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GPS-tracking reveals winter short-stopping and large differences in individual migratory distance among Greylag Geese (*Anser anser*) breeding in Denmark

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The exponential increase in the 'NW/SW European Greylag Goose population' (NGGP) has created demands for more precise estimates of the national breeding populations and improved understanding of their movements to support its effective management. Increased NGGP abundance has been associated with a northeast-ward shift in wintering centre of gravity, suggesting major changes in migratory and wintering patterns. Greater numbers of wintering Greylag Geese wintering numbers in Denmark could originate from increases in the Danish breeding population showing a more sedentary habit and/or from a higher incidence of "winter short-stopping" by birds from elsewhere. Data from the first 16 Greylag Goose deployed with GPS/GSM tracking collars in 2021 and 2022 were used to test the hypothesis that birds in newly colonised Danish breeding areas were more sedentary than the long-distance migratory geese in traditional nesting areas. Contemporary migration patterns showed that some Danish breeders (including examples from newly colonized breeding areas) still migrate to their traditional wintering quarters in southern Spain, but most tagged Greylag Geese stayed in Denmark throughout the annual cycle. These data also provided the first evidence of the occurrence of winter short-stopping among individual Danish Greylag Geese, which after one winter in Spain subsequently wintered in Denmark and the Netherlands, indicating that some individuals can shift between new wintering areas every autumn. Overall, these results show that while most Danish summering Greylag Geese are now largely resident within Denmark, some move to Germany and the Netherlands and a few still undertake the traditional long migration to southern Spain, making assignment of breeding provenance to migrating birds challenging.

1. Introduction

As a result of conservation measures (especially reserve designations and restrictions on hunting), intensification of agriculture, and climate change, the size of many European goose populations has increased significantly during the latter half of the 20th century (Jensen *et al.* 2008, Wisz *et al.* 2008, Fox & Abraham 2017, Fox & Madsen 2017). Most species breed in the Arctic and Boreal biomes and winter in the temperate climate zone of northern Europe, but the Greylag Goose (*Anser anser*) mostly breeds and winters in the temperate zone. The 'NW/SW European Greylag Goose population' (hereafter NGGP) defines, for management purposes, the flyway population which includes migratory geese that breed from northernmost parts of Norway and migrate to winter in southern Spain, as well as partial migrant and resident geese nesting in northwestern lowland Europe (Powolny *et al.* 2018).

The exponential increase in this flyway population (a factor of eight growth in numbers since the 1980s) has led to a demand for precise estimates of the national breeding populations and a better understanding of their movements to support management of the NGGP population overall more effectively, due to the complications arising from the need to relate individuals shot during the hunting season to stock of a given breeding provenance (Johnson *et al.* 2022). Under the auspices of the African-Eurasian Waterbird Agreement (AEWA), the European Goose Management Platform (EGMP) has produced a population-specific Adaptive Flyway Management Programme that provides guidance to resolve and reduce human-goose conflicts and manage exploitation in a sustainable manner (Nagy *et al.* 2021). Such an evidence-based approach to management, however, requires a basic knowledge of the migratory behaviour of different parts of the overall flyway population to fully understand their distribution and overlap in time and space throughout the annual cycle (Bacon *et al.* 2019).

Månsson *et al.* (2022) showed that the migratory distances of Greylag Geese decreased with latitudinal origin in Sweden and that geese tagged in southernmost Sweden spent almost the entire annual cycle in Sweden and Denmark. However, with the major increases in abundance in this population, there has also been a gradual northeast-ward shift in the wintering centre of gravity (Ramo *et al.* 2015) suggesting major changes in patterns of migratory behaviour and winter areas within this population of Greylag Geese.

Numbers of Greylag Geese breeding in Denmark increased seven-fold during 1980–2023 (Vikstrøm *et al.* 2023) and the Danish breeding bird atlases have shown that the breeding range has expanded considerably. From being present in 18% of quadrats across the country in the early 1970s (almost exclusively on the islands in east Denmark; Dybbro 1976), during 2014–2017 it was found to breed in 59% of national quadrats, becoming more widespread, including colonising throughout Jutland in west Denmark, where formerly largely absent (Vikstrøm & Moshøj 2020). Numbers of Greylag Geese counted in Denmark during midwinter counts have also dramatically increased from essentially none prior to 1998 to 80,000–120,000 since 2012 (Nielsen *et al.* 2023). These wintering birds could therefore originate from increases in the Danish breeding population showing a more sedentary habit and/or from increased "winter short-stopping" (*sensu* Elmberg *et al.* 2014) among those breeding to the north and east of Denmark. Either way, it was evident that our previous knowledge of Danish Greylag Goose migration needed updating.

Paludan (1965) described the Danish summering population of Greylag Geese at that time as a winter migrant to Marismas de Guadalquivir (Coto Doñana, 36°58'N, 06°24'W) in southern Spain, an area which was "by far the most important winter quarter for West and Central European Greylag Geese". Bønløkke *et al.* (2006) also described the main wintering quarters for Danish Greylag Geese as southern Spain, but also mentioned that the centre of gravity of the wintering quarters had shifted northwards since the 1950s, a pattern also seen among Greylag Geese from south Sweden (Nilsson & Kampe-Persson 2018). This was recently confirmed by Clausen *et al.* (2023), who showed that the proportion of Danish-ringed Greylag Geese recovered in Spain in winter decreased from *ca.* 75% in the 1950s to almost

none in the 2010s, while those recovered in Denmark increased from almost none to *ca.* 50% over the same period, most marked since the early 1990s (Kampp & Preuss 2005).

