Status, origin and harvest of increasing numbers of Greylag Geese *Anser anser* occurring in Denmark throughout the annual cycle

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Abstract

Breeding census data and September counts show that numbers of Greylag Geese *Anser anser* breeding in Denmark have increased more than six-fold in the period 1990–2020. From around the year 2000, the species has also started wintering in Denmark, where mid-winter counts now exceed 100,000 individuals, supporting a substantial increase in the national harvest (> 50,000 Greylag Geese annually since 2014). Rates of increase for all these measures have, however, declined since 2010. To contribute to the sustainable harvest management of such an important migratory quarry species (comprising Danish-breeding geese as well as those originating outside of Denmark), we need to understand both the origin of birds occurring in Denmark during the hunting season and the winter distribution of Danish-breeding birds, yet we lack contemporary information on either. Resighting and recovery data therefore were used to examine the passage and harvest of birds from other countries and to investigate temporal changes in the winter distribution of geese that bred in Denmark. Norwegian-breeding birds passed through Denmark mainly in early autumn, mostly occurring in western Jutland, whereas Swedish-breeding Greylag Geese peaked in numbers during mid-winter and were most numerous in eastern Denmark. In the last two decades, birds from both Norway and Sweden comprised a larger proportion of the Danish hunting bag than before 2000. Late summer reports of birds marked in Germany and Poland likely reflect moult migrants to Denmark during this period. Although marked breeding Greylag Geese from Denmark traditionally overwintered mostly in Spain, recoveries show they have become increasingly sedentary over seven decades, with many now wintering inside Danish national borders. The Northwest/Southwest (NW/SW) European Greylag Goose population (of which Danish birds form a part) is currently the focus of a developing Adaptive Flyway Management Programme, which requires such knowledge of seasonal movements of birds of different origins to ensure informed decision-making and a knowledge-based approach. Our findings can guide

decision-making concerning Danish harvest legislation, by quantifying how birds of different breeding provenance contribute to the Danish hunting bag. This may assist with defining the allocation of harvest to comply with attaining the national breeding favourable reference population values established for individual countries.

Key words: differential migration, hunting management, migration phenology, ring recoveries, waterfowl.

Across northern Europe, the Northwest/Southwest (NW/SW) European population of the Greylag Goose *Anser anser* has increased substantially in abundance in recent decades (Fox *et al.* 2010; Fox & Madsen 2017). The rapid increase is evident in both summer and winter abundance and has coincided with an expansion in breeding distribution in most countries (Keller *et al.* 2020). Population growth has probably been driven by improved foraging opportunities related to increasing use of agricultural habitats (Fox & Abraham 2017; Fox & Madsen 2017) and a flyway-scale northward shift in wintering distribution at least partly related to milder winters (Ramo *et al.* 2015; Podhrazsky *et al.* 2017; Månsson *et al.* 2022). In the case of Denmark, relaxation of hunting in 1994 (when the closed season was extended to include August) might also have contributed to the increasing trend (Madsen *et al.* 2021). In parallel with the growing population size of Greylag Geese, there have been increasing calls for management actions to mitigate damage to agricultural crops (Fox *et al.* 2017; Montras-Janer *et al.* 2019; Teräväinen *et al.* 2022). As a result, an International Single Species Management Plan and an Adaptive Flyway Management Programme have been adopted for the population, both under the auspices of the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA) and the European Goose Management Platform (EGMP) (Powolny *et al.* 2018; Nagy *et al.* 2021). This, in turn, has led to the definition of two "management units" (MUs) and the formulation of separate population targets. MU1 is migratory, breeding in Norway, Sweden, Denmark and Finland, and wintering to the southwest in the Netherlands, Belgium, Denmark, Sweden, France, Spain and Portugal. The population target of MU1 is 70,000 breeding pairs. MU2 is sedentary; it breeds and winters in Germany, the Netherlands, Belgium and France, and has a population target of 80,000 breeding pairs (Bacon *et al.* 2019; Nagy *et al.* 2021). As part of this process, every country along the flyway of the NW/SW European population has defined national breeding favourable reference population (FRP) values, representing the minimum required level of national breeding abundance to maintain the species as a viable component of its ecosystems (EGM-IWG 2021). The entire flyway population thus covers two management units, each of which covers several national breeding populations.

The objectives of maintaining national breeding FRP values and a target flyway population size relies on adaptive harvest

management and the formulation of national hunting quotas ensuring an appropriate offtake of birds with different breeding provenances. At present, the lack of reliable estimates of national breeding populations in individual range states hampers quantitative analyses of how harvest in different countries affect different breeding stocks (Johnson & Koffijberg 2021; Jensen *et al.* 2022). Nonetheless, knowledge may be gained from determining where and when immigrant Greylag Geese occur in single countries and from assessing the extent to which national breeding populations migrate at all.

Currently, there is little contemporary synthesised information describing the passage of Greylag Geese from other countries (Norway and Sweden in particular) through Denmark. Previous studies from these countries, based on sightings, recoveries and tracking data from neck-collared and GPS-collared birds, suggest that while many Norwegian birds migrate via Jutland (western Denmark), most Swedish birds use the eastern parts as stopover or wintering sites (Andersson *et al.* 2001; Månsson *et al.* 2022). Fully deciphering these patterns might contribute to clarifying variation in hunting exposure between Danish, Norwegian and Swedish birds, and thus support appropriate management decisions required to meet potential differing management needs for these three (and potentially other) national breeding populations.

Limited existing data on the migratory behaviour of marked Danish-breeding Greylag Geese indicate that, throughout the 20th century, most birds left the country in autumn and migrated to winter mainly on the Guadalquivir Marshes in Spain, staging in the Netherlands and France *en route* (Nilsson *et al.* 1999; Andersson *et al.* 2001; Kampp & Preuss 2005; Bacon *et al.* 2019). Recent studies from neighbouring countries have, however, revealed that Greylag Geese now increasingly winter closer to their breeding areas, resulting in a clear northward shift in their wintering range (Voslamber *et al.* 2010; Ramo *et al.* 2015; Podhrazsky *et al.* 2017) – the "winter short-stopping" of Elmberg *et al.* (2014). Some north-Scandinavian birds now actually spend their entire annual cycle in northern Europe (Nilsson & Kampe-Persson 2018; Månsson *et al.* 2022). Given a lack of recent studies on Greylag Goose movements in Denmark (but see Kampp & Preuss 2005; Bacon *et al.* 2019), the extent to which Danish birds also overwinter at northern latitudes has hitherto been unclear. As such, the increasing number of wintering birds in Denmark could have resulted from: 1) north-Scandinavian (especially Norwegian and Swedish) birds "winter short-stopping" to stay in Denmark instead of migrating further to southern Europe, 2) Danish breeders becoming sedentary by staying in Denmark year-round, or 3) a combination of the above.

