Ornis Svecica

Vol. 28, 2018

Swedish Ornithological Society

Ornis Svecica utges av Sveriges Ornitologiska Förening, Stenhusa gård, 380 62 Mörbylånga.
Ornis Svecaica is published by the Swedish Ornithological Society, Stenhusa gård, 380 62 Mörbylånga.
ISSN 1102-6812

ORNIS SVECICA 28: 3–13, 2018

How many observation days are needed to reliably describe bird migration?

Hur många observationsdagar behövs för att tillförlitligt beskriva fågelflyttning?

ANTTI TANSKANEN, RAUNO A. YRJÖLÄ, ULRIKE BAUM, SAKARI TANSKANEN, JÖRGEN ERIKSSON

Abstract

The total number of migrating birds is needed, for example, to estimate collisions risk as part of the assessment process for wind-power parks. This estimation is often based on a small sample of observation days, making estimates uncertain. To determine the number of days needed to obtain reliable figures we used observations of migrating birds obtained from the Signilskär bird observatory, Åland, Finland during the autumn seasons from 2009 to 2013. We sampled 1–14 days during each 14 day time window and used linear extrapolation and Poisson regression with weather covariates to estimate the total number of migrating birds and distribution of estimates. We calculated the head-wind and side-wind components according to the species' most common flight directions. We found that observations should cover at least 90% of the migration period to obtain precise results and 70–90% to obtain results sufficiently reliable to use in practice. Linear extrapolation is the best model for small samples. The larger the proportion of days observed, the better is Poisson regression with weather covariates.

Antti Tanskanen, Karolinska Institutet, Stockholm, Sweden, Email: antti.tanskanen@ki.se
Rauno A. Yrjölä, Environmental Research Yrjölä Ltd, Klaukkala, Finland, Email: rauno.yrjola@yrjola.fi
Ulrike Baum, University of Turku, Turku, Finland
Sakari Tanskanen, Aalto University, Helsinki, Finland
Jörgen Eriksson, Ålands fågelskyddsförening, Mariehamn, Åland, http://www.fagelskyddsforeningen.ax/

Received 20 December 2017, Accepted 11 June 2018, Editor: Jonas Waldenström

Introduction

The effects of artificial structures such as roads, electric wires and wind turbines on animal populations have been extensively studied. Several investigations have shown that these structures may negatively affect populations (Avery 1979, Coffin 2007, Fahrig & Rytwinski 2009). During recent decades the impacts of wind-power plants on birds, have been widely discussed by ornithologists and conservationists, and a publication compilation and several scientific articles have been written about this subject (Drewitt & Langston 2006, Hüppop et al. 2006, Lucas et al. 2007, Stewart et al. 2007, Krijgsveld et al. 2009, Furness et al. 2013).

Large soaring birds of prey are vulnerable, but other bird species also migrate along coastal routes where power plants are usually installed.

The general problems involved in bird migration studies have been discussed in several summary publications (Alerstam 1982, Baker 1984, Berthold 1993). Estimating the number of migrating birds with conventional observation and sampling methods is not an easy task. Visible migrating birds can be observed and counted fairly well under ideal conditions, i.e. when the migration occurs at low altitudes and the visibility is favourable. However, some bird species migrate during the night or at such high altitudes that observers cannot detect them, and radar or other techniques are needed. The birds' migratory behaviour is also dependent on whether they are long- or short-distance migrants. Many long-distance migrants arrive late in spring, leaving early in autumn and migrate during the night. This applies especially to insectivorous species.

The migration of most species lasts several weeks within a season. Only for a few species, such as cranes, does the migration peak last only a few days when the weather conditions are favourable. With some species, such as many water birds, the migration period can last several weeks, and the weather may significantly affect the intensity and duration of the migration.

To reliably estimate the number of birds throughout the migration period, continuous observation should be used from the beginning to the end of the migration. Usually, this is not possible other than in bird observatories that are occupied continuously. Alternatively, the number of migrants can be estimated by observing birds within certain time periods. How many observation days or hours are needed to obtain reliable estimates of the number of migrating birds and how often the observations should be made during migration to minimize effort and maximize accuracy are questions that have remained unanswered so far. Views on the number of observation days needed have varied widely. A review of wind farm bird studies in North America showed that there is a need to standardize surveying methods; observation times and intervals have varied widely among studies, and the observation effort per land area was usually lower when wind parks were larger (Smallwood 2017).

Conservationists usually call for increased numbers of observation days, while the builders of wind-power parks or other infrastructures prefer fewer observation days to minimize costs. In 2016, the Ministry of the Environment in Finland (Ympäristöministeriö 2016) published a recommendation for the number of observation days needed for the spring and autumn migration periods. The recommendation states a minimum of 30 days of observation during migration periods in southern Finland and 20 days in northern Finland. These recommendations may have been based more on precautionary principles rather than on scientific studies.

Migration data are often collected by volunteer birdwatchers who irregularly visit observation sites, i.e. sites that are known to be the best places for migration observation in the region. Thus, the migration data are sparse and do not always give an overall picture of migration. Additionally, weather conditions and working days during the week may affect observation intensity, and observations during fine weather on weekends may be carried over to weekdays and periods of rough weather. Observation intensity may vary between years, which may make it difficult to detect reliable patterns and timing of migration and number of migrants. Observations may not cover the area that is under investigation, and interpolating local migration intensity from nearby places is problematic.

Environmental Impact Assessment (EIA) legis-

Figure 1. Signilskär is located between Åland and Sweden (map source OSM.org).
Signilskär ligger mellan Åland och Sverige.

lation forces those who perform or plan tasks that may alter the environment to evaluate the possible risks to the environment. One example is wind power, since wind turbines may kill migratory birds, and thus the location and arrangement of turbines are crucial factors that impact collision risks. To evaluate the risks, bird migration density is usually monitored in the area where wind- turbine construction has been planned. This needs a microscale estimation of migration behaviour that is usually not known beforehand. In larger areas, observations are made at several points, and observation is usually done following a predetermined sampling scheme.

Limited knowledge is available on the number of observation days required to obtain an estimate of migratory bird counts throughout the migration season with an acceptable level of certainty. There are no definitions of how accurate migration data should be in EIA studies in Finland, for example. Thus, this acceptable level is dependent on who is asked, i.e. authorities, industry or researchers. One recent study from Massachusetts, using migration data from 1969 to 2012, analysed this problem by addressing the question of how much time was needed to describe the changes detected with observations from 5-day weeks throughout the migration season (Stegman *et al*. 2017). The authors showed that with 60% sampling intensity it was possible to detect the same changes as in all the original data. The aim of this study is to evaluate sample size, sampling and extrapolation methods and how they affected the reliability of estimates. We analysed the observation material collected at the Signilskär bird observatory and attempt to estimate how large the observation sample should be to ensure that it describes the number of migrating birds throughout the season with sufficient reliability. We compare linear extrapolation with modelling migration according to weather conditions. We also investigate whether modelling migration according to weather conditions in a single year can be used for estimating migration in some other year with a sample of migration data from that year.

Materials and methods

Study area

The bird observations were made at the Signilskär bird observatory (60° 11.6’ N, 19° 20.5’ E) (Figure 1). It is the oldest such observatory in Finland and is situated between the Åland Islands (distance 10 km) and the coast of Sweden (30 km). Many bird species that migrate during the day use this route to avoid crossing the open sea, especially during the autumn migration. These species include crows, finches and many birds of prey. Signilskär is fairly small, about 1.7 km long and almost 1 km wide. Several small deciduous woods are found on the island, while other areas comprise mainly various meadow biotopes, open rocks and seashore bushes.

