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Spatio–temporal distribution of greylag goose *Anser anser* resightings on the north-west/south-west European flyway: guidance for the delineation of transboundary management units

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In western Europe, the majority of wild goose populations have increased exponentially over the last decades. Such increase is the source of many socio–ecological conflicts. The need for coordinated management actions to handle the goose-related conflicts at the European scale has led to the establishment of a specific European Goose Management Platform (EGMP) under the auspices of the Agreement on the Conservation of African–Eurasian Migratory Waterbirds (AEWA). The north-west/south-west (NW/SW) European population of greylag goose *Anser anser* has been considered as a priority concern, and an AEWA international single species management plan has been recently adopted. Because of the complex structure of the greylag goose population (e.g. spatial differences in migration strategies), and management (e.g. different hunting schemes among the range states), delineation of management units (MUs) based on goose movement characteristics was deemed necessary to further implement effective management actions. Based on neckband marking in various breeding regions and subsequent resighting locations, we conducted spatio–temporal analysis based on kernel methods to infer spatio–temporal and migratory movements of greylag geese in the NW/SW European flyway. The results highlight the existence of contrasted migratory behaviour, dispersal patterns and phenology within the flyway. From these results three international management units could be delineated. The first MU would include migratory birds from Norway. Birds from breeding grounds in Sweden and Denmark would represent the second MU. Finally, a third central MU was delineated, including primarily breeding birds from the Netherlands and northwestern Germany, which do not show migratory behaviour at the flyway scale. The delineation of these MUs has to be considered within an adaptive process, and future studies will enable a refinement of the definition of such units in order to continuously improve the efficiency of management plans.

Keywords: adaptive management, kernel, migration, neckbanding, waterbirds

In western Europe, the majority of wild goose populations have increased exponentially over the last decades (Fox et al. 2010, Fox and Madsen 2017). Such trends are considered to largely result from a combination of reduced harvest pressure and the expansion of modern agricultural landscapes, offering higher quality food than natural foraging habitats, especially during the non-breeding season (Ebbinge 1991, Fox and Abraham 2017). This significant increase of goose populations has caused a rise in socio–ecological conflicts, involving agricultural damage (Follestad 1994, Eythórsson et al. 2017, Fox and Abraham 2017, Koffijberg et al. 2017), flight safety (Bradbeer et al. 2017), human and animal health (Elmberg et al. 2017), and conservation of natural ecosystems (Dessborn et al. 2016, Bakker et al. 2018). The need for coordinated management actions to handle the goose-related conflicts at the European scale led to the estab-

lishment of the European Goose Management Platform (EGMP) in 2016, under the auspices of the Agreement on the Conservation of African–Eurasian Migratory Waterbirds (AEWA). The goal of the EGMP is to provide a framework for a structured, coordinated and inclusive decision-making process for the implementation of a sustainable management of goose populations in Europe. The objective of the joint management is to maintain these populations in a favourable conservation status, while taking into account the concerns of stakeholders (e.g. statutory authorities, farmers, hunting associations, environmentalists) within the pertinent legislative frameworks and regulations (Stroud et al. 2017, <https://egmp.aewa.info/>).

With a mean annual population increase of 9.1% during the period 1995–2009 (Fox et al. 2010), the north-west/south-west (NW/SW) European population of greylag goose *Anser anser* is one of the species causing many conflicts. The NW/SW greylag population ranges from breeding grounds in Norway and Sweden to Spain as the southernmost wintering grounds (Nilsson et al. 1999). Currently the population is estimated at 900 000–1 200 000 individuals (Wetlands International 2015), but there is evidence that this number is likely an underestimate. For instance, the number of shot or otherwise culled geese per year suggests that the real pre-harvest population size must be larger (Powolny et al. unpubl.). The greylag goose is listed on Annex II/A of the EU Birds Directive, which means it is a legally huntable game species in most of the range states with hunting periods varying between and within the states (in general from mid-August to the end of January). However, the species is protected in the Netherlands and part of Belgium, yet derogation shooting and culling is permitted in these countries in response to agricultural harvest losses and air safety risks. The Netherlands ranks among the countries of highest greylag goose abundance (NW/SW flyway), with a large proportion of the entire population being recorded there for most of the year. Voslamber et al. (2010) concluded that >90% of the breeding greylag geese in the Netherlands were resident and showed little dispersion from their breeding sites. During the 1950–1970s reintroduction of greylag geese occurred in the Netherlands, western Germany and Belgium (van den Bergh 1991, Nilsson et al. 1999).

Greylag geese from the NW/SW European flyway breed mainly in Norway, Sweden, Denmark, Germany, the Netherlands and Belgium (Nilsson et al. 1999). During autumn migration, starting from late July, birds breeding in northern countries (Norway, Sweden and Denmark) migrate to staging areas in Denmark, the German Baltic coast and the Netherlands. Some geese winter in the Netherlands while others migrate further south to wintering areas in France (Lac du Der, Andersson et al. 2001, Nilsson et al. 2013) and Spain (Marismas Guadalquivir and Villafáfila, Andersson et al. 2001). Today, increasing numbers of Swedish breeding geese remain in the south of this country during winter (Nilsson 2013, Nilsson and Kampe-Persson 2018), reflecting a general tendency for individual birds to winter closer to the breeding sites (Nilsson 2013, Nilsson and Kampe-Persson 2018). The spring migration starts from January (Fouquet et al. 2009). The phenology of spring and autumn migrations varies between breeding grounds and with environmental conditions (Andersson et al. 2001, Fouquet et al. 2009). During the breeding period, non-breeders (juveniles and failed breeders) aggregate on moulting sites (Nilsson et al. 2001), which are nowadays widespread within the breeding range. Movements to moulting sites may involve long-distance flights (up to hundreds of km, Nilsson et al. 2001), even for birds that show little local dispersion during the rest of the year (H. Kruckenberg unpubl.).

The NW/SW European greylag goose population presents a complex structure. It is composed of sedentary and migratory individuals with different phenology, and present different anthropogenic interests and hunting regulations among range states. As such, the delineation of management units (MUs) was deemed necessary to encompass the time and space dynamics within the flyway. Those MUs would be a first step to better target management actions to stabilize the population and effectively reduce risks and conflicts (Powolny et al. 2018). MUs are defined as functionally differentiated population segments, i.e. having somewhat different seasonal distribution (although may overlap during certain stages of the annual cycle), exhibiting distinct demographic processes and showing somewhat reduced exchange with other segments of the flyway population (Powolny et al. 2018). Previous studies have investigated individual movements based on neckbanding programs, yet they were focusing on specific breeding populations and regions (Andersson et al. 2001, Pistorius et al. 2006, Voslamber et al. 2010). In this study, we aimed to encompass all available neckband marking and resighting data at the flyway level to assess whether it was possible to delineate consistent subgroups of individuals sharing the same spatio–temporal movements within the population. For this, we used a kernel method to display the distribution of neckband resighting locations in space and time. The goal of this exploratory approach was to disentangle the major migratory paths at the flyway scale, to complement earlier studies conducted on regional scales. It was expected that these results, in addition to previous studies, could provide a comprehensive overview of the spatio–temporal dynamics of the population, which could be used to delineate potential MUs. The analysis does not include all urban sedentary populations in continental Europe, which are largely outside the staging and wintering range of the NW/SW flyway population (Kleinhenz and Koenig 2018).