Danish Greylag Geese are part of MU1, and the species is subject to hunting in all Scandinavian countries. In Denmark in particular annual harvest has averaged *c.* 60,000 birds in the years 2015–2020 (Christensen *et al.* 2021), which is by far the largest national bag across the flyway of the species and *c.* one-third of the total harvest covering both management units (Powolny

et al. 2018; but see Johnson & Koffijberg 2021). Besides hunting, substantial numbers of birds are culled annually by means of derogation measures, especially in the Netherlands, and Jensen *et al.* (2022) report an estimate of *c.* 262,000 birds culled in 2020 on a flyway-scale. So far, the spatio-temporal distribution of harvested birds with different origins has been largely unknown, but understanding how the Danish harvest impacts national breeding populations from our neighbouring countries is increasingly important. While MU1 covers breeding birds from all the Nordic countries, and thus management actions and objectives at the level of one entire Fennoscandian population of Greylag Geese, a finer spatial resolution is necessary to meet the requirements of the FRP values defined at the level of individual countries. Greylag Geese occur throughout Denmark with the highest densities of breeding and migrating birds in the eastern parts, but during spring and autumn migration larger numbers of birds are also reported at important stopover sites along the west coast of Jutland and around the Danish Limfjord in northern Jutland (Vikstrøm & Moshøj 2020; Nielsen *et al.* 2023). During 1994–2011, the open hunting season extended from 1 September to 15 January, with January hunting restricted to below the high tide mark in Danish territorial waters. Since 2012, all of January has been included in the open season, and from 2015 onwards January hunting was also allowed above the high tide mark. Since 2018, the season has opened on 1 August, albeit confined to arable fields > 300 m from coasts and wetlands (Madsen *et al.* 2021).

In this analysis, we aim to: 1) describe the changes in the breeding and wintering Greylag Goose abundance and annual hunting harvest in Denmark since the 1980s, 2) clarify the temporal and spatial patterns of Greylag Geese breeding in other north European countries occurring in Denmark, 3) assess the relative contribution of Danish, Norwegian and Swedish birds to the Danish hunting bag, and 4) elucidate any changes in wintering areas used by Danish-breeding birds in the last half a century. Collectively, this information will contribute to an informed basis for assessing the impact of the Danish harvest on different national breeding populations of the Greylag Goose, which may serve as a guide for improved future monitoring and management, as well as for maintaining a sustainable harvest both nationally and at the flyway-population level.

Methods

Changes in abundance and harvest

As a measure of change in relative breeding abundance, we acquired point count data from the Common Birds Census compiled by BirdLife Denmark during 1976–2021 (see Vikstrøm *et al.* 2022 for details). These point counts consist of fixed routes (464 in 2020) covered by the same observer each year, with a number of geographically fixed points (10–20 depending on the length of the transect) that are monitored for all birds seen or heard during a 5 min period. From these counts, annual indices are generated by Birdlife Denmark, based on an index value of 100 for the year in which monitoring commenced (1987 for Greylag Geese). We

extracted all Greylag Goose values from the "breeding bird survey" carried out annually from 1 May–15 June inclusive, covering the time of year when only local breeding birds should be present in the country.

Autumn and winter abundance of Greylag Geese in Denmark were extracted from the national environmental monitoring scheme NOVANA (the National Monitoring and Assessment Programme for the Aquatic and Terrestrial Environment, Nielsen *et al.* 2023). These counts are conducted under the auspices of the Danish Ministry of Environment and reported to Wetlands International. September counts have been completed annually during 1981–2017 and for every second year thereafter, while national mid-winter counts have been conducted annually in mid-January since 1981. The mid-winter counts, covering many species of waterbirds, are conducted as a combination of aerial and land-based surveys, while September counts specifically targeting Greylag Geese are based on land-based surveys alone (see Laursen *et al.* 2008 and Nielsen *et al.* 2023 for details on methodology). While the specifics of this monitoring have changed over time, the aim and approach have always been to conduct a nationwide total count of the number of geese in the country. Coverage from air (and land to a lesser extent) may vary depending on weather, but all major wetlands (the main habitat for Greylag Geese) are always included. The dataset of both counts is extended with supplementary data from "DOFbasen" (citizen science portal of BirdLife Denmark; https://dofbasen.dk/) to cover potential additional sites not covered but supporting Greylag Geese, added using a GIS-based filtering procedure to exclude any potential overlap with the NOVANA counts in time and space. Fully accounting for the minor annual variation in coverage and land-based *vs.* aerial surveys is beyond the scope of the present paper (but see Nielsen *et al.* 2023), and instead we used the official annual estimates to report population development as a smoothed curve ensuring that small annual differences in coverage will have only negligible effects on the abundance estimates. Annual harvest data for 1995–2020 inclusive were extracted from the online Danish bag statistics (Christensen 2022). Analyses of all three count measures and annual harvest were conducted in R 4.2.2 (R Core Team 2022), and smoothed trajectories visualised using the scatter.smooth function from the package "stats" with a smoothing parameter of 0.4 (implying that each smoothed value was based on the closest 40% of all available data points). The Davies test (Davies 2002) from the package "segmented" (Muggeo 2008) was used to identify objectively potential break points (changes in slope) during periods with available data.

Temporal and spatial patterns of occurrence of geese with different breeding provenance

To infer when and where Greylag Geese breeding in different countries occurred in Denmark, we acquired all available data on ringed birds reported from Denmark. This was accomplished by combining datasets from EURING (https://euring.org) and geese.org (https://www.geese.org), which contain ringing and recovery/resighting data respectively, of all Greylag Geese

reported in Denmark up until August 2022. Because the vast majority of dead recoveries were derived from shot birds (95% of all recoveries with known circumstances), any analysis of dead recoveries will be highly biased towards the open hunting season. We therefore analysed dead recoveries and live encounters separately and later discuss important differences between the two. Further to this, January proportions are somewhat underestimated compared with the current situation for all three analyses of dead recoveries, because hunting on land above the high-water mark was not permitted in January until 2015. Greylag Geese have not been marked with neck collars in Denmark for > 20 years, so while we have a relatively consistent time series of dead recoveries, the data on live encounters were too scarce to support robust analyses for this country.

To ensure that geese could be reliably assigned to a national breeding population, only individuals caught and marked between April and July were included in the analysis, based on the assumption that most birds stay close to their breeding areas during this period. We cannot completely rule out that some birds caught as moulting individuals in this period may have originated from breeding populations elsewhere but, as the geographical scale of this study was individual countries, we assume this proportion to be small and insignificant in relation to the overall picture of migratory movements. The aim of the analysis was to clarify contemporary patterns of spatial and temporal occurrence of Greylag Geese from neighbouring countries and, based on the analysis of changes in winter abundance (see Results section), we only included birds reported after the year 2000 when Greylag Geese began to winter in substantial numbers in Denmark. We used half-monthly intervals as our temporal resolution of recoveries/encounters and, to reduce potential effects of pseudo-replication (multiple sightings of the same bird in the same area), individual birds were only included once in each half-month period. Resightings were reported by birdwatchers from all over the country and dead recoveries by recreational hunters throughout Denmark. While both datasets may to some extent be prone to differences in "effort" (*e.g.* more bird watchers around the larger cities), the geographical scale of our comparisons (west *vs.* east Denmark) means that this should not have a major effect on the results. Moreover, the presence of birds of different breeding provenance should be affected in the same way, and the comparison between them therefore unbiased. The spatial patterns of birds from neighbouring countries were investigated by plotting the coordinates (latitude/longitude in degrees and minutes) for fixes in time and space for individual birds in QGIS 3.26.