Bird observations

We used records of autumn migration observations from the years 2009 to 2013. The number of observation days varied from 36 (2010) to 51 (2013) (Table 1). In total, the data comprised 226 days, during which 1 408 146 migratory birds were observed. The number of taxonomic units (species, subspecies or wider units such as ʽlarge raptor’) varied from 157 in 2013 to 206 in 2010 (Table 1). The observations began at the earliest on 20 August (in 2010) and ended at the latest on 3 November (in 2013). A day’s observation period began at sunrise and lasted at least 3 hours. Often, this obligatory morning period was extended to 5–6 h, depend-

Table 1. Observation dates, number of birds observed and number of taxa.
Observationsperioder, antal observationsdagar, antal observerade fåglar och antal taxonomiska enheter.

Year	Dates (dd.mm)	Observation days	Total number of birds observed	Number of taxonomic units
2009	19.–25.8. and 19.9.–31.10.	49	134 271	168
2010	28.8.–1.9. and 25.9.–30.10.	36	184 405	206
2011	27.–31.8, 5.–16.9. and 1.–29.10.	46	256 022	173
2012	15.9.–28.10.	44	451 820	166
2013	14.9.–3.11.	51	381 628	157

ing on the migration intensity, i.e. if the migration continued the observation was prolonged. Migrating birds were observed with binoculars and telescopes, and the observations were marked in the field on paper forms. The data recorded included time, species, number of birds, migration direction and distance from the observation point. We used the daily sum of the bird observations per species and, thus, we do not have individual directions of migratory birds or timing of individual birds.

Weather data

Weather data (wind speed and direction, precipitation) were recorded by the Finnish Meteorological Institute's two closest weather stations (see fmi.fi). The wind measurements were taken at the Hammarland Märket lighthouse (60° 18.1' N 19° 7.9' E), 17 km northwest of the Signilskär bird observatory. The predominant wind direction was the southwest, meaning a headwind for most of the autumn migration. We used a 10-min average wind speed and direction at 6:00 (Coordinated Universal Time UTC) in the morning. This selection was made, because we only had daily sums for migration. The daily precipitation (rain) data originated from Jomala Jomalby (60° 10.7'N 19° 59.2' E), 36 km east of Signilskär (Figures 1 and 2).

Modelling migration

Migration data preparation

We distinguished between five groups of species, i.e. all birds, water birds (European Union for Bird Ringing EURING < 2300) (see EURING codes 2000: http://www.euring.org/data-and-codes/euring-codes), nonwater birds (EURING ≥ 2300), crows (EURING 15 600–15 749) and finches (EURING 16 360–16 389). 'All birds' also included unidentified birds that could not be classified in the other groups. We calculated head-wind, tail-wind and side-wind components for each observation (species and day), ignoring the migrating birds' own speed. Therefore, we assumed that land birds passing Signilskär were heading towards the west and other birds (water birds, gulls, waders, auks; EURING code 0–2300 and 4500–6560 towards the

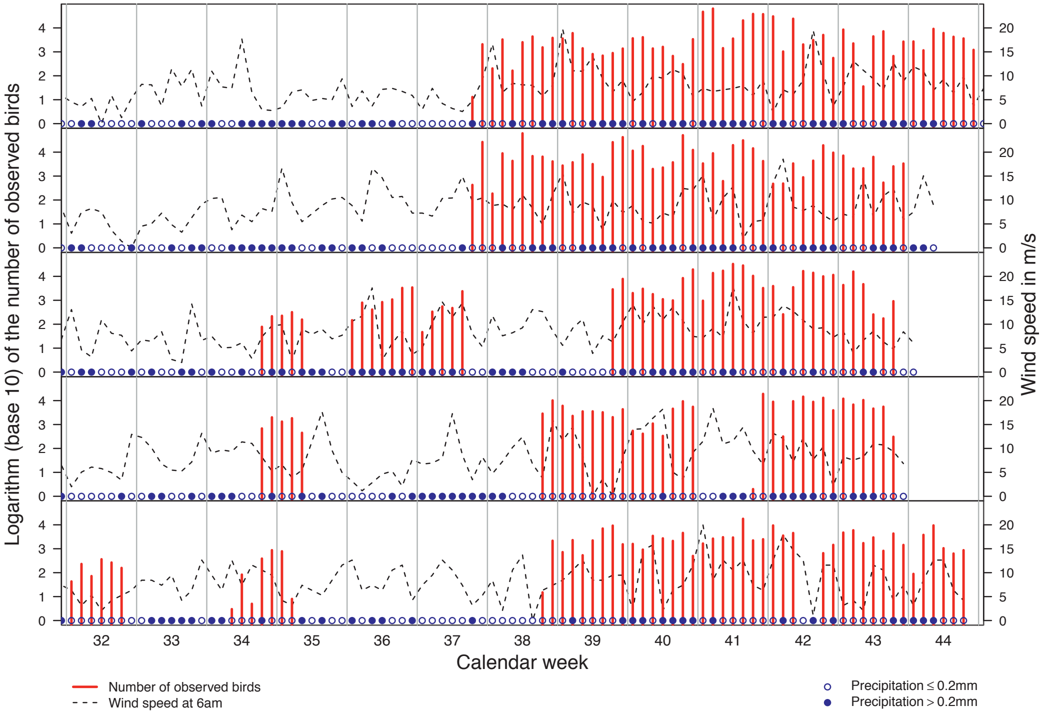


Figure 2. Weather conditions and bird observations 2009–2013 at Signilskär bird observatory.
Väderförhållanden och fågelobservationer 2009–2013 på Signilskär fågelstation.

south. The wind components were categorized into three groups: light (≤ 3 m/s), medium (> 3 m/s and ≤ 9 m/s) and strong wind (> 9 m/s). We used two rain variables, rain on the index day and rain on the previous day, each categorized into two classes, no rain (precipitation ≤ 0.2 mm) and rain (precipitation > 0.2 mm). We grouped the autumn season into 14-day windows, beginning with weeks 35 and 36 in late August and ending with weeks 43 and 44 in early November.

Stratified sampling

To obtain a value that could be interpreted as the total estimate of migration intensity, we selected only those days of a season in which the bird observatory was occupied and migration documented. First, these days were numbered consecutively, independent of their timing, although keeping their order within the season. Subsequently, these days were divided into distinct 14-day windows, beginning with the first 14 days and ending with the last complete set of 14 days. In case the number of observation days in a season was not a multiple of 14, the remaining days not assigned to a time window were not included in the simulation analyses. The 14-day code (35–36 .. 43–44) was assigned to those 14-day periods in which most of the days belonged. Ultimately, we drew either a random or a clustered (continuous days) sample of 1–14 days from each complete set of 14 days. This random sample of days represented the observation days and the others the unobserved days, but here we refer to them as unsampled days, since birds were actually observed. These 14-day periods were selected to ensure coverage of bird observations throughout the season and allow windows of sufficient length to obtain accurate division of time.