To make informed decisions about where and when to regulate harvest of Greylag Geese of this flyway population to safeguard the current Danish breeding population, we need to better understand contemporary timing of migration and ultimate wintering provenance. To support this process, we here present results of the first use of GPS tags on the Danish breeding population of Greylag Geese to describe the differences in migration and wintering patterns of Greylag Geese from Denmark. We hypothesise that (i) some of the Danish breeding Greylag Geese are still long-distance migrants and others are mainly sedentary, that (ii) the Greylag Geese breeding in east Denmark are more likely to migrate to Spain, as these birds are likely descendants from the historical Danish population that traditionally wintered there and that (iii) the Jutland birds that breed in newly colonised areas in Denmark (where numbers have increased substantially) are more likely to show new migratory patterns, including shorter migration and sedentary behaviour.

2. Material and methods

2.1. Sites and captures

A total of 82 Greylag Geese were caught during the breeding seasons 2021 and 2022 at five different locations within two regions of Denmark (Fig. S1); Djursland in eastern Jutland (colonised by breeding Greylag Geese in the early 1990s) and on Zealand (where geese have bred continuously at least since the 1970s; Dybbro 1976). All captured Greylag Geese were rounded up during June when breeders are flightless due to the moulting of flight feathers and before their associated goslings have fledged.

Djursland, 2021: In 2021, 22 geese were caught at Kastrup Mose (56°23'N, 10°22'E) on 7 June and nine additional geese were caught at Vasen, Clausholm (56°23'N, 10°09'E) on 8 June.

Zealand, 2022: In 2022, 35 geese were caught at Lillemaden (55°12'N, 11°10'E) and 12 geese at Krebsgården (55°13'N, 11°11'E) on 31 May on the Island of Agersø, comprising a total of 47 geese. Finally, four birds were caught at Skjoldnæsholm Engsø (55°31'N, 11°51'E) on 1 June.

2.2. Rings and tags

In 2021, we deployed Ornitela OT-N44-3G 45 g GPS/GSM tracking collars on six adult females, one adult male and one juvenile female. All except one adult female, which was predated by a mammal a few days after ringing, contributed to the data sets described below. In 2022, we deployed Druid Flex-2G 44 mm 29 g GPS/GSM tracking collars on 11 adult females, of which nine contributed to the data sets described below. We omitted two that stopped sending data before migratory movements started (Tag #11692, up to 26 June 2022 and tag #11603, up to 17 August 2022; Table S1). All birds were ringed with a standard metal ring (from Zoological Museum of Copenhagen) and a blue plastic leg colour ring and adult birds not fitted with GPS tags were fitted with blue plastic neck collars. Only information derived from the GPS tags is reported in this study.

We instrumented adult females specifically to try and relate factors throughout the annual cycle to breeding propensity, as only adult females showed incubation activity that enabled us to infer, for instance, if geese attempted to nest and failed, abandoned incubation or completed incubation through to potential hatching. To avoid pseudoreplication, we aimed at only deploying tags to geese that were unlikely to be related to each other (*e.g.* eliminating pairs or parent/offspring), another reason for only tagging adult females in large catches. The only tagged male in this sample turned out to be mated to a tagged female and was therefore excluded when calculating mean monthly distances. Since Greylag Geese pair for life, marking males would be largely uninformative relative to the central questions of this study, while we accept that goslings of either sex will behave very differently to adults in ways beyond the scope of the present study.

2.3. Data

Due to the number of geese, the number of functioning GPS transmitters and the variation in power levels of the transmitters (as a result of day length across the year), the number of data points varied greatly across months. At full power, these devices stored a position every 10 minutes, but depending on battery level the frequency dropped gradually down to one position every hour. To ensure a reasonable quality of the GPS data used, only data points with a hdop (horizontal dilution of precision) value < 3 were used in the analysis. The mean (and range) number of positions per included goose were 53,880 (16,138–90,541) for the Djursland geese and 51,123 (36,352–63,007) for the Zealand geese. The Ornitela devices under trials gave an accuracy of > 85% within 20 m of the true position (unpublished data, similar to Clements *et al.* 2021 for smaller units). The Druid devices collected geographical coordinates with a horizontal accuracy of 9.6 ± 5.6 m SE in field tests (based on Li *et al.* 2020a).

We included all data on positions up to 1 June 2023, *i.e.*, about two years for the Djursland geese and one year for the Zealand geese. At that time nine (two from Djursland/2021 and seven from Zealand/2022) of the loggers were still functioning (Table S1). Since the number of full functioning loggers was markedly lower in the second year, we focus on the positions in the first year after tagging. In addition to this, we include data in detail for geese with functioning loggers where we have data to describe their migratory movements in two (n = 3) and three winters (n = 2, covering 2021/2022–2023/2024).

Analysis, mapping and graphical representations were made in Excel and QGIS version 3.34.9.

2.4. Migratory patterns

We classified the migratory patterns observed among individuals into two categories, 'sedentary' including all birds staying within Denmark, defined as being within 150 km from the ringing site, throughout the annual cycle and 'migratory' including all birds leaving the country at any given time of the year. One bird was retrospectively categorised as a 'moulting visitor' to the ringing site, due to its migratory behaviour after ringing.