Methods

Greylag geese were caught in the Netherlands (4503 individuals from 1990 to 2017), Sweden (3481 individuals from 1984 to 2017), Norway (4040 individuals from 1986 to 2017) and to a lower extent in north-western Germany (lower Saxony, 241 individuals from 2016 to 2017 – no data were made available for eastern Germany) and Denmark (115 individuals from 1986 to 1994) (Fig. 1). In total, 12 380 birds were caught, fitted with a metal ring from national ringing centres, and marked with a neckband (see details in Supplementary material Appendix 1, 2). The neckbands were manufactured of laminated UV resistant plastic, engraved with a 3 digit individual code. Collar and digit colours differ among countries of capture (details in <www.geese.org>). From birds caught in the province of Scania (Sweden), neckband retention rate was 97.1% (Persson 2000). While

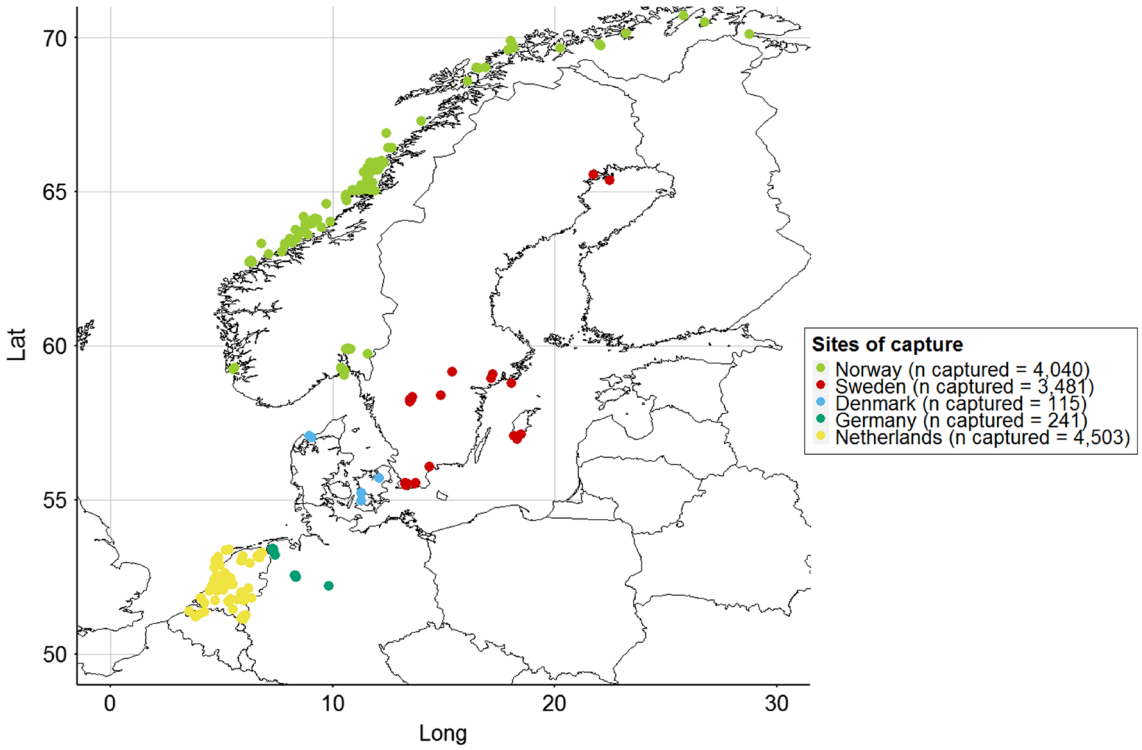

Figure 1. Location of the capture/marking sites.

neckband loss could significantly bias the estimation of survival rates (Nelson et al. 1980, McDonald et al. 2003), such high neckband retention rates should allow robust evaluation of individual migration behaviour, especially when geese are so philopatric to both their breeding (Nilsson and Persson 2001) and wintering grounds (Robertson and Cooke 1999). Sampling effort focused on adults (adult individuals captured with goslings on breeding sites, which are referred as adult breeders thereafter – 30% of captures) and their goslings (49% of captures) as well as non-breeders on moulting sites (21%), and was conducted in priority during the breeding and moulting season (99% of the captures during May, June or July). Greylag goose families were caught when the parents were unable to fly due to wing feather moult and their offspring still had undeveloped wings (Andersson et al. 2001, Voslamber et al. 2010). In inland habitats, they were rounded up when they were grazing on pastures and forced into nets, which had been mounted in advance (Persson 1994). In coastal habitats, most families and moulting non-breeding birds were taken in sweep nets after short pursuits with a boat (Andersson 1990, Andersson et al. 2001).

These neckbandings led to over 457 000 resightings, from which 34% occurred in the very first year after trapping. Each resighting is characterised by a date and a georeference (coordinates – latitude and longitude). We aimed at identifying intra-annual changes in space and time of resighting probabilities, which was expected to be a proxy for the flyway migratory patterns. The marked birds were assumed to behave as non-marked individuals (Clausen and Madsen 2014). We used a kernel product algorithm (Wand and Jones 1995, Keating and Cherry 2009) to draw maps representing the spatial distribution of the probability density function (pdf) of resightings at a given time t. The pdf gives the relative frequency of resighting occurrences in space (latitude and longitude) and time dimensions. All estimations of pdfs were obtained using function 'kernelkcbase' from the adehabitatHR 0.4.15 package (Calenge 2006) with R software ver. 3.4.2 (<www.r-project.org>). The product kernel algorithm from 'kernelkcbase' function is the product of univariate kernel function corresponding to each dimension. For every pdf estimate, the time (date of resighting) was considered as a circular variable, i.e. the birds resighted at time t were so at the same time as birds resighted at time t + 12 months. A biweight kernel function was chosen for the spatial coordinates (Keating and Cherry 2009) and a wrapped Cauchy kernel function to handle the circular distributed temporal covariate (Jammalamadaka and Sengupta 2001). As in Calenge et al. (2010), we combined maps into movies to provide a more didactic overview, allowing a better visual exploration of the speed of movements at the population scale.