Changes in the wintering areas of Danish-breeding Greylag Geese

To clarify potential changes in winter distribution of Danish-breeding Greylag Geese, we used the available information from winter recoveries of birds marked with metal rings in Denmark. As for the analysis above, we defined individuals marked in Denmark in the period April–July as Danish breeding birds. Previous studies of migratory timing (Bacon *et al.* 2019) as

well an ongoing study of GPS-tagged Greylag Geese (https://projects.au.dk/da/can/projekter/gps-sporing) indicate a large efflux of birds from Denmark in early November, presumably reflecting the main wave of autumn migrants. At the same time, Kampp & Preuss (2005) and Andersson *et al.* (2001) found that spring arrival at Danish and Scanian (southern Sweden) breeding sites commenced by early March so, based on these findings, we assumed recoveries from November–February to reflect birds reported either from their wintering quarters or on their way to/from these areas.

The distribution of winter recoveries was assessed per decade and potential changes over time tested using a contingency table (χ^2 test). The outcome of our analysis, founded solely on dead recoveries, was prone to differences in hunting pressure among countries and to changes in hunting pressure along the flyway over time. However, the hunting season for the most important countries included in this analysis (Denmark, Germany, France and Spain) generally covered early autumn to late January (see Powolny *et al.* 2018 for details), with minor deviations among countries and national regions. The species has been protected in the Netherlands since 2001 (Powolny *et al.* 2018), but ever since it has been subject to substantial derogation efforts in parts of the country (EGMP DC 2022). During the 2000s, numbers culled by Dutch derogation efforts increased from *c.* 5,000 to *c.* 50,000 geese (Koffijberg *et al.* 2017) and after 2015 the totals have exceeded 200,000 birds (EGMP DC), although these might be biased high (Johnson & Koffijberg 2021). The analysis was performed in R 4.2.2 (R Core Team 2022) and graphics produced using the "ggplot2" package (Wickham 2016).

Proportional contribution to the Danish harvest

To generate an impression of how the changes in migration patterns and winter abundance might have affected the distribution of birds of different breeding provenance in the Danish hunting bag, all dead recoveries reported as shot in Denmark (n = 1,793) were classified based on their country of origin. Recoveries were grouped into the period before (1950–2000) and after (2000–2020) the emergence of large numbers of wintering birds in Denmark (see Results section). We used a χ^2 test to determine whether changes in the proportion of recoveries by country recorded before and after the year 2000 differed significantly. Likewise, the apparent harvest rate in Denmark was calculated for geese of Danish, Norwegian and Swedish breeding provenance in the same two periods. Harvest rates were expressed as the number of marked geese of a given breeding provenance shot in Denmark/the number of geese ringed in the country of origin in each of the two periods. The numbers of marked birds shot in Denmark for each of the two periods (before : after 2000) originating from each of the three countries were 1,101 : 165 (Denmark), 143 : 130 (Norway) and 100 : 67 (Sweden). Data on the numbers of ringed geese in the three countries were derived from EURING and total sample sizes for each period (before : after 2000) totalled 6,100 : 2,068 (Denmark),

4,110 : 2,592 (Norway) and 5,836 : 2,120 (Sweden). This comparison assumes birds to be marked and shot in the same period, which may be violated for geese surviving from one period to the next. However, while a few geese marked prior to 2000 may have survived until after 2000, the same can be said about geese ringed prior to 1950 surviving into the earliest period, which is why we consider severe bias to be unlikely.

Results

Changes in abundance and harvest

The breeding bird index of Danish Greylag Geese revealed an overall breeding population growth across the last three decades (Fig. 1A), demonstrated by a six-fold increase and an index value of 628 in 2021. The increase was particularly steep during the years 1997–2017, as illustrated by the breakpoints identified at the start

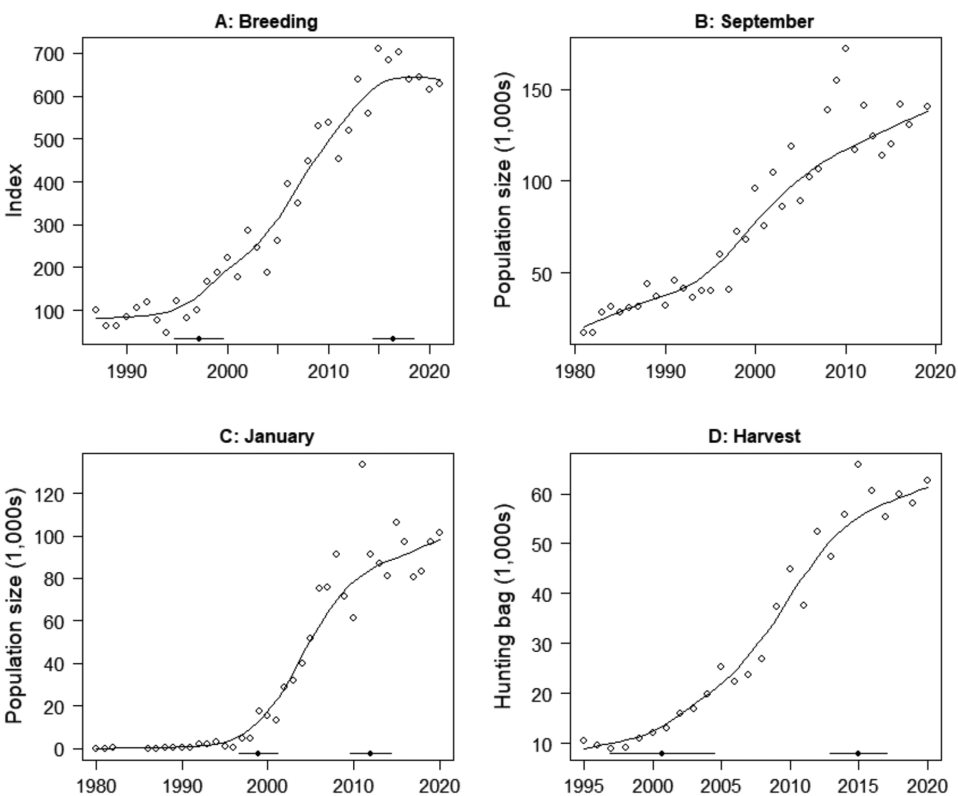

Figure 1. Annual variation in: (A) breeding index, (B) September counts, (C) January counts and (D) hunting harvest of Greylag Geese in Denmark, during the period 1980–2021. Solid lines indicate smoothed trajectories (see Methods), and at the bottom filled circles show the position (± s.d.) where statistically significant break points occurred in the data. Note: breeding index is for years 1987–2021, with the index set to 100 in the baseline year 1987.

and end of this period (Davies test: $K = 10$, $P < 0.001$). Data from the last five years indicate a levelling-off in the index and a stabilisation of the numbers breeding in Denmark.