We describe the movements of each individual Greylag Goose by the distances (km) to the ringing site, presented as mean monthly distances. To describe the nature of active migration, we measured the distance from the last stopover site within Denmark (after periods of foraging at various sites in Denmark), from the initiation of the autumn migration (*i.e.* the point at which each individual initiated a series of movements in a unified direction more than 200 km from its previous staging site) to the southernmost wintering point (Coto Doñana), likewise we only include the active migration during spring migration from Coto Doñana (defined as for autumn departure from Denmark) until the first stopover site in Denmark. The total length of the migration and the migration period hence covers the distance/time from the last stopover site in Denmark before migration to the first stopover site in Denmark after migration. The speed of the active migration is the distance moved divided by the hours during active flight.

3. Results

The results are presented by breeding region and by migratory strategy within relevant seasons, summarised in Table 1.

3.1. Migratory patterns

All four geese tagged at Kastrup Mose, Djursland showed traditional migratory behaviour and left the country to winter in southern Spain, while the three geese tagged at the nearby site (*ca.* 15 km away), Vasen, Clausholm were sedentary.

Seven of the nine geese tagged in the region of Zealand were sedentary, while one migrated to the Netherlands and another turned out to be a visiting moulting bird at Agersø, which soon after regaining the ability to fly left for Flensburg, on the Danish/German border (*ca.* 130 km away), never subsequently returning to its ringing site.

Table 1. Summary of the included GPS-tagged Greylag Geese (*Anser anser*) in this study. Migrants are defined as birds leaving the country during migration (> 150 km from ringing site); sedentary as birds staying in Denmark throughout the annual cycle. One goose migrated away from the ringing site soon after ringing and stayed in the same area (northern Germany) hereafter and is hence considered to be a moulting visitor to the ringing site at the time of capture.

Ringing year	Ringing region	Ringing site	Number of geese	Migrants	Sedentary	Moulting visitor
2021	Djursland	Kastrup Mose	4	4	0	0
		Vasen, Clausholm	3	0	3	0
		Total	7	4	3	0
2022	Zealand	Agersø	8	1	6	1
		Skjoldnæsholm Engsø	1	0	1	0
		Total	9	1	7	1
Total			16	5	10	1

3.2. Monthly movements

3.2.1. Geese ringed on Djursland

The difference in migratory behaviour is illustrated by the mean monthly distance from the ringing site between the migrants and the sedentary group (Fig. S2). During July–October, the two groups behaved similarly with a mean distance from the ringing site of less than 25 km.

At the end of October increasing movements were seen in both groups, but with large differences between them. The migratory birds left for Spain, *ca.* 2,500 km in direct line from the ringing site and returned during February. The monthly mean distance from the ringing site also increased for the sedentary birds but monthly means were substantially lower reaching a maximum mean of 97 km in December.

After returning to the breeding site in February, all four migratory individuals stayed in the vicinity in March–April (mean monthly distance: 4 km). The same pattern was found for the only remaining sedentary goose (mean monthly distance: up to 15 km) (see Table S1).

At different times during the breeding season, which apparently was unsuccessful for all of the tagged birds concerned, the migrant group moved away from the ringing site, mostly further north, presumably on moult migration (see below).

3.2.2. Geese ringed at Zealand

Seven of the nine included geese marked on Zealand, stayed near the ringing site during the breeding season and moved only short distances away during August–December (mean monthly distances of 19–35 km, Figs. 1 and S3). From January they returned to the breeding sites where they stayed throughout the breeding season.

Two geese behaved differently from the general pattern of the others (Figs. 1 and S3). One (#11612) left the ringing site in mid-July and migrated to the Denmark–Germany border area *ca.* 130 km southwest of the ringing site. It stayed here the rest of the study period (Fig. 1). We tentatively interpret this to be a breeding bird from elsewhere that only appeared at the catching site to moult (see below).

The other goose (#11640) was the only Greylag Goose from Zealand that migrated. It stayed near the ringing site until mid-October when it migrated *ca.* 600 km southwest to spend the winter in southwestern Netherlands. It returned to the breeding site in mid-January and stayed here the rest of the spring.

3.3. Migrants to Spain

Four of the Djursland caught Greylag Geese migrated to Spain and stayed there during