As a first step, the pdf of resightings was estimated from the overall dataset. Resightings of individuals during the first year after trapping (365 days after trapping) were discarded because they may present multiple local resightings at the trapping site and the migratory movements were constrained by the date of trapping. In total, 292 333 resightings from 8503 individuals were kept for the analysis. As previous studies highlighted heterogeneity in phenology, wintering and migratory strategies among birds captured in Norway, Sweden and the Netherlands (Andersson et al. 2001, Pistorius et al. 2006, Voslamber et al. 2010), we next estimated separate pdfs based on the country of initial capture (i.e. ringing). Because breeding individuals show a strong philopatry to breeding sites (Nilsson and Persson 2001), only resightings from individuals captured as adult

breeders were kept in the analyses (which ensured that the country of capture was the actual country of breeding). Because only few resightings were available from north-western German adult breeders, we did not discard resightings from the first year after trapping for the kernel analysis. The produced pdfs were considered as a proxy for the spatio–temporal dynamics of the individuals from each country of breeding. It resulted in 36 891 resightings from 800 individuals captured in Sweden; 6149 resightings from 322 captured in Norway; 65 241 resightings from 1577 individuals captured in the Netherlands; 1367 resightings from 111 individuals captured in north-western Germany; and 359 resightings from 31 individuals captured in Denmark. Pdfs were all defined with a smoothing in time dimension of 0.1 and in spatial dimension (latitude and longitude) of 1. Smoothing parameters were chosen subjectively, based on visual observation of kernel estimates (Silverman 1986 and see details in Calenge et al. 2010, Supplementary material Appendix 1). This approach is advised for exploratory purposes, as it provides more insight into the structure of the data (Calenge et al. 2010). Resulting pdfs were represented with the smallest areas where the probability of resighting a neckband were equal to, given that it is resighted at this date, 50% (in black), 70% (in dark grey) and 90% (in light grey). To be the most integrative, we focused mainly on the largest surface area (90%, hereafter referred to as 'Density patch') to assess spatio–temporal variations in resighting probabilities.

Results

The pdf estimated from the overall dataset presented a clear NW/SW temporal dynamic of resighting probabilities. One density patch was observed on the coast of Norway from late March to early September. Multiple density patches were observed in Sweden: one was present from March to September in the province of Södermanland, close to Stockholm, while another remained across the year in the province of Scania in south Sweden. Further south, a persistent density patch was observed throughout the year in the Netherlands. Density patches appeared in Spain and France from early November to mid-March (Fig. 2, Supplementary material Video 1).

When focusing on adult breeders captured in Norway, the pdf still presented a NW/SW temporal pattern (Fig. 3). Neckbands were resighted on the Norwegian coast but with surface area of probability densities of resighting shrinking in size from early September to February. Density patches appeared in the Netherlands and Denmark in July and August, respectively. The density patch in Denmark disappeared in early November. At the beginning of November, density patches appeared in the north (Villafáfila) and south (Marismas Guadalquivir) of Spain. In February a density patch temporally appeared on the Atlantic coast of France (Baie de l'Aiguillon). The density patch in the Netherlands started to shrink in April and disappeared in May. Density patches re-appeared in Denmark and northern Germany between February and April. In Spain, density patches lasted until late March/early April (Fig. 3, Supplementary material Video 2). Density patches briefly appeared in March in south Sweden, but no patches were observed in Sweden during the breeding season (May, June and July).

The pdf of resightings for Swedish-breeding birds showed probability densities of resighting with static surface area in the province of Scania throughout the year. As with Norwegian breeders, the pdf also presented a NW/SW temporal pattern for Swedish-breeding greylag geese. Between March and mid-October, density patches were observed at the

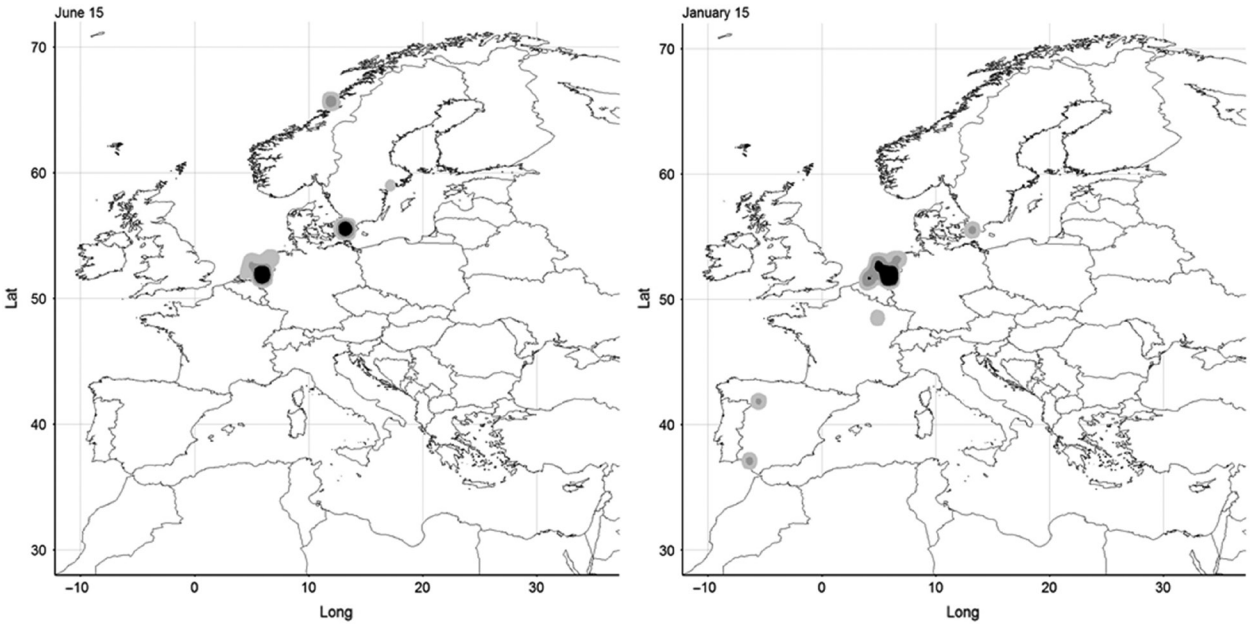

Figure 2. Maps of probability density function of resighting on 15 June (left) and 15 January (right), representing the breeding and wintering periods, respectively. The black areas correspond to the smallest area where the probability of resighting a neckband, given that it is resighted at this date, is equal to 0.5. The dark grey areas correspond to the smallest area where this probability is equal to 0.7. The light grey areas correspond to the smallest area where this probability is equal to 0.9. For a complete understanding of the results, see Supplementary material Video 1.