Outside the breeding season, numbers of Greylag Geese in Denmark have also increased substantially in autumn and winter over the last four decades (Figs. 1B & 1C). September counts increased from *c.* 15,000 individuals in the early 1980s up to *c.* 140,000 in the latest (2019) count, with a peak count in 2010 of *c.* 170,000 birds. January counts went from almost no birds in the 1980s and 1990s to *c.* 102,000 birds in 2021. The highest recorded mid-winter count (*c.* 133,000 birds) was observed in 2012. While there was no statistical support for changes in the slope of the September counts (Davies test: $K = 10$, $P = 0.307$, n.s.), the January count data supported two breakpoints (Fig. 1C). The first of these indicated a steep rise in January numbers around the year 2000 and the second break was associated with a slightly slower increase in winter abundance from just after 2010 (Davies test: $K = 10$, $P = 0.001$). Collectively, these patterns suggest that Greylag Goose abundance has increased substantially in all seasons over the last three decades, that the species (either Danish breeders or other north-Scandinavian birds) started wintering in Denmark from *c.* 2000 and that the growth in breeding and winter abundance has levelled off in recent years.

Annual harvest averaged around 10,000 birds in the mid-1990s but rose sharply during 2000–2015 to reach an annual bag of *c.* 60,000 Greylag Geese in recent years; hence, a six-fold increase over the last three decades (Fig. 1D). Two significant breakpoints were identified around 2000 and 2015 (Davies test: $K = 10$, $P = 0.034$), suggesting the onset of a substantial increase in harvest followed by a levelling-off in numbers shot, respectively.

Temporal and spatial patterns of occurrence of geese with different breeding provenance

Resightings of Norwegian-breeding birds revealed that their numbers in Denmark peaked in mid-August to mid-October and that relatively few birds remained in Denmark during winter (Fig. 2A). In early spring (late February–early April) numbers increased again, presumably as the result of spring migrants returning north. Looking at the dead recoveries, these confirm a large influx of Norwegian birds to the country in early autumn and much lower numbers during winter (Fig. 2B). This picture is heavily biased by the timing of the Danish hunting season, however, which until 2017 started on 1 September and ended in January. As a result, the early influx of Norwegian birds in August was not picked up by this analysis and it was not possible to detect any spring peak.

Live encounters of Swedish-breeding geese revealed a different pattern compared with the Norwegian ones. The proportions of resightings were relatively low in early autumn and gradually built up during autumn and early winter to peak in early January–mid-March (Fig. 3A). Smaller numbers of Swedish birds were seen in Denmark during summer as well. As for the Norwegian birds, the Swedish dead

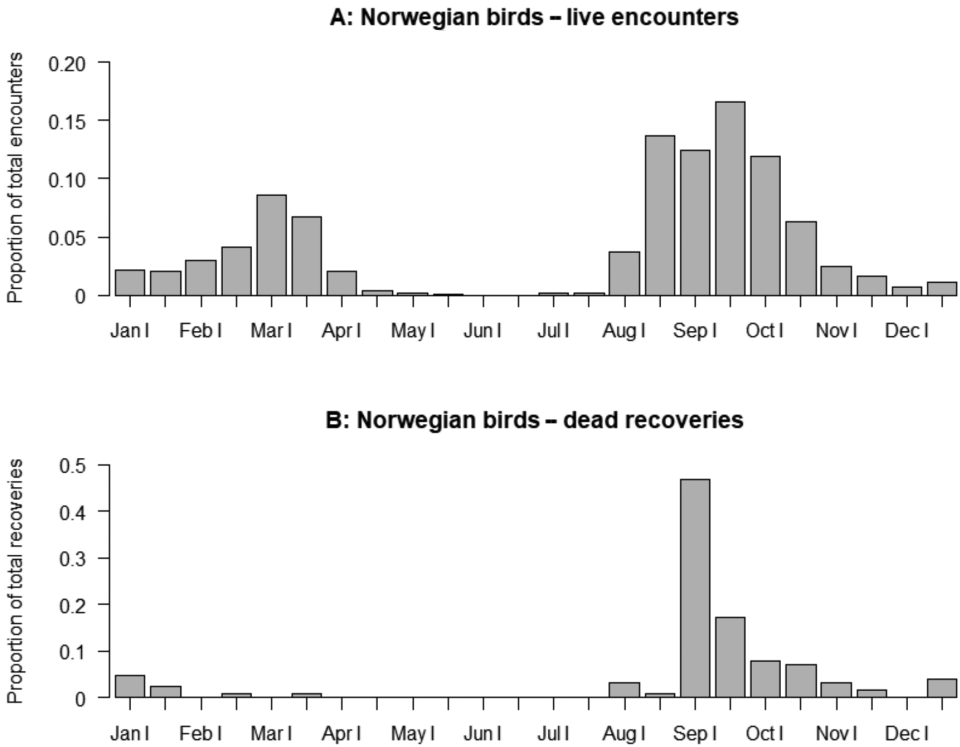

Figure 2. Half-monthly distribution of Greylag Geese fitted with metal rings, neck collars or GPS-collars in Norway in April–July resighted (A, n = 1,527) or recovered (B, n = 128) in Denmark during 2000–2022. For most of this period, the open Danish hunting season covered September–January. Note the difference in scale of the y-axes between plots.

recoveries were highly influenced by the timing of the Danish hunting season, but the pattern seemed to confirm that Swedish birds were more numerous in winter than in autumn (Fig. 3B).

The contemporary (after 2000) dead recovery data from Danish geese showed that most birds were reported in September (the start of the hunting seasons up until 2018), but also that Danish breeders were harvested to some extent across the entire autumn and winter (Fig. 4). The proportions of dead recoveries during summer were expectedly higher for these birds compared with Norwegian and Swedish geese, given the Danish breeding provenance of this group.

The spatial distributions of Norwegian and Swedish Greylag Geese reported in Denmark were markedly different (Fig. 5), and birds from these two countries seemed to be spatially segregated when present in Denmark. Greylag Geese from Norway were concentrated in Jutland (96% of all reports), especially along the west coast, with only few and scattered reports in