Statistical models

To estimate the total number of migrating birds, we used two types of statistical regression model, linear extrapolation and Poisson regression, to model the migration density, depending on weather conditions and calendar time. First, we used linear regression with no explanatory variables. If we denote N_{obs} the observed number of birds and N_{tot} the estimated total number of birds, T_{obs} the observation time and T_{tot} the total time, we obtain equation (1),

$$N_{tot}=\left(T_{tot}/T_{obs}\right) N_{obs}$$

i.e. linear extrapolation over unsampled time. Since we used the same sample size in each 14-day window, this ratio of observation days is constant over the time windows, and the observed number of birds is multiplied by the ratio; e.g. with observations of 3 days from each 14-day window, the multiplier is 14/3 = 4.67. This is the simplest model that extrapolates number of birds over unobserved time.

In our second and third approaches, we used Poisson regression models. Let's denote the logarithm of the number of birds observed (Nlog) and the weather variables of that day (headwind, tailwind, sidewind, rain, rain previous day), then the time in the season on the respective day of interest (14-day calendar time) is WT. The equation is then (2) $Nlog=intercept+\beta'WT$, where intercept is the migration intensity under reference conditions (light wind, no rain, calendar weeks 41–42), β the coefficient vector and WT the binary variable vector (0/1) of each weather and time category. The wind components are also dependent on the birds' assumed flight direction, as described earlier.

In the second approach, we built the Poisson model, based on the data from the sampled days in each simulation, i.e. the regression coefficients may differ between the simulations, depending on the sampled days. The log number of migrating birds on an unsampled day was estimated, using values of regression covariates associated separately for each day's weather conditions and summing up the exponent-transformed results from each day. For example, if 5 days of each 14-day window were sampled, the regression coefficients (weather) were calculated, based on this sample, and these coefficients were used to calculate the estimated migration intensity for the remaining 9 days in each 14-day window. In the third approach, we built the Poisson model, based on the migration and weather data from all observation days for each year separately (Table 3). With these coefficients, we estimated the number of migrating birds in the previous year (estimate in 2009 with coefficients from 2010) and similarly the following year. This was done by fitting the model covariates on unsampled days as in the second approach. Finally, the total number of migratory birds was calculated as the sum of the estimated number of birds on unsampled days and the birds counted on sampled days.

Simulations with the resampling technique

We simulated the effect of shorter observation time with the resampling technique. One simulation consisted of sampling a fixed number of days from each 14-day window, selecting observations of one bird group for these selected days. We applied the models (one of three described earlier) to the

Table 2. Number of days needed for sampling from a 14-day time window to yield 95% of the simulated migration estimates with 10%, 30% and 50% marginal error of the total number of migrating birds observed. The underlying statistical models were a) random selection of days and linear extrapolation, b) selection of clustered, continuous days and linear extrapolation, c) random selection of days and Poisson regression with weather covariates based on the days selected.
Antal stickprovsdagar som behövs ur ett fjortondagarsfönster för att nå 95% av den simulerade skattningen med 10%, 30% och 50% marginalfel för totala antalet observerade fåglar. Underliggande modeller var a) slumpvis valda dagar och linjär extrapolering, b) sammanhängande dagar och linjär extrapolering, c) slumpvis valda dagar och Poisson-regression med vädervariabler.

Original data		Observation days needed in 14-day windows within different error limits and 95 % of simulations within limits		
Species group	Individuals observed	10% error a/b/c	30% error a/b/c	50% error a/b/c
All birds	1 305 428	14 / 14 / 14	9 / 11 / 11	6 / 8 / 9
Water birds	136 894	14 / 14 / 14	10 / 10 / 12	7 / 8 / 11
Nonwater birds	1 162 298	14 / 14 / 14	10 / 11/ 11	6 / 8 / 11
Crows	519 977	14 / 14 / 14	11 / 14 / 13	9 / 12 / 12
Finches	236 205	14 / 13 / 14	14 / 11 / 14	11 / 10 / 13

unsampled days to estimate the number of migratory birds for unsampled days. This was repeated 10 000 times to ensure a covering set of different days to be in the simulation. In all, we repeated the sampling and modelling steps 22.4 million times, i.e. we ran 10 000 simulations for each year, combination of species group, number of days selected from a 14-day-window, sampling strategy and statistical model. The median of these 10 000 simulated estimates was interpreted as the estimate of the total number of migratory birds.

Finally, we calculated the number of days needed to observe in each 14-day window to obtain an estimate that deviated less than 10%, 30% and 50% from the observed total number of migrating birds with 95% probability. This was calculated from all

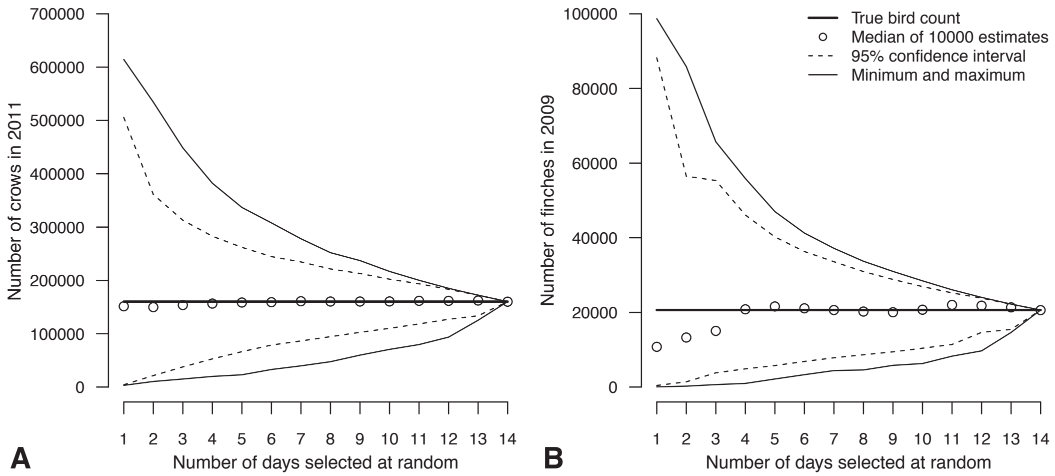


Figure 3. Results from simulating 140 000 stratified random samples estimating the migration of (A) crows (Hooded Crow *Corvus corone cornix* L., Eurasian Jackdaw *C. monedula* L., Rook *C. frugilegus* L. and *C.* L. sp.) in 2011 and (B) finches (Chaffinch *Fringilla coelebs* L., Brambling *F. montifringilla* L. and *F.* L. sp.) in 2009 based on linear extrapolation.
Resultat från simulering av 140 000 slumpvisa stickprov för skattning av flyttningen av (A) kråkfåglar (gråkråka, kaja, råka och obestämda) 2011 samt (B) finkfåglar (bofink, bergfink och obestämda) 2009 med linjär extrapolering.

Table 3. Exponent-transformed Poisson model coefficients for the years 2009–2013 and all birds combined. Reference categories (with value 1) are light winds, no rain and 14 days covering weeks 41–42. NA indicates the absence of observations.
Exponenttransformerade koefficienter från Poisson-modell för åren 2009–2013 och med alla fåglar kombinerade. Referenser med värde 1 är svag vind, inget regn och 14 dagar veckorna 41–42. NA anger avsaknad av observationer.