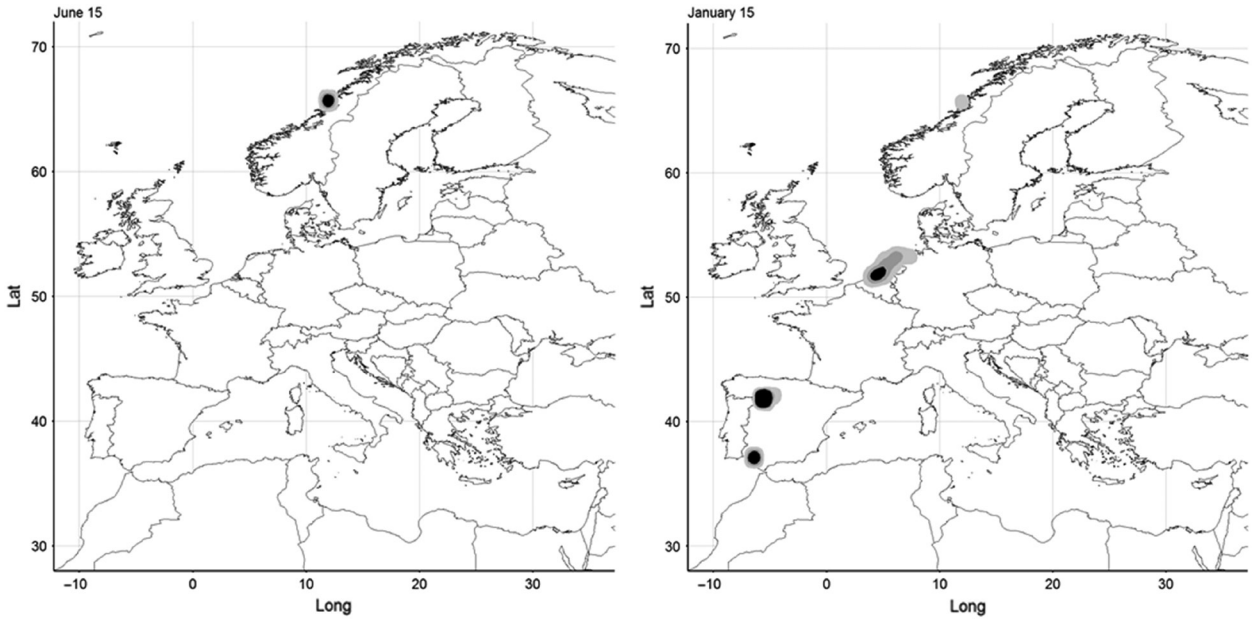

Figure 3. Maps of probability density function of resighting on 15 June (left) and 15 January (right), representing breeding and wintering areas for adult breeders captured in Norway, respectively. The black areas correspond to the smallest area, where the probability of resighting a neckband, given that it is resighted at this date, is equal to 0.5. The dark grey areas correspond to the smallest area, where this probability is equal to 0.7. The light grey areas correspond to the smallest area, where this probability is equal to 0.9. For a complete understanding of the results, see Supplementary material Video 2.

proximity of Stockholm, in Södermanland, and the lake of Vänern, further west. In October, density patches appeared in the Netherlands, eastern France (Lac du Der) and southern Spain (Marismas Guadalquivir), as well as in the north of Spain (Villafáfila) from mid-November. Density patches in Spain and the Netherlands completely disappeared at the end of February. The density patch observed in eastern France was persistent until late March (Fig. 4, Supplementary material Video 3). Interestingly, no density patch from adult breeders captured in Sweden was observed in Norway during the breeding season.

Resighting probabilities for adult breeding birds captured in Denmark also presented a NW/SW pattern (Fig. 5, Supplementary material Video 4). A density patch was observed

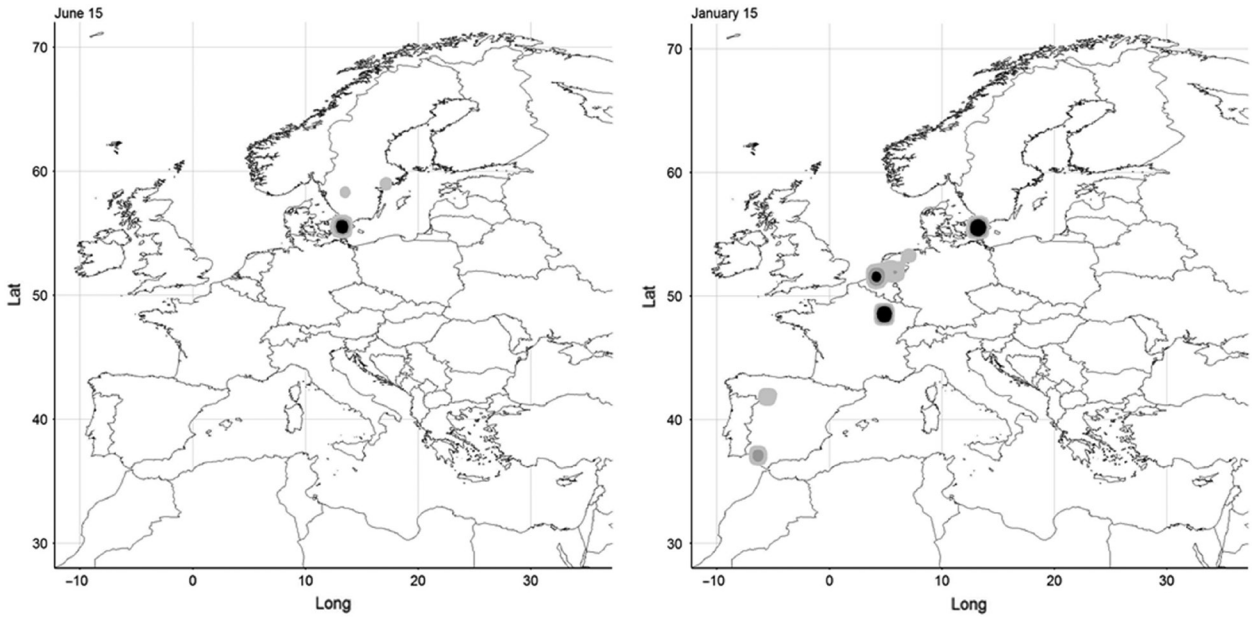

Figure 4. Maps of probability density function of resighting on 15 June (left) and 15 January (right), representing breeding and wintering areas, for adult breeders captured in Sweden, respectively. The black areas correspond to the smallest area, where the probability of resighting a neckband, given that it is resighted at this date, is equal to 0.5. The dark grey areas correspond to the smallest area, where this probability is equal to 0.7. The light grey areas correspond to the smallest area, where this probability is equal to 0.9. For a complete understanding of the results, we strongly recommend viewing the Supplementary material Video 3.