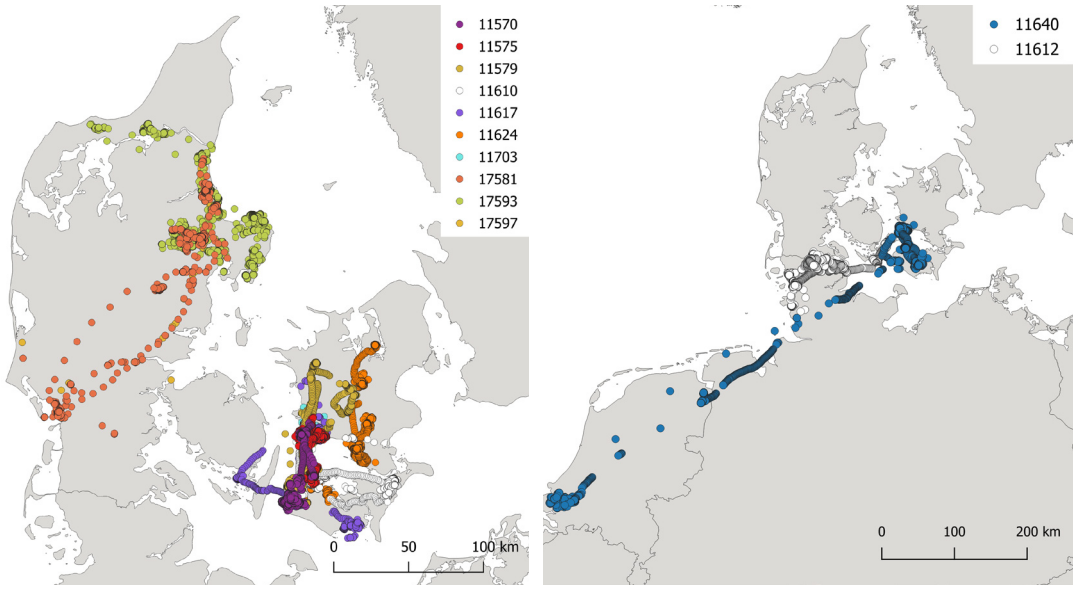

Fig. 1. Movements of Greylag Geese (*Anser anser*) during the first year after being tagged. Left: All sedentary individuals (staying in Denmark throughout the annual cycle): Three tagged in Vasen, Clausholm, Jutland, Denmark in 2021 and seven tagged at Zealand (Agersø and Skjoldnæsholm Engsø) in 2022. Right: One migratory and one moult migrant to the catching site (see text); both tagged at Agersø, Zealand in 2022. Notice different scales of the two maps.

winter. All four went to Coto Doñana at the Mediterranean coast, but one of these returned *ca.* 220 km northeast to the Colada Reservoir (Embalse de la Colada in Córdoba 38°31'N, 05°00'W) after 14 days and stayed there until it initiated its northward spring migration (Figs. 2 and 3). The speed of the migration and number of staging sites used during the migration are shown in Table S2.

The four geese showed individual variation in their onset of autumn migration (22 Oct–21 Nov) and the timing of return to the breeding area (5–28 Feb), resulting in a staging period at the winter sites of 72–95 days and a total length of the active migration period covering 77–119 days. They spent between three and 19 days to migrate the *ca.* 2,500 km to the southernmost destination (Coto Doñana) and between four and 17 days on the return spring migration (Table 1).

The migratory routes and the staging sites along the flyway varied between individual geese (Table S2; Figs. 1 and 2). Staging sites were recorded in Germany, Netherlands, France, and Spain. Some of the stops were short, often only a few hours, one day or overnight before continuing the flight. Others were longer, *e.g.* goose #17594 that stayed a week or more in Germany and again in the Netherlands on the southward migration and in the Netherlands on the northward migration (Table S2). All longer stops tended to be north of 51°N, *e.g.*, the longest stops during the two migration journeys were in the Netherlands, mostly in the southern part of the country (Table S2, Fig. 3).

3.4. Active migration

The use of GPS enabled a much better understanding of the details of the migration than the knowledge we have from standard ringing and colour ringed birds.

The tagged Greylag Geese did not migrate all the way to the wintering site in one direct flight but took breaks en route, and the migratory movements were consequently divided into several discrete stages. The autumn migration to Spain involved a mean of 3.75 (range 2–5) active migratory periods and the spring migration a mean of 6 (4–7) active migratory periods. Maximum distances in flight by each of the four geese ranged between 863 and 2,164 km during autumn and

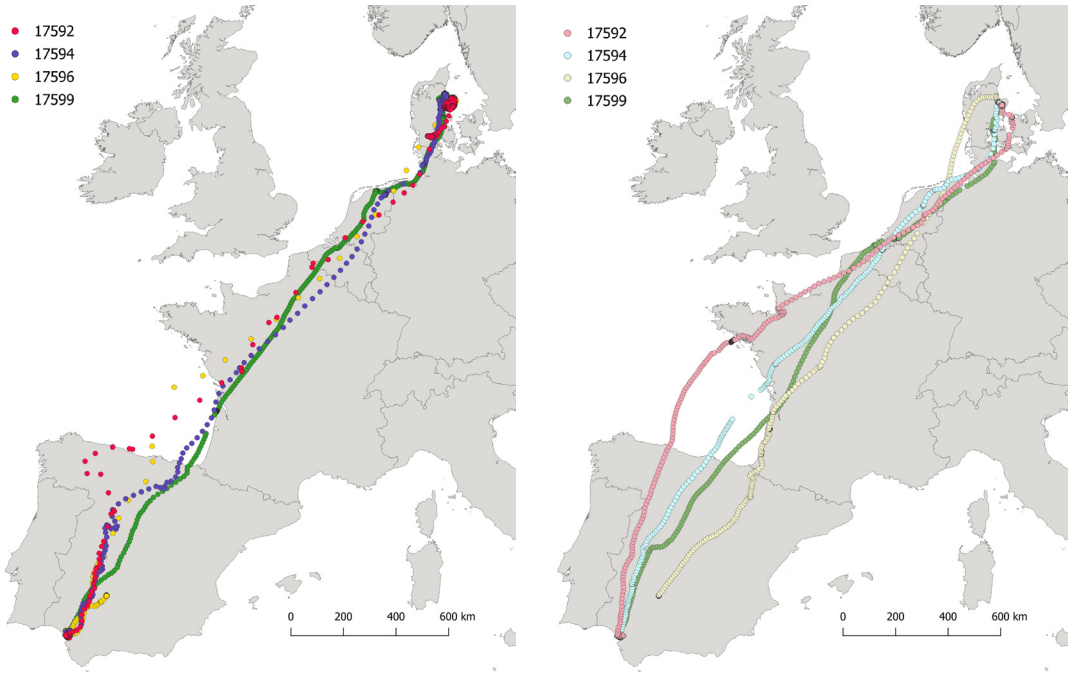

Fig. 2. Migratory routes of four Greylag Geese (*Anser anser*) tagged in Kastrup Mose, Denmark in 2021 and wintering in Coto Doñana, Spain during the winter 2021/2022. Left: Autumn migration. Right: Spring migration up to 31 March. The same colours (but paler in spring) in the two seasons represent the same individuals. Note that the frequency of positions generated by the devices differed between individuals and periods.