Covariates	2009	2010	2011	2012	2013
Intercept	2114.1	2411.2	7553.5	8570.1	6734.5
medium headwind	1.99	2.17	1.95	0.96	1.33
medium tailwind	0.96	0.95	0.28	0.69	0.31
strong headwind	0.93	0.3	0.12	2.4	0.05
strong tailwind	0.82	1.2	0.49	0.25	0.66
rain index day	0.77	1.18	0.77	0.45	1.43
rain previous day	0.38	1.2	0.85	0.75	0.45
medium sidewind	0.91	1.07	0.59	1.59	2.89
strong sidewind	1.74	0.82	0.97	0.87	1.09
Weeks 35-36	0.1	0.21	0.04	NA	NA
Weeks 37-38	0.27	NA	0.13	0.92	0.09
Weeks 39-40	0.8	1.29	0.83	1.33	0.13
Weeks 43-44	0.77	1.18	0.65	0.32	0.25

5 years, 10 000 simulations each year, and 95% of these amounted to 47 500 simulation estimates. We calculated the minimum number of days needed to obtain estimates that were within the ± 10%, 30% and 50% boundaries from the observed number of migratory birds in the corresponding year to fulfil this cumulative 95% probability over all 5 years.

Results

Table 2 presents the number of days needed to achieve estimates within a 10%, 30% and 50% marginal error of the total number of migrating birds observed in 95% of the simulations. In practice, all days must be sampled to achieve results within the 10% marginal error. In tolerating a higher marginal error of up to 50%, only 50–70% of the days are needed, depending on the bird species. When linear extrapolation was used, random selection of days was more efficient than selection of clustered, continuous days. The species group of finches formed an exception, because selecting continuous days appeared to be more efficient than selecting days randomly. Moreover, linear extrapolation required fewer observation days to generate a result within a particular error margin than a Poisson model, which utilised the migration year's weather data, except for the crow taxa. For crows, the Poisson model performed slightly better than linear extrapolation, based on clustered days, although the linear extrapolation based on randomly selected days best predicted the number of migrating birds.

Figure 3 depicts how the variation in the results based on linear extrapolation converges fairly smoothly. After 4–5 out of 14 days, the estimate improved constantly with each additional day.

In modelling migration based on the weather data from the observation days themselves, the Poisson model used in the second approach performed poorly when only a few days were selected (Figure 4). To achieve reliable estimates, more than half of the 14 days must be sampled. However, when almost all days were sampled, this method was more accurate than linear extrapolation.

Table 3 shows the regression coefficients yielded by Poisson regression analyses in modelling migration, given the weather data for each year from 2009 to 2013 (third approach). The general picture suggests that medium headwinds were associated with higher numbers of migrating birds than those observed on a standard day, while the other wind conditions were associated with lower numbers of migratory birds, for most years. The variation between years was wide. For example, while the strong head-wind exponent-transformed coefficient in 2012 was estimated at 2.4, it was estimated at 0.05 for the following year. Furthermore, the numbers of migratory birds observed were lower during the early weeks of each season, with the exponent-transformed regression coefficients remarkably smaller than 1.

Figures 5A and 5B illustrate how the Poisson model performs for one year's (2010, 2011) migration, given the weather regression coefficients of another year (2011, 2010, respectively). The median of 10 000 simulated migration counts fitted fairly well to the actual total migrating bird count observed, irrespective of the number of observation days. However, the variation converged very slowly. Figures 5C and 5D were created, using weather data of 2009 to model the migration in 2010 and vice versa. Although the migratory bird counts on a 'standard day' in 2009 and 2010 were estimated to be similar and the regression coefficients were similar (Table 3), the model either severely underestimated (Figure 5C) or overestimated (Figure 5D) the migratory bird counts.

Discussion

We showed that to obtain very precise results with 95% probability from bird migration, almost all days are needed for observation during the migration season. However, if more error is allowed, a lower number of days may be needed. If an error level of ± 50% of the observed number of migratory birds is accepted, the observation should cover at least 50% of the days to estimate the total number of all species. If the target is to estimate the migratory bird counts for certain species for which the migration time window is known, observation can be focused on that time. For example, if we are interested in migration of golden eagles (*Aquila chrysaetos* (L.)) in Åland, we need to make observations during their migration period from mid-September to November. The more specific question we ask and the smaller number of individuals we target introduce further randomness and uncertainty. For example, single species such as the common crane (*Grus grus* (L.)) may undergo very concentrated peak migration that varies over the years. Thus, it may be difficult to estimate how many days are needed for accurate counts and how to schedule this effort. This was shown in our results, where the same accuracy for the migratory sums of all species needed 15–20% less time than for crows and 30–40% less than for finches. When we summed up the counts for all species, these daily sums were much more evenly distributed throughout the migration season than for single species or species groups. To model single species migration and extrapolate over unobserved time there usually are several days with zero numbers of migratory birds in the daily observation data. For these types of data, zero-inflated Poisson regression or a negative binomial model could be more precise than Poisson regression.

If we assume a migration season of 3 months from mid-August to mid-November, it contains eight 14-day periods. This yields approximately 45 days of observation required to expect an estimate to be within the 50% error margin and 60 days for the 30% error margin of the numbers of migrating birds observed. If consecutive days are used, approximately 20% more days are needed. One consecutive period may save travelling time and cost compared with separate days.

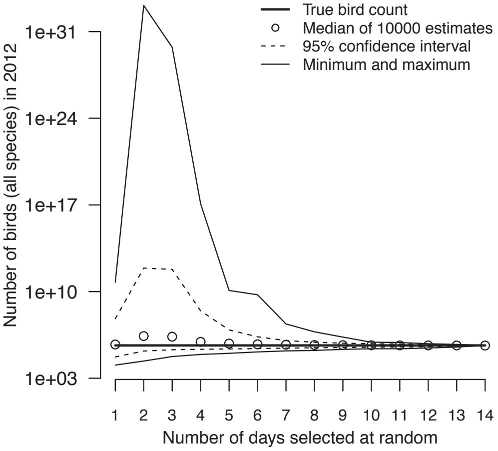


Figure 4. Results from simulating 140 000 stratified random samples estimating the number of migrating birds (all species) in 2012, based on Poisson regression models fitted to the observation day data.
Resultat från simulering med 140 000 slumpvisa stickprov för skattning av antalet flyttande fåglar av alla arter år 2012, baserat på Poisson-regression för observationsdata.