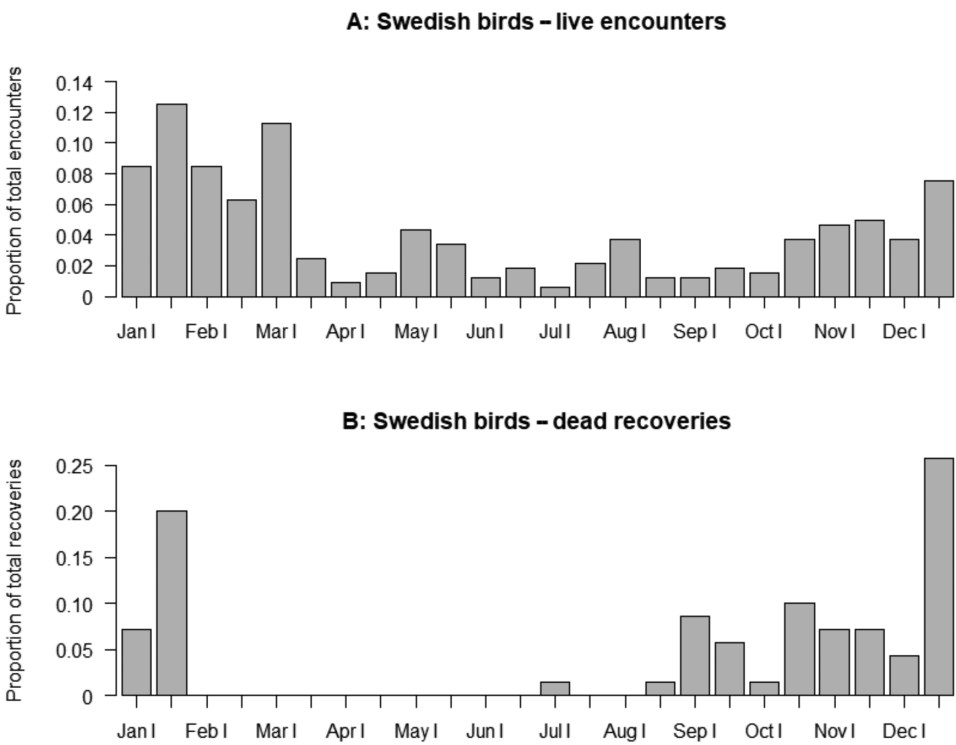

Figure 3. Half-monthly distribution of Greylag Geese fitted with metal rings, neck collars or GPS-collars in Sweden in April–July resighted (A, $n = 320$) or recovered (B, $n = 71$) in Denmark during 2000–2022. For most of this period, the open Danish hunting season covered September–January. Note the difference in scale of the y-axes between plots.

eastern parts of the country. Birds from Sweden, on the other hand, had a clear easterly distribution, with the majority of birds (78%) reported on Zealand and Funen and occasional reports along the east coast of Jutland.

In addition to Norwegian and Swedish birds, smaller numbers of German, Polish, Dutch and Finnish birds were also resighted in Denmark (Fig. 6). German ($n = 49$) and Polish ($n = 33$) birds showed a similar pattern, with peak numbers in late summer (July–August) and occasional sightings in autumn and winter. Birds from Germany and Poland were mainly reported in southeast Denmark, close to their country of origin (Fig. 7). Dutch birds ($n = 127$) showed no clear temporal pattern and were reported from all regions of the country, although most numerous on the Jutland peninsula (Fig. 7). The few Finnish birds ($n = 15$) showed a pattern of occurrence very similar to the Swedish birds and were found in Denmark mainly during mid-winter and only in the southeastern parts of the country (Figs. 6 and 7).

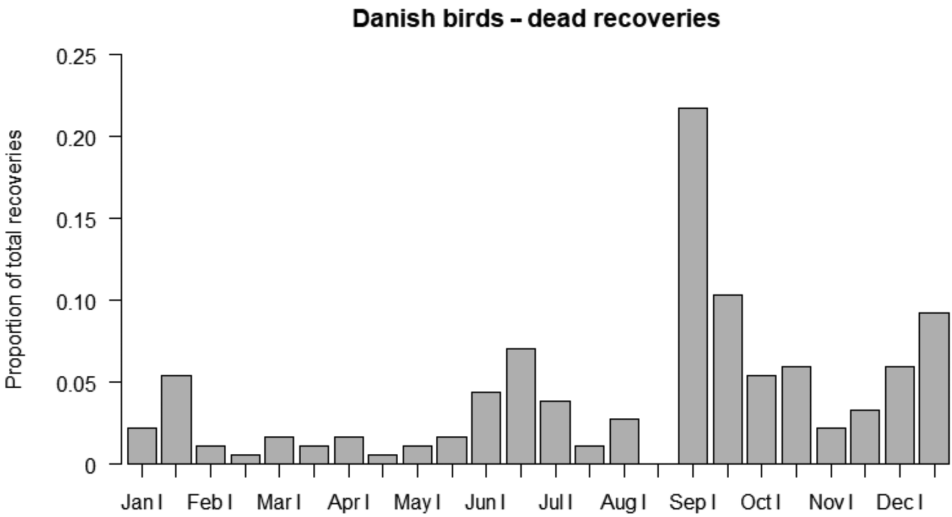

Figure 4. Half-monthly distribution of Danish-breeding Greylag Geese recovered (*n* = 184) in Denmark during 2000–2022.

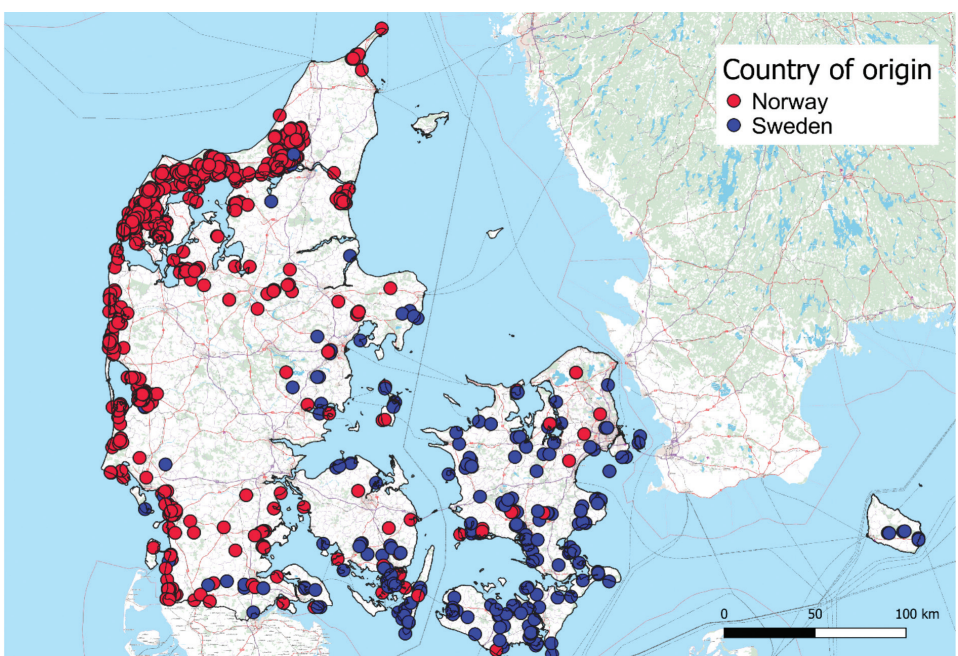

Figure 5. Spatial distribution of Norwegian-breeding (red, *n* = 1,655) and Swedish-breeding (blue, *n* = 391) Greylag Geese reported in Denmark during 2000–2022. The map combines both live resightings and dead recoveries.