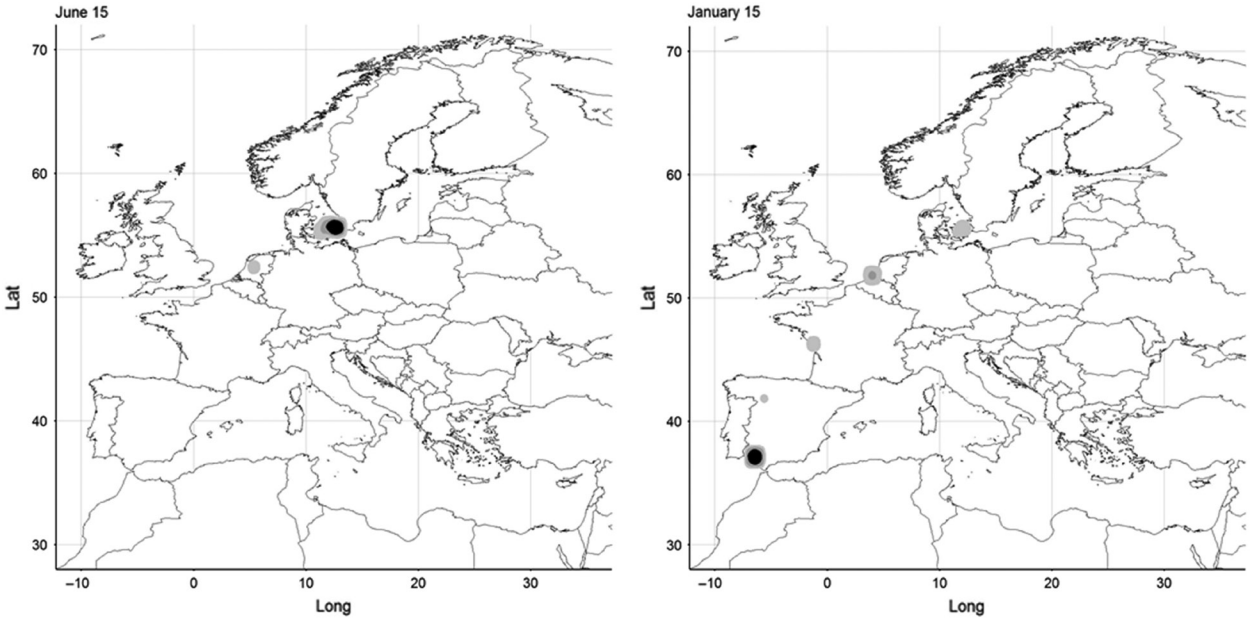

Figure 5. Maps of probability density function of resighting on 15 June (left) and 15 January (right), representing breeding and wintering areas, for adult breeders captured in Denmark, respectively. The black areas correspond to the smallest area, where the probability of resighting a neckband, given that it is resighted at this date, is equal to 0.5. The dark grey areas correspond to the smallest area, where this probability is equal to 0.7. The light grey areas correspond to the smallest area, where this probability is equal to 0.9. For a complete understanding of the results, see Supplementary material Video 4.

in the province of Zealand in Denmark throughout the year, but presented its largest surface area from March to November. Density patches were observed in the Netherlands from early September to July, and also appeared in north-western Germany during the same period. From early October to May a density patch appeared in southern Spain, as well as more sporadic density patches appearing in northern Spain and western France.

For adult breeders captured in the Netherlands, only one large density patch was observed over the Netherlands and overflowing on the surroundings countries (western Germany and northern Belgium). In particular, no resighting density patches were observed for these birds in southern countries (Spain and France). This is further supported by the low proportion of adult breeders captured in the Netherlands and resighted in France (0.4%) or Spain (1.4%) (Fig. 6, Supplementary material Video 5). Yet, 10.2% of the adult breeders captured in the Netherlands were resighted in Germany (Supplementary material Appendix 1).

Finally, density patches from adult breeders captured in north-western Germany remained in the vicinity of the trapping sites (Fig. 1, 7, Supplementary material Video 6). Almost no resightings of north-western German adult breeders were recorded in the other countries of the flyway, with the exception of the Netherlands where 15.3% of the north-western German adult breeders were resighted (Supplementary material Appendix 1).

Discussion

Based on neckband resighting dates and locations, a spatio-temporal analysis using kernel methods allowed infering migratory patterns of greylag geese in the NW/SW European flyway. Beyond a mere distribution map of neckband resighting locations, the kernel method produced a comprehensive representation of the migration movements at the flyway scale.

Migratory patterns

Migration phenology of adult breeders depended on the origin of adult birds, and was very consistent with previous studies conducted at regional scales (Andersson et al. 2001, Voslamber et al. 2010). Adult breeders from Norway, Sweden and Denmark presented spatiotemporal fluctuations of resighting probabilities along the flyway, supporting clear migratory movements (Dingle and Drake 2007). During autumn migration, adult breeders originating from Norway appeared to reach staging sites in the Netherlands earlier than birds from Sweden and Denmark. Conversely, Norwegian birds arrived later at their Spanish wintering grounds than Swedish and Danish birds, which could be explained by longer staging periods of the former birds in the Netherlands (Andersson et al. 2001). As observed by Nilsson et al. (2013), the Lac du Der in eastern France was a significant wintering area only for birds breeding in Sweden. Interestingly, probability densities of resighting Swedish adult breeders remained constant across the year in the south of Sweden. This is concordant with Nilsson and Kampe-Persson (2018) who reported that the number of birds wintering in southern Sweden has markedly increased since 2000. This may be a consequence of changes in migratory habits caused by factors such as changes in agricultural practices and milder winters (short-stopping sensu Elmberg et al. 2014, Nilsson and Kampe-Persson 2018). Conversely, during winter the probability density of resighting Norwegian adult breeders in Norway was depleted. During spring migration, a density

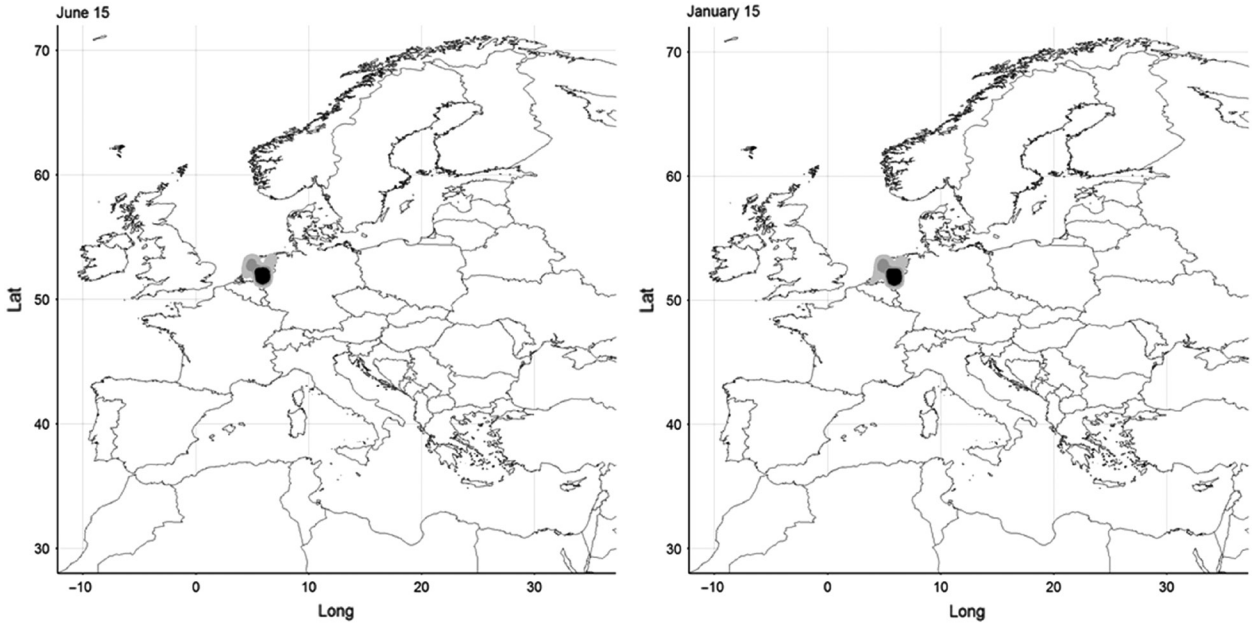

Figure 6. Maps of probability density function of resighting on 15 June (left) and 15 January (right), representing breeding and wintering areas for adult breeders captured in the Netherlands, respectively. The black areas correspond to the smallest area, where the probability of resighting a neckband, given that it is resighted at this date, is equal to 0.5. The dark grey areas correspond to the smallest area, where this probability is equal to 0.7. The light grey areas correspond to the smallest area, where this probability is equal to 0.9. For a complete understanding of the results, see Supplementary material Video 5.