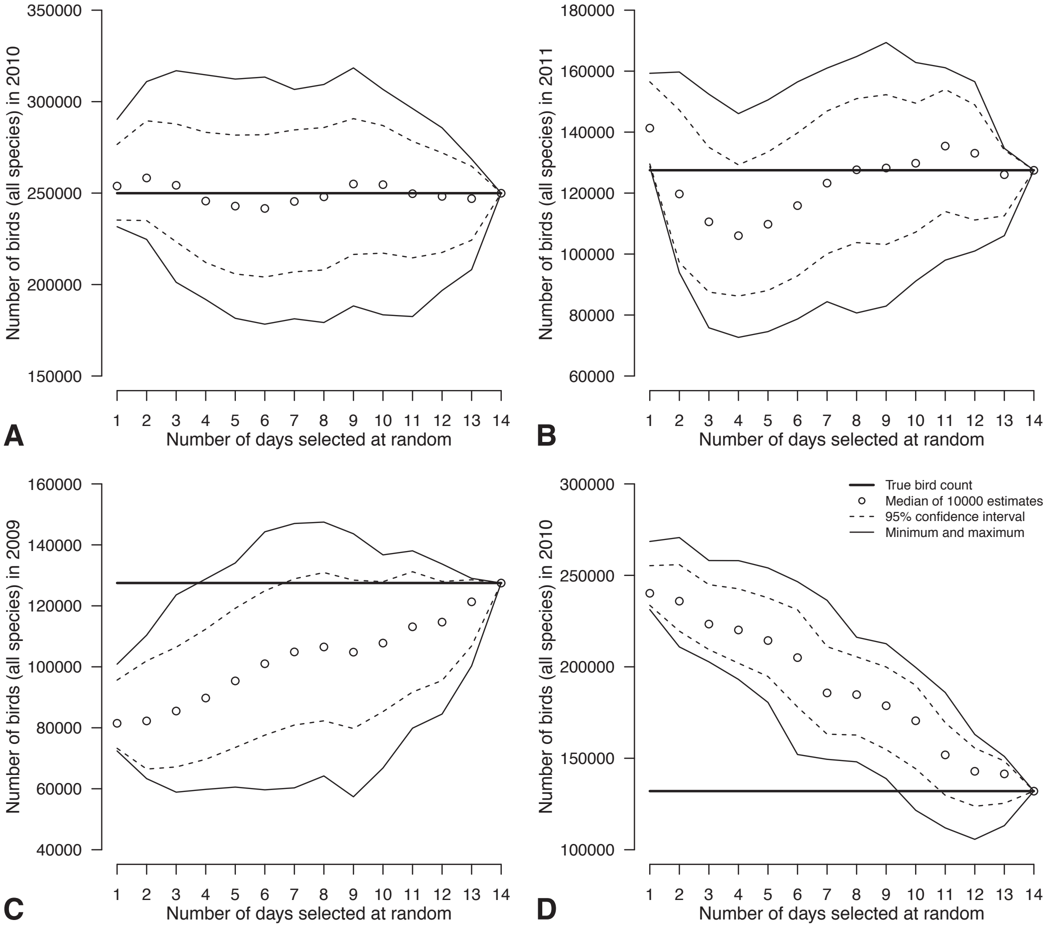


Figure 5. Results from simulating 140 000 stratified random samples estimating the number of migrating birds (all species) in (A) 2010, (B) 2011, (C) 2009 and (D) 2010, based on Poisson regression models fitted to the migration data of (A) 2011, (B) 2010, (C) 2010 and (D) 2009.
Resultat från simulering med 140 000 slumpvisa stickprov för skattning av antal flyttande fåglar av alla arter år (A) 2010, (B) 2011, (C) 2009 och (D) 2010 i förhållande till observationsdata åren (A) 2011, (B) 2010, (C) 2010 och (D) 2009.

This study shows how unreliable observations of less than 50% of the time are. If reliable estimates of migratory bird numbers are needed, e.g. in EIA studies, potential migration time must be focused on intensely. This includes not only days, but also time within days. In this study, we did not focus on how many hours per day are needed, but the same principles apply. If observation is only during early morning, individual species or some of all species may be missed. Timing during the day should also be randomized to some extent, so that migration densities during the day can be estimated. In our data, the daily observation time varied and may have resulted in increased variation in the daily sums of different birds. This was due to the nature of the data. An ordinary compulsory morning session lasts three hours, but if the migration is lively, volunteers may continue to observe longer and more often than when migration is weak.

Linear extrapolation with randomly selected days yielded the best results of the methods tested. Only estimating finch migration numbers by observing continuously over several days was better. This may have been due to the uneven distribution of migrating finches within the 14-day window, since these species showed better matching to total migrating bird numbers than did even the probability for each day. The Poisson model from the observed data and weather data yielded very accurate results when almost all days were sampled in most simulations. In some simulations, the estimated number of migratory birds deviated strongly from the observed number when the observation days' weather and number of migratory birds did not match with those estimated, e.g. when the observation days were rainy and showed lively migration, while the remaining (unsampled) rainy days showed low migration intensity. In this case, the coefficient for the rainy days was overestimated in the model. In the third approach, weather covariate values, the coefficients modelled from the sampled days could be made for different species or species groups separately. Modelling migration for raptors and waterfowl may result in very different parameters, and combining these two or all species may produce incompatible parameters. In our example, modelling the migration of crows with weather conditions showed better fit than for finches.

We used stratified sampling with 14-day windows and equal numbers of days in each time window. The excess effort spent on days with low number of migratory may be counterproductive. Thus, more efficient results could be achieved with a sampling strategy in which more observation days are included in periods during which target species are observed in abundance. Using time windows for selecting observation days is crucial. It ensures that observations are made throughout the season and thus for all species of interest, but results in slight underestimation of migrating bird numbers, which is due to the time distribution of migration. Many birds migrate in a fairly short period, and forced observation from days of zero migration is probably the reason for this underestimation.

Linear extrapolation is a useful method when observations cover only a small portion of the entire migration season. When a larger portion of the season is covered, predicting migrating bird numbers from observations with weather data will become preferable. The advantage in modelling migrating bird numbers, using weather data, is that collecting local weather data is inexpensive with automated weather stations. The methods we used are examples of modelling, while others such as the log-linear regression model (van Belle *et al*. 2007) may use weather data for better estimation of the number of migratory birds and thus may reduce the number of days needed to accurately compare the methods presented here.

The impact of weather clearly varied over the years. This was at least partly dependent on some weather conditions being rarer in some years than in others. For example, if there is only one day of heavy headwind in a certain year and long periods during another year, then migratory birds can easily avoid this single day compared with the long periods. This was clearly seen in 2012, where strong migration with strong headwinds was observed and no migration with medium headwinds, in contrast to all other years.

The response to weather conditions varied between bird species. Thus, a more effective way of modelling would be to divide birds into groups sufficiently large to show similar responses to wind and rain conditions. This could be done with a separate data-mining procedure to find meaningful taxonomic groups or expert evaluation by migration observers. For most species, the number of birds observed was too small and sparse over time for weather-modelling purposes. In this study, we used weather modelling separately for crows and finches. Weather conditions may reroute migration or change its altitude. In the Signilskär area, tail-wind conditions with good visibility forced pigeons (*Columba* sp. L.) and Eurasian jackdaws (*Corvus monedula* L.) to migrate at high altitudes directly over the Sea of Åland south of Signilskär, making flocks invisible to observers on the island, but visible at Eckerö on the mainland before taking height and crossing the Sea of Åland. Many raptors use thermal-convection flows and select their routes accordingly. The relatively high migration intensity observed under head-wind conditions is thus somewhat biased, because the birds fly low at sea level, using islands when crossing the Sea of Åland. This increases the probability of an observer recording them compared with birds flying high over the open sea. When the purpose of observation is to record the number of migrating birds in a certain area, a single year's observations may not reflect the average year's numbers, and the same effort could be made more efficient when scheduled over several years instead of one.

Conclusions

To yield reliable estimates of how many birds migrated during a time period, one must observe and count the number of migrating birds on at least half of the days. Linear extrapolation results in good estimates of the total numbers when the estimation is based on only a small proportion of the total number of observation days. The larger the proportion of days covered, the better the models with weather covariates perform.

Acknowledgements

We thank all volunteer birdwatchers, especially Ari Lehtinen and Jari Helstola for their valuable work. This study would not have been possible without their effort. We also thank two reviewers for their excellent comments and James Thompson for English proofreading.

Literature Cited

Alerstam, T. 1982. *Fågelflyttning*. Bokförlaget Signum. Lund. 295pp

Baker, R.R. 1984. *Bird navigation: the solution of a mystery?* Hodder & Soughton ltd. London. 256pp.