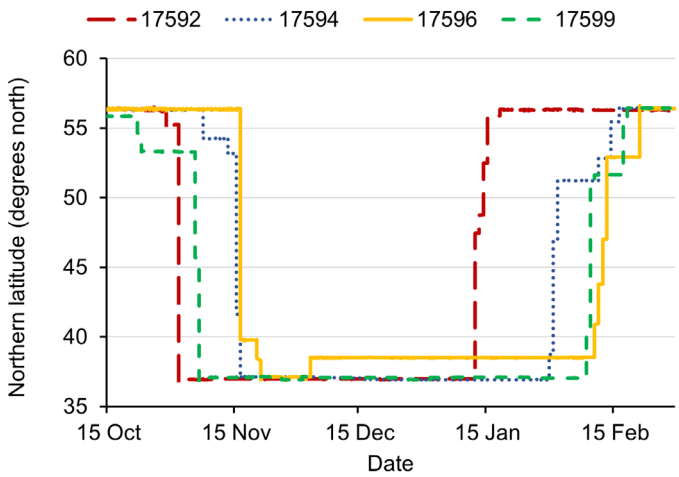

Fig. 3 Seasonal changes in latitude of four GPS-tagged migratory Greylag Geese (*Anser anser*) during 15 October 2021 to 1 March 2022 illustrating their migratory speed and staging sites from the tagging site in Kastrup Mose, Djursland to their wintering quarters in Coto Doñana, Spain.

715–1,623 during spring. The longest recorded distance was 2,164 km for a goose (#17596) that within 24 hours flew from Denmark to Badajoz in Spain during autumn. The mean speed during active flight was 69 km/h during autumn and 64 km/h during spring (Table 2).

3.5. Moult movements

After the four migrants to Spain returned to the breeding area, they all stayed locally until we registered subsequent movements away from this area, which appeared to constitute moult

Table 2. Speed of active migration among the four Greylag Geese (*Anser anser*) that migrated to Spain. Notice that the total length does not sum up to the total length of 2,500 km, since these only include true migratory movements and not the pre- and post-migratory local movements, *i.e.*, start and end of migration does not necessarily start at or lead to the ringing site.

Season	Activity	#17592	#17594	#17596	#17599	Mean
Autumn	Migration periods (No)	3	5	2	5	3.75
	Length (Km; Sum)	2,352	2,448	2,481	2,417	2,424
	Hours (Sum)	40	38	28	37	38
	Km/h (Mean)	58.3	65.3	88.6	64.5	69
	Max distance	1,152	863	2,164	1,014	
Spring	Migration periods (No)	4	7	7	6	6
	Length (Km; Sum)	2,356	2,470	2,462	2,332	2,405
	Hours (Sum)	32	44	40	37	153
	Km/h (Mean)	74.0	55.9	62.1	63.3	64
	Max distance	715	991	776	1,623	

migrations. These movements occurred at different times (between 17 April and 15 May) in different directions and to different destinations *ca.* 90–400 km from the ringing site (Figs. 4 and 5). We infer from the timing of these movements and the staging sites, which are all known or potential moulting areas (Fig. 5) that they were related to cases of unsuccessful breeding attempts followed by moult migration away from the vicinity of the breeding area.

The only remaining goose in the sedentary group showed no post-breeding movements away from the ringing site, *i.e.* it stayed within 15 km throughout the breeding season.

3.6. Subsequent winter movements

The migratory patterns shown by the remaining Djursland geese during the winters 2022/2023 (n = 3) and 2023/2024 (n = 2) revealed different patterns.

In the winter 2022/2023, the remaining two geese among the four Spanish-wintering migrants did not undertake a similar migration as the year before but mostly stayed in Denmark near the ringing site (mean monthly distance: 7–25 km) with December as the exception for one goose (#17594), which departed from the ringing site 21 November for a stopover *ca.* 100 km SW before migrating to stay at the German Wadden Sea (*ca.* 360 km away) during 7 December to 1 January. The remaining sedentary goose stayed within a monthly mean distance of maximum 60 km from the ringing site the year round until transmissions stopped in December 2022.

In winter 2023/2024, goose #17594 departed for a new wintering site, this time at Ijsselmeer in the Netherlands (52°39'N 5°23'E), where it stayed during 29 November to 30 December 2023. Goose #17592 repeated the pattern from the former winter by staying at Djursland throughout the winter.