patch from Norwegian birds was observed in western France in February. This is in accordance with Fouquet (1991), who observed extended staging of Norwegian birds in France during spring migration. Swedish birds appeared to leave their wintering grounds in Spain and the Netherlands earlier than adult breeders from Norway. Breeding sites in Norway may provide lower resource availability than the wintering grounds and spring staging sites in the Netherlands, so that breeding birds could prolong their stay in those areas to build-up greater energy reserves (Nilsson et al. 1999). The low resighting probabilities of Norwegian adult breeders in south Sweden may represent prospective and short staging behaviour before going to the breeding grounds in Norway. In accordance with Nilsson and Persson (2001), the results

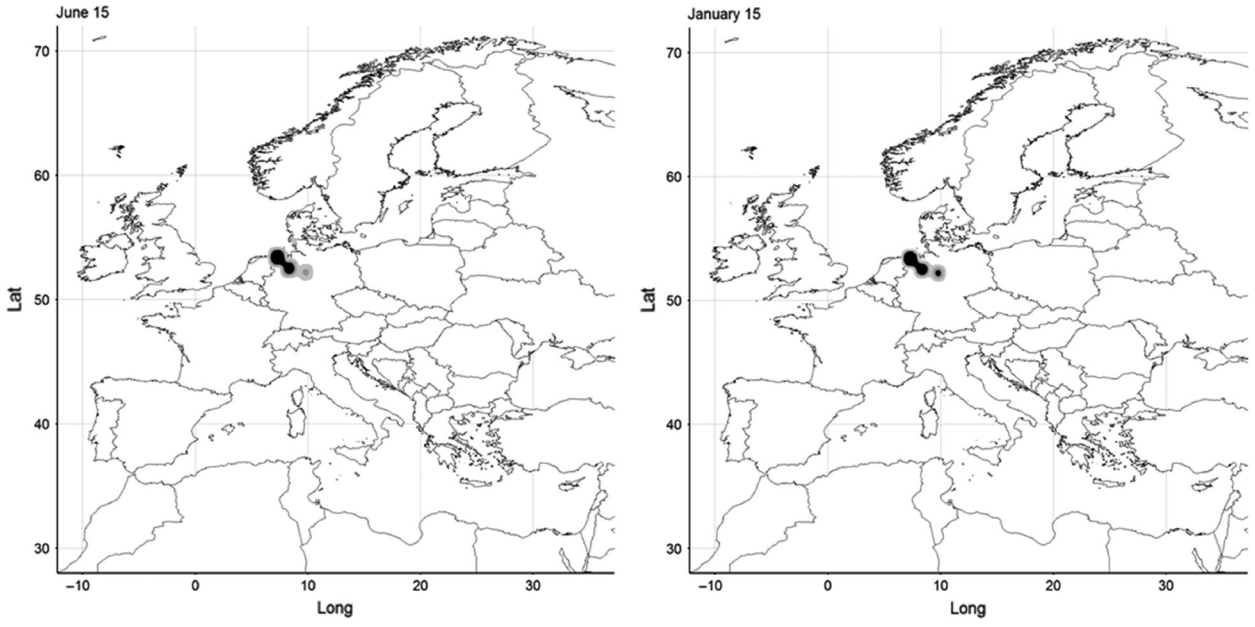

Figure 7. Maps of probability density function of resighting on 15 June (left) and 15 January (right), representing breeding and wintering areas for adult breeders captured in north-western Germany, respectively. The black areas correspond to the smallest area, where the probability of resighting a neckband, given that it is resighted at this date, is equal to 0.5. The dark grey areas correspond to the smallest area, where this probability is equal to 0.7. The light grey areas correspond to the smallest area, where this probability is equal to 0.9. For a complete understanding of the results, see Supplementary material Video 6.

from the kernel methods highlighted a strong philopatry of Norwegian, Swedish and Danish birds to their respective breeding grounds. This observation is further supported by the low proportions of resightings in Sweden for Norwegian breeding birds (2.5%) and resightings in Norway for Swedish breeding birds (0.5%, Supplementary material Appendix 2). In addition, adult breeders from Denmark had low resightings proportions in Norway and Sweden (respectively 2.5 % and 0%). During the breeding period, density patches outside their respective breeding grounds may actually indicate moulting areas (Fox et al. 1995, Andersson et al. 2001). As opposed to the breeding birds from Norway, Sweden and Denmark, adult breeders from the Netherlands did not appear to migrate from their breeding grounds (Voslamber et al. 2010). Long migratory movements were not recorded for adult breeders from north-western Germany either. Conversely, it is known that greylag geese ringed in eastern Germany present migratory movements to the Netherlands and Spain (Heinicke and Köppen 2007). This is in accordance with Bairlein et al. (2014), supporting the idea that breeding populations in eastern Germany may be more migratory compared to those in north-western Germany.

Limits and future prospects

Although we were interested in the probability density that a greylag goose was present at a given place and date, our dataset only allowed representing the probability density that a neckbanded greylag was resighted at a given place and date. Movement analysis from marked individuals commonly has limits set by unequal distribution of ringing and observer effort in space and time (Korner-Nievergelt et al. 2010). Such heterogeneity in space and time may tamper the link between resighting probability and actual probability of presence, and consequently bias comparisons and the interpretation of the results. Yet, our results are strongly supported by ring recovery atlases (Fransson and Pettersson 2001, Bakken et al. 2003, Bønløkke et al. 2006, Nilsson 2017), in which the distribution of ring recoveries closely matches the present results from neckbands resightings. We are therefore confident that kernels from the different breeding grounds provide a correct picture of migratory movements at the flyway scale. However, it is still possible that heterogeneity in ringing effort and monitoring periods will have misrepresented the dynamics especially for countries with few ringed birds (Germany, Denmark). Further research should focus on the observer and ringing effort disparities in space and time. Confronting our results to tracking data from individuals fitted with GPS transmitters may be a first step into detailing this issue. More importantly, no neckbanding data were (made) available from eastern Germany and western Finland. Part of the birds from these regions may present migratory movements along the NW/SW flyway (Andersson et al. 2001, Heinicke and Köppen 2007, Bairlein et al. 2014). Therefore, it appears necessary to intensify ringing effort and to develop further collaborations with German and Finnish ringing programs, in order to overcome these gaps. As our study was conducted at the European level the results may miss local specificities of migratory behaviour (Voslamber et al. 2010). However, as the ambition was to delineate MUs at a transboundary scale, local specificities was not of prime priority. Nevertheless, effective management policies for the flyway will require the combination of local and broad scale interventions (Boyd et al. 2008). It will also require a better understanding and prediction abilities regarding climate change and the effect of agricultural practices on greylag goose wintering strategies, short-stopping and phenology throughout the flyway (Pistorius et al. 2006, Fouquet et al. 2009, Ramo et al. 2015, Nilsson and Kampe-Persson 2018). Ringing studies have shown the migration and dispersal of greylag geese have undergone major changes over the past decades. Swedish breeding birds increasingly remain in Sweden to winter (Nilsson 2013), whereas most breeding birds from the Netherlands nowadays show little dispersal from their breeding sites (Voslamber et al. 2010). Hence, the centre of gravity of the wintering range within the flyway has shifted northwards (Ramo et al. 2015). In addition, variations in wintering strategies may be related to individual characteristics. Kruckenberg and Borbach-Jaene (2004) demonstrated that site fidelity of greylag geese depended greatly on the mating status of the individuals. Clausen et al. (2018) observed some frequent changes in individual wintering strategies between years for pink footed geese *Anser brachyrhynchus*, partly related to sex and age. Thereby, multi-state models (Lebreton and Pradel 2002) are currently being developed to quantify such long-term shifts and individual related variations in wintering strategies (Bacon et al. unpubl.).