Van Belle, J., Shamoun-Baranes, J., van Loon, E. & Bouten, V. 2007. An operational model predicting autumn bird migration intensities for flight safety *Journal of Applied Ecology* 44, 864–874 doi: 10.1111/j.1365-2664.2007.01322.x

Berthold, P. 1993. *Bird migration. A general survey*. Oxford University Press. Oxford. 239pp.

Avery, M.L. 1979. Review of avian mortality due to collision with manmade structures. *Bird Control Seminars Proceedings. Paper 2.*

Coffin, A.W. 2007: From roadkill to road ecology: A review of the ecological effects of roads. Journal of Transport Geography 15: 396–406.

Drewitt, A.L. & Langston, R.H. 2006. Assessing the impacts of wind farms on birds. Ibis 148: 29–42.

Fahrig, L. & Rytwinski, T. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society 14: 1–20.

Furness, R.W., Wade, H.M. & Masden, E.A. 2013. Assessing vulnerability of marine bird populations to offshore wind farms. Journal of Environmental Management 119: 56–66.

Hüppop, O., Dierschke, J., Exo, K.-M., Fredrich, E. & Hill, R. 2006. Bird migration studies and potential collision risk with offshore wind turbines. Ibis 148: 90–109.

Krijgsveld, K.L., Akerhoek, K., Schenk, F., Dijk, F. & Dirksen, S. 2009. Collision risk of birds with modern large wind turbines. Ardea 97: 357–366.

Lucas, M. de, Janss, G.F., Ferrer, M. & eds. 2007. Birds and wind farms. Risk assessment and mitigation. Quercus.

Smallwood, K.S. 2017. Monitoring birds. In: Perrow, M.R. (ed.) Wildlife and Wind Farms, Conflicts and Solutions. Volume 2, Onshore: Monitoring and Mitigations. Conservation Handbooks, Pelagic Publishing, Exeter, UK.

Stegman, L.S., Primarck, R.B., Gallinat, A.S., Loyd-Evans, G.T., & Ellwood, E.R. 2017. Reduced sampling frequency can still detect changes in abundance and phenology of migratory landbirds. *Biological Conservation* 210(April): 107–115. Available at: http://dx.doi.org/10.1016/j.biocon.2017.04.004.

Stewart, G.B., Pullin, A.S. & Coles, C.F. 2007. Poor evidence-base for assessment of windfarm impacts on birds. *Environmental Conservation* 34:1.

Ympäristöministeriö 2016. Linnustovaikutusten arviointi tuulivoimarakentamisessa. *Suomen ympäristö* 6/2016, in Finnish http://urn.fi/URN:ISBN:978-952-11-4624-4.

Sammanfattning

Vid miljökonsekvensbedömning av t.ex. planerad etablering av vindkraftverk behövs vanligtvis en utvärdering av risken att fåglar kolliderar med verken. För detta behövs en uppskattning av antalet fåglar som passerar området. Denna utvärdering utgörs vanligtvis av ett stickprov av tiden, till exempel delar av höstflyttningsperioden. Ett problem i sammanhanget är att det är svårt att veta hur stora stickprov som bör tas för att osäkerheten i uppskattningen skall hamna på en rimligt låg nivå. I denna studie simulerar vi hur många observationsdagar det behövs för att uppnå olika säkerhetsnivåer i beskrivning av höststräcket av fåglar och jämför olika metoder med flyttningsobservationer från Signilskärs fågelstation, Åland, Finland, från höstarna 2009 till 2013.

Hösten delades i tvåveckorsperioder och vi simulerade stickprovsförfarande med från en till 14 dagar av varje period. Proven togs antingen som enstaka dagar eller som en period av succesiva dagar. Vi använde linjär extrapolation och Poisson-regression med väderobservationer som kovariat. Vi kalkylerade mot- och sidovindskomponenter för flyttfåglar enligt den vanligaste flygriktning som används i vädermodellen.

Resultaten visar att för en relativt noggrann uppskattning behövs sträcket räknas cirka 90% av tiden, och för resultat som avviker högst 30% från det verkliga antalet observerade flyttfåglar behövs det 70% till 90% av tiden räknas. Den bästa modellmetoden är linjär extrapolering då proven är under 50% av tiden och Poisson-vädermodellen då tiden är över 50% av den totala tiden. Som en tumregel ger 50% av totaltiden en felmarginal på 50% och 70% av tiden en felmarginal på 30%. Det är därför bättre att sprida ut samma antal observations dagar på flera år (säsonger) i stället för under en säsong, då det är stor variation mellan åren.

ORNIS SVECICA 28: 14–18, 2018

Flock-fishing deep-diving piscivores (Great Crested Grebe *Podiceps cristatus*, Great Cormorant *Phalacrocorax carbo*, Common Merganser *Mergus merganser*) at Lake Vombsjön, southern Sweden, and those that exploit them

Flockfiskande och djupdykande fiskätare (skäggdopping Podiceps cristatus, *storskarv* Phalacrocorax carbo, *storskrak* Mergus merganser) *i Vombsjön, Sydsverige, och de som utnyttjar dem*

HANS KÄLLANDER

Abstract

Lake Vombsjön in southern Sweden is visited by large numbers of Great Crested Grebes *Podiceps cristatus* (>2000), Great Cormorants *Phalacrocorax carbo* (sometimes >1000) and Common Mergansers *Mergus merganser* (up to 2000) in late autumn and early winter. Different species exploit them. Great Crested Grebes are used especially by commensal Common Gulls *Larus canus*; the gulls take advantage of fish that flee towards the surface. Common Gulls also use cormorants and mergansers in the same way but also try to kleptoparasitize them. Both Herring Gulls *Larus argentatus* and Great Black-backed Gulls *Larus marinus* kleptoparasitize these two species, while Red Kites *Milvus milvus*, Grey Herons *Ardea cinerea* and Carrion Crows *Corvus corone* use them commensally. White-tailed Eagles *Haliaeetus albicilla* seem to use both methods to obtain fish. On 50% of one hundred visits during November to March, eagles were seen flying low over the fishing flocks. They would fly a metre or so above the flocks and then accelerate and attack a bird holding a fish. The bird would then either try to escape by a rush or by diving, dropping the fish which the eagle seized. Interestingly, the flock-fishing birds showed no fear reactions towards the eagles but appeared to regard them similarly to large gulls.

Hans Källander, Villavägen 6, 241 65 Harlösa, Sweden.
E-mail: hans.kallander@telia.com

Received 12 March 2018, Accepted 13 June 2018, Editor: Dennis Hasselquist

In late autumn and early winter, large numbers of Great Crested Grebes *Podiceps cristatus*, Great Cormorants *Phalacrocorax carbo* and Common Mergansers *Mergus merganser* visit the 12 km^2 large Lake Vombsjön in southern Sweden. Great Crested Grebes often reach high numbers already in October, but usually peak in November when sometimes more than 2000 individuals may be present at the lake. Cormorants are present year-round, but numbers are usually highest in November–December. Being rather variable, these numbers often are around 800 individuals but have occasionally been well above a thousand. Common Mergansers, finally, seem to arrive at somewhat varying times during autumn, probably depending on the timing of ice formation on lakes further to the north. Sometimes a fishing flock of more than 2000 has been recorded. All three species are exploited by several other bird species that try to obtain a share of the fish these species capture or make accessible. Here I will briefly describe these species and their methods to obtain fish. The data on which this note is based were mainly collected during 2004 to 2017. Often observations were directly talked into a tape recorder and later transcribed.