4. Discussion

Although the number of tagged geese was low, these first ever results from deploying GPS tags on Danish breeding Greylag Geese confirmed the hypothesis (i) that some Danish breeders still migrate to their traditional wintering quarters in Southern Spain. Evidence from tagged goose movements also supported rejection of our hypotheses (ii) that Danish migrants to Spain originated from the established part of the population and (iii) that breeding geese in newly colonized parts of Denmark would be those that have evolved more

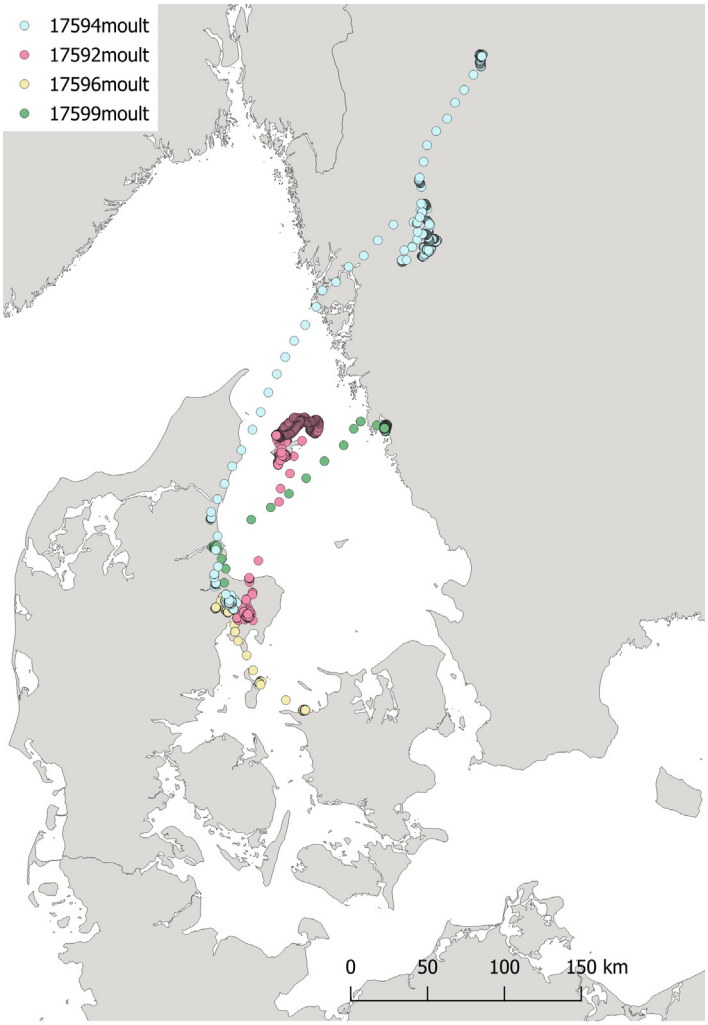

Fig. 4. Post-breeding movements of four Greylag Geese (*Anser anser*) away from the breeding area in Kastrup Mose to moulting sites in Sweden and Denmark during 1 April to 31 May 2022. Prior to these movements, all four geese returned to the site where they were tagged, after wintering in Coto Doñana, Spain during the winter 2021/2022.

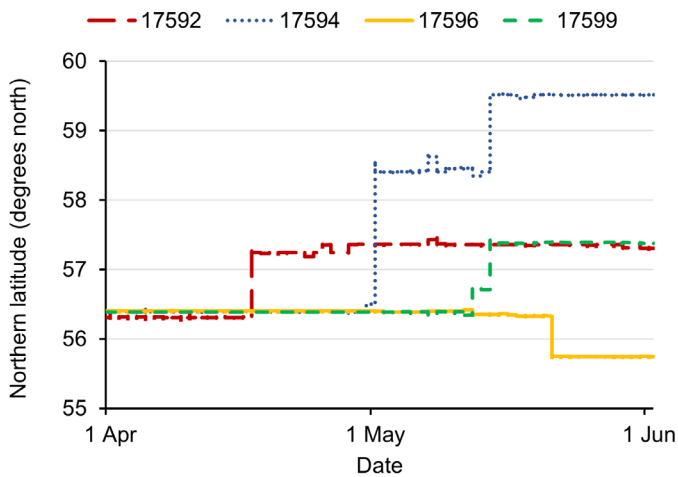

Fig. 5. Seasonal changes in latitude of four GPS-tagged Greylag Geese (*Anser anser*) between 1 April and 31 May 2022, the year after being tagged at Djursland (56°23'N, 10°22'E). Staging sites at 31 May: #17592: Nordre Rønner, Læsø, Denmark (57°21'N, 10°55'E); #17594: Karlstad, Vänern, Sweden (59°31'N, 13°25'E); #17596 Saltbækvig, Denmark (55°44'N, 11°09'E); #17599: Kungsbackafjorden, Sweden (57°23'N, 12°06'E).

sedentary wintering patterns. Contrary to expectations, tracking data revealed that the four geese that migrated to southern Spain all came from an area in Jutland, where breeding Greylag Geese were unknown 30 years ago, while none from the long-established Zealand population undertook any long movements (albeit but one went to the Netherlands). Further GPS tagging of geese from breeding populations throughout Denmark are needed to investigate the degree to which Greylag Geese still migrate to Spain in winter and if they are associated with particular areas or conditions.

These data also provided the first evidence of the occurrence of winter short-stopping of individual Danish Greylag Geese, since both Spanish wintering geese still with functioning tags spent the subsequent winter in or near Denmark, in marked contrast to the previous winter following marking. The winter when the four geese migrated to Coto Doñana turned out to be a very severe drought winter in Spain with exceptionally low water levels (Fox *et al.* 2023). One of the geese even decided not to stay at Coto Doñana in that winter, but instead moved to winter at a resort not previously known to support wintering Greylag Geese further north and inland, supporting evidence to suggest that the long journey had not been entirely worth it for that individual. We speculate that these individuals short-stopping in the following winter reduced their migration distance based on their experiences of the previous year to avoid experiencing another winter with poor feeding conditions.

