a need for continuously updated knowledge, e.g. to coordinate monitoring, harvest quotas and networks of protected areas. Today, Greylag geese originating from the three northerly catch sites in our study area constitute a common management concern for all countries within the flyway, i.e., from Sweden to Spain, which then also in general terms supports the current delineation of the two management units (Powolny et al. 2018; Heldbjerg et al. 2021). Even so, and although the flyway embraces many countries, Greylag geese originating in these three northern catch sites spend much of their annual cycle within Sweden, and almost all of it in Sweden, Denmark, the Netherlands, and Germany. Greylag geese tagged at the two southernmost sites spent 97 and 100% of their time in Sweden and Denmark only. Consequently, the appropriate delineation of management units may vary from a regional to an international scale depending on the origin of geese and the migratory habits in specific areas. In other words, management strategies used for the Greylag geese treated as residents (i.e. MU2—Central European breeders) may actually also be applied to part of the Swedish population. The spatiotemporal patterns demonstrated in this study also reveal that Greylag geese seem to stay close to their respective catch site from April to September. This period would therefore be best suited for monitoring the population size of Greylag geese breeding in Sweden, if the aim is to estimate the national breeding population size, provided that a possible influx from Norway and/or Finland is either negligible or possible to control for. Since changes in migration strategy are likely to go on, continued mapping of movements and migration strategies of European Greylag geese is much needed for proper interpretation of collected data and for designing appropriate management and monitoring schemes.

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Declarations

Conflict of interest The authors declare no competing interests.

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