Study site

Lake Vombsjön has a maximum depth of c.15 m, 13% are more than 10 m deep, and 55% are between 5 and 10 m deep while 30% are less than 5 m deep. The lake has a rich fish fauna with perch *Perca fluviatilis*, roach *Rutilus rutilus*, bream *Abramis brama*, björkna *Blicca blicca*, rudd *Scardinius erythrophthalmus*, ruffe *Gymnocephalus cernua*, bleak *Alburnus lucidus* and others. Since 1948 the lake is regulated and is acting as a water reservoir for Malmö, Lund and several other cities. The shores are rather low and covered with deciduous trees except in the south where the shores are steeper and border to a large pine plantation, Vombs Fure. Suitable observation points exist both in the west (including a bird observation tower) and in the north-east (Öveds badstrand) and east. There are embankments along the shore from south-east to north-east, and in north and west.

The hosts and their exploiters

Great Crested Grebe, Common Gull, Black-headed Gull and Herring Gull

Great Crested Grebes were used predominantly by Common Gulls *Larus canus* that circled above fishing grebes, in particular over denser aggregations, and plunge-dived among the grebes. This association with the grebes may be entirely commensal, the gulls looking for small fish that have fled towards the surface in response to the diving activities of the grebes. Attempts at stealing fish held in the grebe's bill were observed occasionally but so far only two successful attacks were recorded despite more than 50 days of observation. This does not preclude that kleptoparasitism could have occurred more often than the observations suggest – distances were often quite long and details difficult to see. What speaks against kleptoparasitism, however, is the observation that dense flocks of Common Gulls occasionally were seen hovering and diving towards the water surface well away from any grebes, which suggests that they had located a shoal of small fish without the aid of grebes. Sometimes it seemed as if Common Gulls saw the grebes through the water and dived towards them when they were surfacing, but in no case did this result in the gull obtaining the fish. Black-headed Gulls *Croicocephalus ridibundus* also sometimes circled together with Common Gulls above fishing flocks of grebes, and on eight occasions Herring Gulls *Larus argentatus* were seen associated with fishing Great Crested Grebes. In contrast to Common and Black-headed Gulls, Herring Gulls were sitting on the water intently watching surfacing grebes. On six occasions they attacked a grebe that surfaced with a fish in its bill, but every time the grebe dived instantly so all kleptoparasitic attempts by Herring Gulls were unsuccessful.

Great Cormorant, Common Merganser and the large gulls

Great Cormorants and Common Mergansers share many features in common and are treated together here even though they usually formed monospecific flocks. However, successful dives, signalled by either fish in the bill of a surfacing piscivore or by violent attempts at intraspecific kleptoparasitism often acted as an impetus for the other species to join and form a mixed feeding flock. Sometimes a flock of Common Gulls or Black-headed Gulls hovered over mergansers or cormorants, especially in early autumn, apparently trying to kleptoparasitize them (once a Common Gull managed to steal a fish from a merganser and also negative attacks on cormorants were seen). In winter, these small gulls were usually less common and both mergansers and cormorants mostly had Herring Gulls and Great Black-backed Gulls *Larus marinus* associated with them, the former often being up to ten times more numerous than the latter. These large gulls either circled over the fishing flocks or swam among the diving mergansers or cormorants in an alert posture. Sometimes Great Black-backed Gulls attempted to monopolize fishing flocks by driving away other Black-backs (but usually not Herring Gulls). Cormorants or mergansers surfacing with fish, especially big ones, regularly resulted in kleptoparasitic attacks by Herring and Great Black-backed Gulls and often also by both conspecifics and the other species of diving piscivore. These attacks often led to a turmoil when the attacked bird tried to evade the attacks. Sometimes the fish wandered from one kleptoparasite to another. Quite often when a Herring Gull had stolen a fish and flew off to eat it undisturbed, it was immediately attacked in the air by a Great Black-backed Gull and often lost it. Sometimes there was a tug of war between, usually, a cormorant and a gull with the cormorant sometimes managing to keep its fish. The large gulls sometimes seemed reluctant to attack a cormorant with fish. This is understandable because on numerous occasions cormorants were seen trying to bite gulls that came too near. Nonetheless, kleptoparasitism no doubt was a very important feeding method of the two large species of gull. However, distances were often too long to establish how successful the gulls were at stealing from the two species (cf. Källander 2006).

One of the interesting things to observe in these feeding flocks was how the different species used cues unintentionally given away that indicated their foraging success. Thus, when one or more individuals at either end of the flock surfaced with big fish, other birds immediately flew there and dived (or in case of the gulls, tried to kleptoparasitize). This constant surveying of the fishing success of others was very common among all parties involved (also see under White-tailed Eagle below).

Grey Heron and the fishing flocks

A few times Grey Herons *Ardea cinerea* flew out to a fishing flock and circled above it. Once the heron even landed on the water and stayed there for quite some time intently watching the fishing success of the flock. At other lakes I have several times seen both Grey Herons and Great White Herons *A. alba* associating with flock-fishing Great Cormorants. At Lake Krankesjön, for instance, both species of heron associated with cormorants fishing in shallow water and they even seemed to be able to predict where swimming cormorants would reach vegetation where the herons could settle. These observations are interesting mostly from the question how herons can know that cormorants indicate increased fish availability. Have they seen cormorants surface with fish in the bill and learnt to associate them with fish shoals?

Red Kite and the fishing flocks

Red Kites also appeared above the fishing flocks, usually flying rather high monitoring the flock below. A number of times, they stooped from considerable height and either picked up a small fish or interrupted the stoop. The relatively few times that they obtained fish, it was just picked up close to the flock and appeared to have nothing to do with kleptoparasitism.

White-tailed Eagle and the fishing flocks

The most impressive use of the flock-feeding piscivores involved White-tailed Eagles *Haliaeetus albicilla.* Kleptoparasitism is a well-known feeding metod in the genus *Haliaeetus* and has been studied especially in Bald Eagles *H. leucocephalus* (Grubb 1971, Fischer 1985, Jorde & Lingle 1988, Bennetts et al. 1990, Brown 1993). On nearly 50% of about one hundred visits to Lake Vombsjön during November to March, White-tailed Eagles were seen using the fishing flocks of cormorants and mergansers as an aid to obtain fish. The eagles usually circled low over the flock, in windy weather conditions mostly flying against the wind until they reached the end of the flock where they made a wide arc and drifted back to where they had started. From time to time they would rise somewhat in the air, hover and then let themselves sink towards the surface with outstretched legs. Sometimes they landed on the water where they would stay for a moment before rising again with or without a fish in the talons. Such events may have indicated commensalism where the eagles simply tried to pick up small fish that had swam towards the surface to evade the diving piscivores. Such small fish were regularly eaten in flight.

The eagles would also fly low over the flock and then accelerate towards a cormorant or merganser with fish. Eagle attacks on birds with fish often occurred when a bird tried to evade kleptoparasitic attacks by either conspecifics or gulls. Usually the attacked bird would drop the fish and dive quickly, the eagle picking up the fish. Having secured it, the eagle would immediately head for trees on the shore, sometimes harassed by one or more other eagles. In such situations, surprisingly often the eagle would drop its fish (because of dominance relations between the eagles?) which was then either captured in the air, usually by the pursuer, or (about ten times) was seen falling to the water and thus getting lost for both the owner and the pursuer.