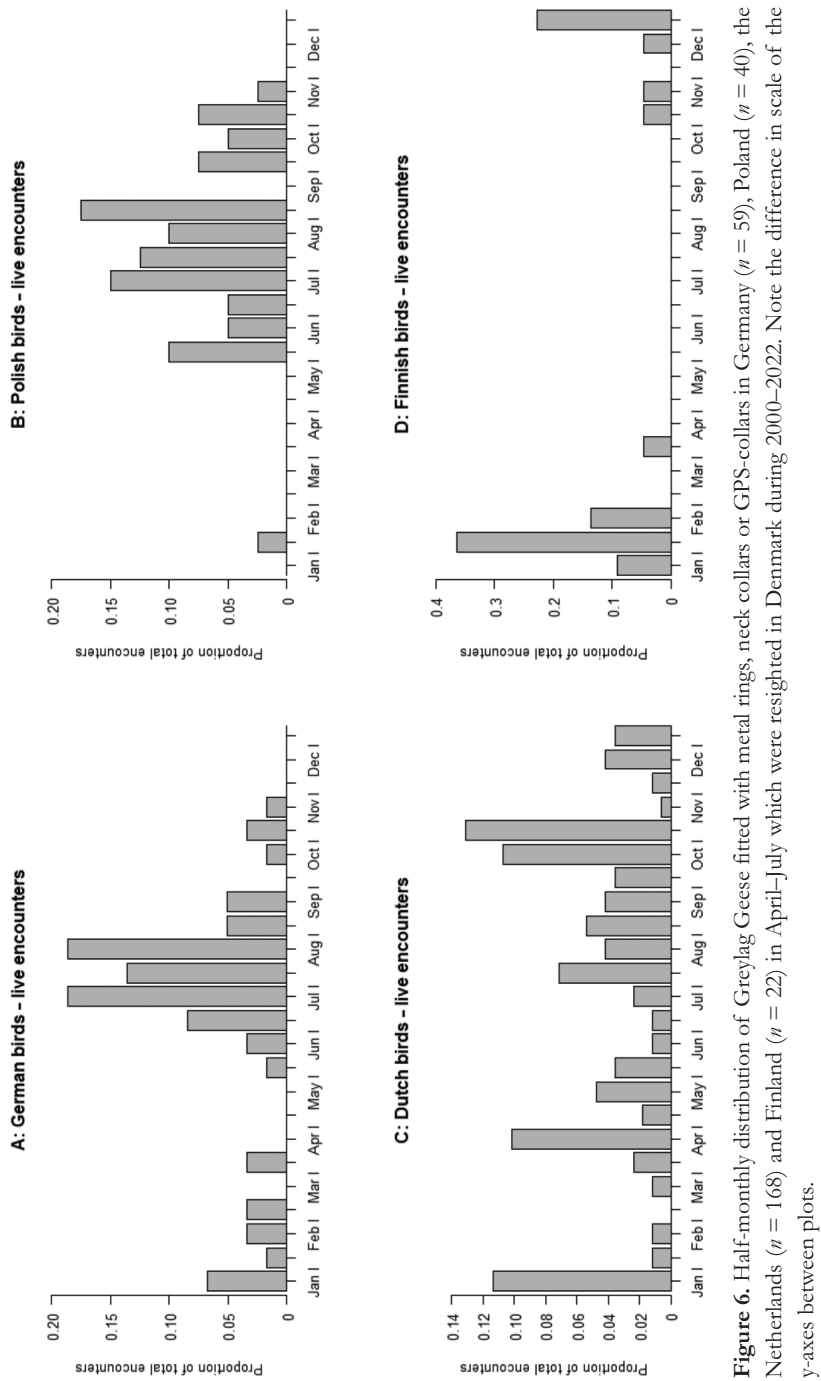

Figure 6. Half-monthly distribution of Greylag Geese fitted with metal rings, neck collars or GPS-collars in Germany ($n = 59$), Poland ($n = 40$), the Netherlands ($n = 168$) and Finland ($n = 22$) in April–July which were resighted in Denmark during 2000–2022. Note the difference in scale of the y-axes between plots.

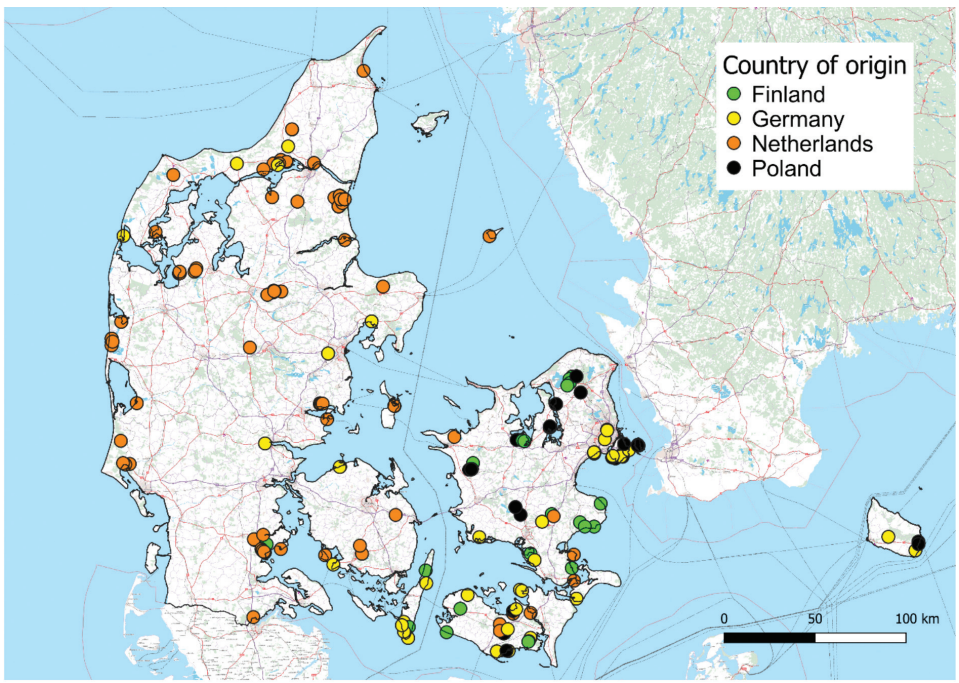

Figure 7. Spatial distribution of German- (yellow, n = 66), Polish- (black, n = 41), Dutch- (orange, n = 171) and Finnish-breeding (green, n = 24) Greylag Geese reported in Denmark during 2000–2022. The map includes both live resightings and dead recoveries.

Occasional resightings of birds from Czechia (6), Great Britain (1), Latvia (1) and Lithuania (2) were too few to decipher temporal or spatial patterns, as were the data on dead recoveries from all countries other than Norway and Sweden (n < 10 in all cases).

Changes in the wintering areas of Danish-breeding Greylag Geese

The distribution of winter recoveries from Danish-breeding Greylag Geese has changed significantly over the last seven decades (two-way contingency table of country and decade, χ^2_{18} = 367.8, P < 0.001, Fig. 8). The proportions recovered in the southernmost wintering areas in Spain (mainly the Guadalquivir Marshes) declined considerably over this period, and the gradual abandonment of this traditional wintering area was paralleled by a slightly higher use of wintering areas in France and, in particular, a steep increase in the number of birds wintering in Denmark near their breeding sites.