Management units

From our current results and previous studies (Andersson et al. 2001, Voslamber et al. 2010), a minimum of three MUs may be delineated at the flyway scale. These management units preferably represent populations that show similarities in their migratory patterns and phenology. Because of the low connectivity between breeding grounds in Norway and Sweden, and the differences in migratory phenology, breeding populations from Norway and Sweden could be delineated as two distinct MUs (MU1 and MU2, respectively). Individuals from these two MUs can be subsequently observed in the Netherlands and neighbouring countries, being used as staging and wintering areas during spring and autumn migration from/to more southern wintering sites (France and Spain, Andersson et al. 2001). At a local scale, Andersson et al. (2001) observed that birds from Sweden and Denmark were using similar staging and wintering areas in the Netherlands and Spain. Birds from Sweden and Denmark are commonly considered as a unique migratory population, the western Baltic population (Nilsson et al. 1999, Andersson et al. 2001), and our results also highlighted their separate arrival on staging and wintering sites from arrival date of Norwegian birds. As such, we suggest integrating the Danish breeding birds within MU2, together with birds breeding in Sweden. Adult breeders from the Netherlands and north-western Germany did not exhibit migratory movements between breeding and wintering sites at the flyway scale, but rather presented short distance movements and moulting dispersal within the two mentioned regions (Voslamber et al. 2010,

H. Kruckenberg unpubl.). Therefore, we considered north-western Germany and the Netherlands as a unique MU (MU3). Because Belgium only presented staging sites of relatively limited importance (Nilsson et al. 1999) and mostly hosts a population originating from reintroductions in the 1950s (Nilsson et al. 1999), Belgium was considered to belong to MU3, together with the Netherlands and north-western Germany. The lack of data from birds breeding in eastern Germany and western Finland limited our capacity to include them in the MUs delineation process. Andersson et al. (2001), Heinicke and Köppen (2007) and Bairlein et al. (2014) highlighted migratory behaviour from individuals ringed in those regions. However, caution should be taken as those regions are actually overlapping the NW/SW and the central flyways (Dick et al. 1999, Andersson et al. 2001, Guillemain et al. unpubl.). Therefore analysis of existing data and further studies are required before assigning these regions to specific MUs. Even if birds from the different units meet during different periods of the year on staging, moulting and wintering areas, such a MU delineation may give the opportunity to apply time specific management actions that will target specific breeding populations. For example, during autumn migration birds from the second MU (Swedish and Danish breeders) arrive in the Netherlands later than bird from the first MU (Norwegian breeders). The timing of potential management procedures in the Netherlands or in France may hence allow targeting birds from one or the other MU, without impacting the others.

This study is a first step into building an international adaptive management action plan for the greylag goose. Fundamentally, it provides a smoother and more dynamic display of data structured in space and time than simple maps of resighting occurrences. As such, it contributes to a clear understanding of the dynamics of the flyway and allows stakeholders and managers implementing proper management actions through space and time. This study produced results to delineate management units based on biological attributes (spatio–temporal distribution). The further process of delineation will require to consider additional attributes, as science alone cannot support management decision. The delineation of management units will have to consider the different threats, conflicts and conservation status (and consequent hunting legislation, Powolny et al. 2018) across the flyway. Also, the number of management units will have to be relevant in the face of administrative burden, attainable management effort and/or objectives. As the delineation of MUs is considered through an adaptive process, future studies and findings will enable refining the definition of such units in order to continuously improve the efficiency of the management plan.

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References

Andersson, A. 1990. Autumn migration of greylag geese *Anser anser* ringed in Gotland. – Baltic Birds 5: 23–27.

Andersson, A. et al. 2001. Migration patterns of Nordic greylag geese *Anser anser*. – Ornis Svecica 11: 19–58.

Bairlein, F. et al. 2014. Atlas des Vogelzugs: Ringfunde Deutscher Brut- und Gastvögel [Atlas of bird migration: ringing recoveries of German breeding and migrating birds].

Bakken, V. et al. 2003. Norsk ringmerkingsatlas. Vol 1. – Stavanger Museum, Stavanger.

Bakker, E. S. et al. 2018. High grazing pressure of geese threatens conservation and restoration of reed belts. – Front. Plant Sci. 9: 1–9. <https://doi.org/10.3389/fpls.2018.01649>.

Bønløkke, J. et al. 2006. The Danish bird migration Atlas. – Forlaget Rhodos and Zoologisk Museum, Københavns Univ.

Boyd, C. et al. 2008. Spatial scale and the conservation of threatened species. – Conserv. Lett. 1: 37–43.

Bradbeer, D. R. et al. 2017. Crowded skies: conflicts between expanding goose populations and aviation safety. – Ambio 46: 290–300.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. – Ecol. Model. 197: 516–519.

Calenge, C. et al. 2010. A new exploratory approach to the study of the spatio-temporal distribution of ring recoveries: the example of teal (*Anas crecca*) ringed in Camargue, southern France. – J. Ornithol. 151: 945–950.

Clausen, K. K. and Madsen, J. 2014. Effects of neckbands on body condition of migratory geese. – J. Ornithol. 155: 951–958.

Clausen, K. K. et al. 2018. Highly dynamic wintering strategies in migratory geese: coping with environmental change. – Global Change Biol. 24: 3214–3225.

Dessborn, L. et al. 2016. Geese as vectors of nitrogen and phosphorus to freshwater systems. – Inland Waters 6: 111–122.

Dick, G. et al. 1999. Greylag goose *Anser anser*: central Europe/north Africa. – In: Madsen, J. et al. (eds), Goose populations of western Palearctic. A review of status and distribution. Wetlands Int. Publ., pp. 202–213.