We might also speculate that poor hydrological conditions in Coto Doñana that winter affected their body condition through carryover effects, which could explain why all four birds failed to breed (at different phases of the breeding cycle) in the following year and instead each undertook a moult migration away from Denmark (each to a different area) after returning to the breeding areas, although we cannot reject the possibility that conditions at the breeding site also influenced the probability of successful breeding. The early spring 2022 was exceptionally dry in Denmark, with the driest March ever recorded (since 1874; DMI 2022), which may have left small ponds in the farmland landscape hydrologically unsuitable as breeding sites for Greylag Geese in that season. Moreover, this might also have conspired to make hydrological conditions later in the season unsuitable for moulting Greylag Geese, hence it seems likely that their post-breeding migration to moulting areas at larger wetlands improved their probability of survival compared to staying on smaller ponds in the farmland. Finally, we cannot exclude the possibility that capture and tagging of the geese could also have influenced their breeding propensity. Studies on the related species, Pink-footed Goose (*Anser brachyrhynchus*) showed that capture and GPS-tagging lowered their probability to produce hatchlings in that year (Schreven *et al.* 2024). However, these birds were ringed just prior to the spring migration and other studies on the same species only revealed limited behavioural effects for a few weeks after handling and tagging (Clausen *et al.* 2020).

Generally milder winters and improved feeding conditions in Denmark (and north Europe) have improved wintering conditions for this population of Greylag Geese, enabling them to remain further north later in the non-breeding season than ever before. Climate change has both reduced the thermoregulatory costs of geese remaining so far north and reduced the threat of ice and snow cover, that denies them access to winter pasture and, increasingly, winter cereals (Clausen *et al.* in revision). The use of different land cover types, including grassland, crops and natural wetlands, by the tagged geese in Denmark reported in this study is the subject of current analysis (Clausen *et al*. in revision), but it seems likely there are increasing fitness benefits associated with remaining in Denmark in winter now. Simultaneously, conditions at their formerly most important wintering site in Coto Doñana have been deteriorating in recent decades (Camacho *et al.* 2022, De Felipe *et al.* 2023, Green *et al.* 2024), and a response in the form of changing migratory patterns (*i.e.* short-stopping) seems likely.

Although Greylag Geese are considered relatively winter site loyal and conservative in their use of habitat (*e.g.* Swann & Brockway 2007,Swann *et al.* 2015), subordinate geese (by virtue of their low dominance status) are often explorative and the first to find enhanced foraging opportunities, to which they subsequently attract other geese (Stahl *et al.* 2001). These mechanisms could explain the ability of the population as a whole to

adapt to novel foraging opportunities outside areas they have traditionally occupied. Annual changes in the migration/wintering patterns of individuals are known among Pink-footed Geese, with an average of 54% changing wintering strategy from one year to the next, although with large individual variation. Individually, these changes were not related to hunting pressure or winter temperature but could be partly explained by a tracking of food resources (Clausen *et al.* 2018).

The remaining two geese among the four that went to Spain proved to be short-stopping in Denmark and Germany in the following winter. Moreover, one of the birds wintered in Ijsselmeer in the Netherlands in the third winter and therefore showed a different migratory pattern in three subsequent winters: Coto Doñana, Spain, German Wadden Sea, and latterly Ijsselmeer in the Netherlands. The other bird stayed in Denmark in the two winters following its winter in Coto Doñana (Fig. S4). While we accept there are limits to what we can conclude from only two birds, these results indicate that some individuals have the ability to choose between wintering areas every autumn. We will need information from a larger number of tagged geese to understand if this decision is a random one or if the migratory pattern (long distance, short-stopping or no migration) is somehow related to the condition of the birds or to life-history traits and also if it differs between regions.

It was unexpected that all tagged geese from one site on Djursland wintered in Spain while all three from the neighbouring site stayed in Denmark for the winter. This raises the question as to whether geese decide every winter, whether they should stay to winter near their breeding areas or go and how far, rather than as individuals annually following the route to traditionally used winter quarters dictated by their parents, as is the case for many Arctic-nesting goose species. Again, confirmation awaits a larger study with more birds and longer lasting tags to verify this.

Most of the Zealand Greylag Geese were sedentary and stayed within a limited distance (*i.e.* a few hours flight from the catch site) throughout the annual cycle, despite the expectation that these long-established populations would include individuals most likely to travel to Spain. Even among the geese in this region we had two birds that showed aberrant patterns. The one that went to the Netherlands to winter proved that even in the eastern parts of the country, breeding Greylag Geese may still undertake migratory movements. Moreover, the same bird went to the same area again in the following winter. The other goose, which was caught during moult at Agersø but clearly had its breeding origin in the area near Flensburg in Germany, showed that during the post-breeding season, aggregations can be a mix of local breeding birds and birds from other sites (confirmed by the four birds from Kastrup Mose that moulted at four different sites in Denmark and Sweden). The origin of moulting Greylag Geese at our catch sites is not known, but resightings in Denmark of colour ringed Greylag Geese from other countries (Clausen *et al.* 2023) has proven there is a general pattern that local breeding birds mix with those from elsewhere. The origins of individuals among the large aggregation of moulting Greylag Geese on the island of Saltholm between Denmark and Sweden showed that the geese came from different directions but mainly within a few hundred kilometres (Fox *et al.* 1995). Nilsson *et al.* (2001) showed that the distance to moulting sites for breeding Greylag Geese from Scania, southernmost Sweden decreased from *ca.* 600 km (Netherlands) to *ca.* 50 km (Saltholm) with an increase in the population in the 1990s.