Proportional contribution to the Danish harvest

Based on the breeding provenance of marked birds shot in Denmark, the composition of the Danish harvest changed significantly before and after year 2000

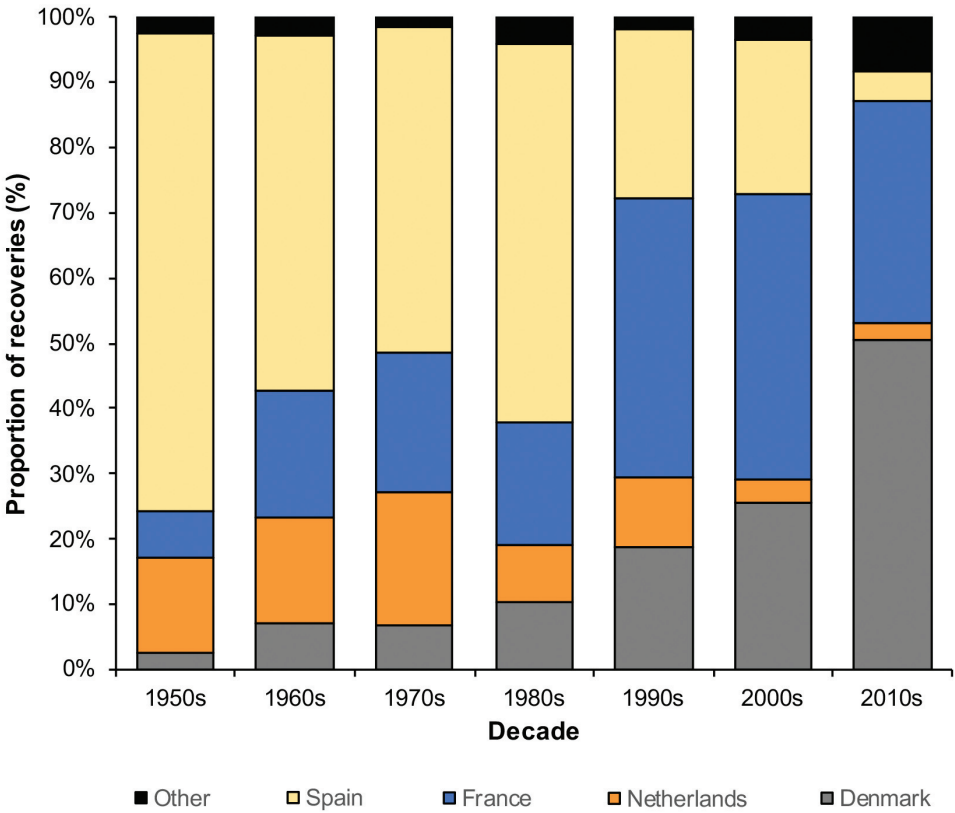

Figure 8. Distribution of winter recoveries (November–February) of Greylag Geese breeding in Denmark, expressed per country and decade, during 1950–2020. Sample sizes for the seven decades (1950s–2010s) were 41, 210, 117, 116, 112, 55 and 85 respectively.

(χ^2_3 = 210.8, $P < 0.001$, Table 1). Before 2000, *c.* 79% of the dead recoveries were of Danish origin, while Norwegian and Swedish birds made up 10% and 7% respectively. After 2000, the proportion of birds of Danish breeding provenance had fallen to 41%, while Norwegian geese accounted for 33% of shot birds and Swedish geese made up 18%. A similar development was found in our simple expression of harvest rates, as the rate for Danish birds fell from 18% to 8% before and after the year 2000 respectively, while conversely the harvest rate of both Norwegian and Swedish birds increased (Table 1).

Discussion

Our analyses revealed recent increases in the abundance of Greylag Geese in Denmark in summer, autumn and winter, reflected in a parallel pattern in the national harvest bag. The pattern in all three abundance measures and the national harvest indicated that

Table 1. Proportional distribution of Greylag Geese of different breeding provenance in the Danish hunting bag (based on dead recoveries of birds reported as shot) and harvest rate of the same populations in the Danish harvest (numbers shot/numbers ringed), before and after the year 2000.

Breeding provenance	Distribution of bag (%)		Harvest rate (%)	
	Before 2000	After 2000	Before 2000	After 2000
Denmark	79.3	40.7	18.0	8.0
Norway	10.3	33.1	3.5	5.0
Sweden	7.2	18.3	1.7	3.2
All other countries*	3.2	7.9	–	–

*Including birds from Belgium, Czech Republic, Finland, Germany, Lithuania, the Netherlands and Poland.

the rate of increase was lower in the most recent years, albeit not significantly so for September counts. The increases in autumn and winter numbers may result partly from Danish breeders adopting a sedentary lifestyle and partly from northern breeders increasingly using Denmark as a stopover and/or wintering area. With respect to the breeding origin of geese hunted in Denmark, our data suggest that contemporary annual harvests contain a larger proportion of Norwegian and Swedish birds than prior to the emergence of large wintering numbers in Denmark. These figures should be treated with caution, however, as they will be affected by the proportions of marked birds in and from individual countries at any one time, which cannot be estimated reliably because of substantial uncertainty regarding the size of national breeding populations (Johnson & Koffijberg 2021; Jensen *et al.* 2022). Consequently, the result is only indicative of real patterns and the actual contribution of birds of different breeding provenance may differ from those presented here. Nonetheless, harvest rates in Denmark showed a similar change in the proportional contribution between these three national breeding populations, supporting an increased proportion of birds from northern Scandinavia in the bag after the turn of the millennium.

Our data revealed profound differences in migration phenology between birds from Norway and Sweden. While the vast majority of Norwegian birds seemed to pass through Denmark during early autumn (see Bacon *et al.* 2019; Boos *et al.* 2019), Swedish birds had their peak occurrence in mid-winter and were most numerous in Denmark during January and February (see Månsson *et al.* 2022). Consequently,

Norwegian birds seem mainly to be transient migrants en route to winter quarters further south (Andersson *et al.* 2001), while Swedish birds are to a greater extent winter visitors, whose numbers in Denmark may be weather-dependent and related to the presence of snow/ice conditions in southern Sweden. As a result, changes in September abundance were probably driven mainly by Danish- and Norwegian-breeding Greylag Geese, while changes in January numbers probably reflect the abundance of primarily Danish and Swedish birds. In addition, annual variation in the January count probably related to winter conditions in both Sweden and Denmark, which may explain the relatively low count in 2010 coinciding with the coldest January in Denmark during the last two decades and the highest count in January 2012, which was mild.

Interestingly, the geographic distribution of Norwegian and Swedish birds occurring in Denmark was also markedly different. The distinctive east–west gradient in the frequency of occurrence of Greylag Geese from these two countries highlighted that Swedish and Norwegian birds were to a large extent both spatially and temporally segregated in Denmark. Earlier studies indicated a differential use of separate migratory routes and stopover sites by Greylag Geese from Norway and Sweden (Andersson *et al.* 2001; Månsson *et al.* 2022), which can now be confirmed. In addition, our results emphasise a difference between Swedish and Norwegian birds in terms of migration phenology that to our knowledge has not previously been described. Boos *et al.* (2019) found that Norwegian birds from the northeasternmost parts of Norway (eastern Finnmark) migrated via the east coast of Sweden to arrive in Denmark and the Netherlands in late October. These birds seem to follow a route similar to the Swedish birds, which may partly explain the otherwise rare reports of Norwegian geese in the east of Denmark. Nevertheless, other Norwegian birds observed in eastern Denmark originated from central Norway. Seen in the light of managing the effects of hunting on national breeding populations, these differences in occurrence between Norwegian and Swedish birds provide important information upon which to base future harvest management, targeting specific birds within a geographical and temporal context. Thus, Greylag Geese shot in western Jutland in early autumn will mainly be Danish or Norwegian birds, whereas individuals shot in eastern Denmark during mid-winter will primarily be Danish or Swedish birds, potentially including a minority of birds from Finland as well.