Dingle, H. and Drake, V. A. 2007. What is migration? – BioScience 57: 113–121.

Ebbinge, B. S. 1991. The impact of hunting on mortality rates and spatial distribution of geese, wintering in the Western Palearctic. – Ardea 79: 197–209.

Eythórsson, E. et al. 2017. Goose management schemes to resolve conflicts with agriculture: theory, practice and effects. – Ambio 46: 231–240.

Elmberg, J. et al. 2014. Interpreting seasonal range shifts in migratory birds: a critical assessment of 'short-stopping' and a suggested terminology. – J. Ornithol. 155: 571–579.

Elmberg, J. et al. 2017. Potential disease transmission from wild geese and swans to livestock, poultry and humans: a review of the scientific literature from a One Health perspective. – Infect. Ecol. Epidemiol. 7: 1300450.

Follestad, A. 1994. Background for a management plan for geese in Norway. – NINA Utredning 65: 1–78, Norwegian with English summary.

Fouquet, M. 1991. Migration et hivernage de l'oie cendrée (*Anser anser*) en France. Rôle et importance du Centre-Ouest. – Oiseau Revue Francaise d'Ornithol. 61: 111–130.

Fouquet, M. H. et al. 2009. Greylag geese *Anser anser* depart earlier in spring: an analysis of goose migration from western France over the years 1980–2005. – Wildfowl 59: 143–151.

Fox, A. D. and Abraham, K. F. 2017. Why geese benefit from the transition from natural vegetation to agriculture. – Ambio 46: 188–197.
Fox, A. D. and Madsen, J. 2017. Threatened species to super-abundance: the unexpected international implications of successful goose conservation. – Ambio 46: 179–187.
Fox, A. D. et al. 1995. Moulting greylag geese *Anser anser* on the Danish island of Saltholm; numbers phenology, status and origins. – Wildfowl 46: 16-30.
Fox, A. D. et al. 2010. Current estimates of goose population sizes in western Europe, a gap analysis and assessment of trends. – Ornis Svecica 20: 115–127.
Fransson, T. and Pettersson, J. 2001. Swedish bird ringing atlas – Volume 1. – Naturehistorika riksmuseet and Sveriges Ornitologiska Förening.
Heinicke, T. and Köppen, U. 2007. Vogelzug in Ostdeutschland I – Wasservögel Teil 1. Berichte Vogelwarte Hiddensee 18, Hiddensee.
Jammalamadaka, S. R. and Sengupta, A. 2001. Topics in circular statistics. – World Scientific.
Keating, K. A. and Cherry, S. 2009. Modelling utilization distributions in space and time. – Ecology 90: 1971–1980.
Koffijberg, K. et al. 2017. Responses of wintering geese to the designation of goose foraging areas in the Netherlands. – Ambio 46: S241–S250.
Kleinhenz, A. and Koenig, A. 2018. Home ranges and movements of resident greylag geese (*Anser anser*) in breeding and winter habitats in Bavaria, south Germany. – PLoS One 13(9): e0202443.
Korner-Nievergelt, F. et al. 2010. Improving the analysis of movement data from marked individuals through explicit estimation of observer heterogeneity. – J. Avian Biol. 41: 8–17.
Kruckenberg, H. and Borbach-Jaene, J. 2004. Do greylag geese (*Anser anser*) use traditional roosts? Site fidelity of colour-marked Nordic greylag geese during spring migration. – J Ornithol. 145: 117–122.
Lebreton, J. D. and Pradel, R. 2002. Multistate recapture models: modelling incomplete individual histories. – J. Appl. Stat. 29: 353–369.
McDonald, T. L. et al. 2003. Tag loss can bias Jolly-Seber capture–recapture estimates. – Wildl. Soc. Bull. 31: 814–822.
Nelson, L. J. et al. 1980. The effect of band loss on estimates of annual survival. – J. Field Ornithol. 51: 30–38.
Nilsson, L. 2013. Censuses of autumn staging and wintering goose populations in Sweden 1977/1978-2011/2012. – Ornis Svecica 23: 3–45.
Nilsson, L. 2017. Migration of greylag geese *Anser anser* according to recoveries of birds marked with traditional leg-rings in Sweden. – Ornis Svecica 27: 132–138.
Nilsson, L. and Kampe-Persson, H. 2018. Changes in migration and wintering patterns of greylag geese *Anser anser* from southernmost Sweden during three decades. – Ornis Svecica 28: 19–38.
Nilsson, L. and Persson, H. 2001. Natal and breeding dispersal in the Baltic greylag goose *Anser anser*. – Wildfowl 52: 21–30.
Nilsson, L. et al. 1999. Greylag goose *Anser anser*: Northwest Europe. – In: Madsen, J. et al. (eds), Goose populations of western Palearctic. A review of status and distribution. Wetlands Int. Publ., pp. 182–201.
Nilsson, L. et al. 2001. Moult and moult migration of greylag geese *Anser anser* from a population in Scania, south Sweden. – Bird Study 48: 129–138.
Nilsson, L. et al. 2013. France as a staging and wintering area for greylag geese *Anser anser*. – Wildfowl 63: 24–39.
Persson, H. 1994. Neck-banding of greylag geese *Anser anser* in Scania, 1984–1993. – Anser 33: 101–106.
Persson, H. 2000. Neck collar retention in a greylag geese *Anser anser* population. – Ornis Svecica 10: 155–160.
Pistorius, P. A. et al. 2006. Temporal changes in spring migration phenology in the Norwegian greylag goose *Anser anser*, 1971–2004. – Wildfowl 56: 23–36.
Powolny, T. et al. (eds) 2018. AEWA International single species management plan for the greylag goose (*Anser anser*) – Northwest/Southwest European population. – AEWA Technical Series, Bonn, Germany.
Ramo, C. et al. 2015. Latitudinal-related variation in wintering population trends of greylag geese (*Anser anser*) along the Atlantic Flyway: a response to climate change? – PLoS One 10: e0140181.
Robertson, G. J. and Cooke, F. 1999. Winter philopatry in migratory Waterfowl. – Auk 116: 20–34.
Silverman, B. W. 1986. Density estimation for statistics and data analysis. – Chapman and Hall.
Stroud, D. A. et al. 2017. Key actions towards the sustainable management of European geese. – Ambio 46: S328–S338.
van den Bergh, L. M. J. 1991. De Grauwe Gans als broedvogel in Nederland. RIN-rapport 91/1. – RIN, Arnhem/Leersum/Texel, in Dutch.
Voslamber, B. et al. 2010. Dutch greylag geese *Anser anser*: migrants or residents? – Ornis Svecica 20: 207–214.
Wand, M. P. and Jones, M. C. 1995. Kernel smoothing. – Chapman and Hall/CRC.
Wetlands International 2015. Waterbird population estimates, 5th edn. Summary report. – Wetlands Int., Wageningen, the Netherlands.

Supplementary material (available online as Appendix wlb-00533 at <www.wildlifebiology.org/Appendix/wlb-00533>). Appendix 1, Video 1–5.