Classic migration theory hypothesizes that longer-distance migrants should minimize spring migration duration to enhance fitness by earliest occupation in best body condition of the best quality territories (Kokko 1999) and earliest first laying (Moore *et al*. 2005). Earlier nesting is associated with greater clutch size (Rowe *et al*. 1994) and better-quality offspring with higher survival rates during their first migration (Perrins 1970, McNamara *et al*. 1998). Most avian migration studies show that spring migration is faster than autumn migration (Nilsson *et al*. 2013), but this is not always the case among geese. For many Arctic breeding geese, spring migration takes significantly longer than that in autumn, for instance among Far East Greater White-fronted Geese (*Anser albifrons*, Deng *et al.* 2019) and Tundra Bean Geese (*Anser serrirostris*, Meng *et al.* 2022). In contrast, Swan Geese (*Anser cygnoides*), breeding in Mongolian-Manchurian steppe wetlands and wintering in China, undertake spring migration

faster than autumn migration (Batbayar *et al*. 2013) as do Far East Asian Greylag Geese (Li *et al.* 2020b), which also breed in the steppe region. Our results from Danish nesting long-distance migrants to Spain suggest that the duration of autumn and spring migration differed little (3 vs. 4 days, 19 vs. 17, 7 vs. 14 and 16 vs. 10 respectively for the four birds) but varied in length due mainly to stopover duration in northern Europe that varied between birds. These results seem to confirm that while internally consistent, the difference in duration of autumn versus spring migration in different goose populations vary in relation to conditions encountered along their migration routes (as witnessed in studies of other goose populations), necessitating a more nuanced development of hypotheses to explain their relative length (*e.g.* Deng *et al*. 2019).

Overall, these results showed a surprising degree of variation in wintering behaviours among Danish summering Greylag Geese, but clear evidence that the majority of birds now summering in traditionally occupied and newly colonized areas are largely resident within Denmark, with some moving further to Germany and the Netherlands and a few still undertaking the traditional long migration down to southern Spain. The evidence of short-stopping by individuals shows the flexibility in migration behaviour in this population and adds to the complexity of determining the breeding origin of birds shot in the autumn and winter, in relation to supporting the management process under the AEWA management plan for this population (Powolny *et al.* 2018). For this reason, we encourage more tracking of geese from even more geographically disparate areas in greater numbers to better understand the factors affecting decisions relating to wintering and moulting provenance by birds of differing summering origins.

GPS-seuranta paljastaa talviajan lyhytpysähtelyn ja suuret erot muuttomatkan pituudessa Tanskassa pesivien merihanhi-yksilöiden (*Anser anser*) välillä

Luoteis- ja lounais-Euroopan merihanhikannan (*NW/SW European Greylag Goose population, NGGP*) räjähdysmäinen kasvu on lisännyt tarvetta tarkentaa kansallisten pesimäkantojen arvioita ja parantaa ymmärrystä hanhien liikkeistä kannan tehokkaamman hallinnan tukemiseksi. Kannan runsastuminen on liitetty talvehtimisen painopisteen siirtymiseen kohti koillista, mikä viittaa muutoksiin muuttokäyttäytymisessä ja talvehtimisalueissa. Tanskassa talvehtivien merihanhien määrän kasvu voi johtua joko kasvaneesta, paikallaan pysyvästä pesimäpopulaatiosta ja/tai ilmiöstä, jossa yhä useammat muualla pesivät linnut pysähtelevät alueella talviaikana (*winter short-stopping*). Ensimmäisten 16 merihanhen GPS/GSM-lähettimillä varustettujen yksilöiden (vuosina 2021 ja 2022) avulla testasimme hypoteesia, jonka mukaan uusilla Tanskan pesimäalueilla pesivät hanhet ovat paikallaan pysyvämpiä kuin perinteisillä pesimäalueilla pesivät pitkän matkan muuttajat.

Nykyiset säännönmukaisuudet muuttokäyttäytymisessä osoittivat, että jotkut Tanskassa pesivät hanhet (mukaan lukien uusilla pesimäalueilla pesivät yksilöt) muuttavat edelleen perinteisille talvehtimisalueilleen Etelä-Espanjaan, mutta useimmat merihanhet pysyivät Tanskassa koko vuosikierron ajan. Havaitsimme myös ensimmäistä kertaa talviajan lyhytpysähtelyn esiintymistä yksittäisten merihanhien keskuudessa; eräät hanhet talvehtivat ensimmäisenä talvenaan Espanjassa, mutta siirtyivät sen jälkeen talvehtimaan Tanskaan ja Alankomaihin, mikä osoittaa, että yksilö voi vaihtaa talvehtimisaluettaan joka syksy. Kokonaisuudessaan tulokset osoittavat, että vaikka useimmat Tanskassa kesää viettävät merihanhet pysyvät pääosin Tanskassa, osa liikkuu Saksaan ja Alankomaihin, ja muutamat tekevät edelleen perinteisen pitkän muuttomatkan Etelä-Espanjaan, mikä tekee pesimäalueen määrittämisestä muuttolinnuilla haastavaa.

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Online supplementary material

Supplementary material available in the online version of the article (https://doi.org/10.51812/of.143127) includes Tables S1–S2 and Figures S1–S4, presenting detailed information on the breeding sites, moulting sites and migration for the individual birds.