The mid- and late summer reports of birds breeding in Germany and Poland indicates that geese from these countries appear in Denmark as moult migrants, mainly in the southeast parts of the country. In the early 1990s, Fox *et al.* (1995) found that moulting Greylag Geese on the island of Saltholm (situated in Øresund) originated primarily from adjacent areas in Denmark and Sweden, but recently Nilsson & Hermansson (2019) have described a northbound moult migration of continental-breeding geese to Lake Hornborgasjön in Sweden and this phenomenon may have become increasingly common in recent decades or previously

overlooked. The Swedish birds reported in Denmark during mid-summer likely result from geese moving to Denmark during the remegial moult – a phenomenon known to occur on Saltholm (Fox *et al.* 1995; Nilsson *et al.* 2001). In addition, there may also be some exchange across national borders even for breeding birds. This seems especially likely in eastern Denmark, where Denmark and Sweden are separated only by the Great Belt (a stretch of open water from 4–30 km wide) and breeding populations from the two countries may not in reality be separate.

The differences in temporal distribution of live resightings *versus* recoveries of dead birds highlights the shortcomings of the latter when working on quarry species. While dead recoveries may be good indicators of seasonal variation in hunting mortality, they are often highly biased in terms of describing phenology and migratory timing due to large differences in reporting probability between the open and closed hunting season. Our analysis of changes in wintering distribution of Danish-breeding Greylag Geese builds entirely on dead recoveries and may consequently be prone to changes in hunting pressure/legislation (*e.g.* in Denmark in 1994 and 2017) and/or reporting rates (Robinson *et al.* 2009) over time and space. In terms of geographical bias in particular, our analysis could underestimate the importance of countries where the species is protected, as has been the case in the Netherlands since 2001 (Powolny *et al.* 2018). However, Greylag Geese are subject to substantial derogation control in the Netherlands, with > 200,000 individuals culled annually in recent years (EGMP DC 2022). At least parts of these derogation efforts take place in autumn and winter, when Danish birds should be present in the country (EU Birds Directive Derogations 2020). Given this level of culling, our dataset includes surprisingly few Dutch recoveries. Recent studies have highlighted that current estimates of Greylag Goose offtake and population size may be highly biased in some countries, which hampers interpretations of reporting probability and absolute harvest in any detail (Johnson & Koffijberg 2021; Jensen *et al.* 2022). However, in most countries included in our analysis (*e.g.* Spain, France, Germany and Denmark), Greylag Geese have been subject to a similar open season throughout the study period. If we assume reporting probability to be similar across these countries, proportional changes in dead recoveries over time should not be heavily biased except for the effects of changes in national season lengths across the seven decades. In this respect, the main changes may have been extensions of the open season in Denmark to include August and January, but the timing of these changes (2018 and 2014 respectively) are too recent to have had a significant effect on the changing pattern of recoveries depicted here. Despite the limitations of having to rely solely on dead recoveries, it seems likely that Danish-breeding Greylag Geese today winter in Denmark to a greater extent and, hence, that an increasing part of the national breeding population has become sedentary over the last 50 years. In addition, the migratory part of the Danish-breeding population now migrates considerably shorter distances between summer and

winter quarters compared with the start of the study period, as has previously been described on flyway-scale (Ramo *et al.* 2015).

Interestingly, the pattern and duration of rapidly increasing numbers was similar for geese breeding and wintering in Denmark. While this could suggest a connection between the two, we should be prudent in over-interpreting these relatively limited data. Winter Greylag Goose abundance is the product of Danish birds supplemented to an unknown extent by birds breeding in northern Scandinavia, where national breeding populations have likewise grown considerably (Powolny *et al.* 2018; Liljebäck *et al.* 2021). The total numbers wintering in Denmark are also likely to be affected by winter severity. In parallel with the emergence of the wintering trait in Denmark, fewer Danish Greylag Geese now migrate to the traditional wintering areas in southern Spain. GPS-tracking studies have likewise found that Swedish Greylag Geese are increasingly abandoning these southernmost wintering areas, with some individuals from northern Sweden migrating to Germany and the Netherlands to winter (Månsson *et al.* 2022; Nilsson *et al.* 2022). The continued use of France as a wintering area for Danish geese described in this study probably reflects the same pattern, and other central-western European countries (especially the Netherlands, the importance of which may have been underestimated in our analysis) may still serve as important wintering grounds for Danish breeders as well. Studies of more neck- or GPS-collared birds are needed to confirm this hypothesis and to overcome the limitations of using only dead recovery data presented here.

The change in migratory behaviour of both Danish and other Scandinavian Greylag Geese has come about effectively within just a couple of decades. This indicates that changes in annual movements were driven mainly by behavioural adaptation and social transmission rather than being genetically based, as has also been suggested by other recent studies of migratory changes in geese (Clausen *et al.* 2018a; Nilsson *et al.* 2022). The ultimate drivers of this change may relate to a combination of improved winter foraging opportunities, milder winters and successful conservation leading to population growth (Ramo *et al.* 2015; Fox & Abraham 2017; Fox & Madsen 2017; Podhrazsky *et al.* 2017; Clausen *et al.* 2018b). The great similarity in both magnitude and timing of the developments in harvest and abundance of Greylag Geese in Denmark suggest that changes in the Danish hunting bag may to a great extent reflect population development. The growing proportion of Danish breeders wintering in Denmark would imply that national harvest may increasingly take a toll on local breeding birds. However, our data indicate that although the harvest of Danish breeders may have risen in absolute terms, the proportional contribution of these birds to the total harvest has decreased after year 2000 at the expense of birds from further north. This probably reflects an increase in the frequency and duration of stopovers among birds from Norway and Sweden, as well as growing proportions of individuals that breed in northern Scandinavia among the Danish-wintering birds. This is supported by the fact that, although the Danish breeding index increased six-fold over our

study period, a large proportion seemed still to winter south of the country. Consequently, the increase in abundance during the wintering period will have to be partly fuelled by birds from elsewhere.

To ensure appropriate future harvest management of Greylag Geese and compliance with the national FRP values, quantifying how birds of differing breeding provenance contribute to different national hunting bags is increasingly important. Norwegian and Swedish bird are increasingly subject to hunting in Denmark, but exactly to what extent is presently unknown, due to a lack of national breeding population censuses for MU1 and potentially differential investment in marking of Greylag Geese in the different states, which hamper our ability to determine the international hunting pressure on the different national breeding stocks. Ongoing initiatives in relation to the European Goose Management platform (EGMP) seek to overcome these data gaps in the coming years (Jensen *et al.* 2022). Meanwhile, based on the available descriptive data, we show that differences in the temporal and spatial patterns of occurrence of birds originating from outside Denmark might be used to direct future harvest management in Denmark for geese breeding in northern Scandinavia. This may guide decision-making concerning the Danish harvest legislation until better options are available. Improved, coordinated capture–mark–recapture programmes across the region would be an important contribution to improve our predictions of how future potential changes in hunting management and allocation of the harvest may affect the different national breeding populations.

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