The approach of an eagle from the shore trees was always preceded by all gulls taking to the air; in fact, this reaction of the gulls was a very reliable cue indicating that an eagle was on its way. Usually, the gulls did not return to the fishing flock until the eagles had left, but on a few occasions large gulls settled at the far end of the fishing flock while eagles were still flying over the flock.

The most interesting feature of this association between eagles, cormorants and mergansers was that the latter mostly showed no fear reactions in response to the eagles despite these often passing less than a metre above them. It seemed as if they regarded the eagles in the same way as they regarded the large gulls that were associated with them. Only three or four times did cormorants or mergansers show an escape reaction when eagles were present. On these few occasions, the eagles were flying higher than usual and stooped from a greater height and it seemed that this behaviour elicited the flight response. Since there was often much flying between different parts of a fishing flock, some of these flights may not have been triggered by the eagles.

Often more than one eagle flew simultaneously over the fishing flock (the maximum number recorded at the same time was seven), often without any obvious interactions between them. Adults appeared to have higher success rate than younger eagles when kleptoparasitising cormorants and mergansers. Some 16 successful attempts were recorded for adults versus circa seven for juveniles. In practice, the difference was more pronounced than these figures show: first winter eagles were seen about three times as often above the fishing flocks as were adults.

Hooded Crow and the fishing flocks

On a few occasions I observed a Hooded *Crow Corvus corone cornix* hovering close to the water surface at the fishing flock more than a hundred metres from the shore and once or twice crows were seen leaving the flock with a fish in the bill. Once a Common Gull and a crow were aiming at the same fish but the gull was faster and got it.

Discussion

Fish constitutes a valuable food for many species of birds. Individual fish are often quite large and it should come as no surprise that conflicts between various birds over fish are numerous. One such conflict is between actively fishing bird species (hosts) and the species that kleptoparasitize them. In this kind of interaction, one would expect hosts to use one or more tactics to avoid losing prey and kleptoparasites to try and overcome these tactics. As reported in the present note, a number of species try to use flock-fishing deep-diving waterbirds to obtain food that would otherwise be either unavailable to them or difficult to find and capture. Of the species studied here, gulls were the most ubiquitous. Although the commensal exploitation of Great Crested Grebes and also of Great Cormorants and Common Merganser by Common Gulls and less often by Black-headed Gulls probably have a very small impact on any of these species; especially as the success of the gulls at getting fish seemed to be very low. In fact, one could really ask whether spending considerable time circling above flocks of these three deep-diving species, from time to time diving head-long into the water, could be profitable. Sometimes one even gets the impression that the mere sight of fish in the bills of these deep-divers acts as an irresistible signal that food is potentially available.

With the large gull species, Herring and Black-backed Gull, the situation is clearer. Both use cormorants and mergansers as hosts stealing from them when the opportunity arises. The conflict is clear: The hosts try to avoid losing their prey while the kleptoparasite makes efforts at obtaining it. No wonder then that cormorants and also mergansers were seen biting at gulls, which therefore sometimes seemed to be hesitant to attack. Once a cormorant even pursued (in flight) for about one hundred metres a Herring Gull that carried a fish. The competition for fish was fierce also between the gulls. As reported earlier (Källander 2006), Great Black-backed Gulls regularly robbed Herring Gulls of the fish prey they had stolen. Even Black-backed Gulls themselves were often harassed in the air when they had a fish and both Herring and Great Black-backed Gulls with fish often flew up to a hundred metres before settling on the water to ingest it un-attacked. Also, among both mergansers and cormorants attempts at intra-specific kleptoparasitism were very common as were inter-specific kleptoparasitism in these species. Attacked birds either rushed along the surface or dived to evade their pursuers.

That White-tailed Eagles kleptoparasitize Common Mergansers has been observed at two other localities in Sweden (Lake Åsnen, where huge numbers of Common Mergansers gather in late autumn and early winter (Hallberg 2001) and Lake Hjälmaren (Å. Pettersson in litt.) and it seems likely that the association occurs at many Swedish lakes where cormorants or mergansers gather.

References

Bennetts, R.E., McClelland, B.R. & Caton, E.L. 1990. Aerial piracy by Bald Eagles: success of aggressorns and followers. *Northwestern Natur*. 71: 85–87.

Brown, B.T. 1993. Winter foraging ecology of Bald Eagles in Arizona. *Condor* 95: 132–138.

Fischer, D.L. 1985. Piracy behaviour of wintering Bald Eagles. *Condor* 87: 246–251.

Grubb, T.C. 1971. Bald Eagles steal fish from Common Mergansers. *Auk* 88: 928–929.

Jorde, D.G., and Lingle, G.R. 1988. Kleptoparasitism by Bald Eagles wintering in south-central Nebraska. *Journal Field Ornithol*. 59: 183–188.

Hallberg, L.-O. 2001. Åsnen – örnarnas sjö. Kungsörnen 2001: 9–15. (In Swedish.)

Källander, H. 2006. Interspecific kleptoparasitism by four species of gull *Larus* spp. In South Sweden. *Ornis Svecica* 16: 127–149.

Watson, J.W., Garrett, M.G. & Anthony, R.G. 1991. Foraging ecology of Bald Eagles in the Columbia River estuary. *J. Wildl. Manage*. 55: 492–499.

Sammanfattning

Senhöst och vinter gästas den 12 km^2 stora Vombsjön av imponerande antal skäggdoppingar (ibland >2000), storskarvar (c.1000) och storskrakar (upp till minst 2000). Alla tre utnyttjas av olika arter som försöker få del av de fiskar dessa dykande fåglar för upp till ytan. Här beskrivs kortfattat dessa arter och de metoder de använder för att komma åt fisk. Data insamlades huvudsak-

ligen under senhöst och vinter 2004–2017 då ett hundratal besök gjordes vid sjön. Vombsjön har en ganska rik fiskfauna, som domineras av abborre, gärs, mörtfiskar och löja. Sjön är som djupast c.15 m men en knapp tredjedel är mindre än 5 m djup. De talrika skäggdoppingarna under senhösten utnyttjas företrädesvis av fiskmåsar, vilka kretsar över ansamlingarna av doppingar och störtar sig huvudstupa ner mellan doppingarna. Det förefaller som om utnyttjandet främst består i att doppingarnas dykande får småfisk att fly mot ytan, där de kan fångas av måsarna. Skarvar och storskrakar däremot är i hög grad utsatta för kleptoparasitism (födostöld) av gråtrut och havstrut. Också fiskstölder inom såväl som mellan dessa båda dykande arter är vanliga och leder ofta till stridigheter. Inte minst i samband med sådana attraheras de båda trutarterna och också havsörnar. De senare verkar ha två olika taktiker att få fisk. Antingen flyger de lågt över fiskeflocken, går upp och spanar, varpå de låter sig sjunka mot ytan med utsträckta ben. I det fallet förefaller det oftast handla om småfisk som försökt undkomma mot ytan (och som sedan fångas vid ytan innan de åts och i luften). Den andra metoden är att flyga lågt över fiskeflocken för att accelerera mot en skarv eller skrake som fångat en litet större fisk som tar tid att svälja. Den attackerade fågeln försöker antingen rusa över vattenytan eller, oftare, dyka, varvid den släpper fisken som örnen plockar upp. Havsörnar har setts flyga lågt över fiskeflockar under cirka 50% av 100 besök vid Vombsjön under november – mars (som mest sju örnar samtidigt). Det som mest fascinerar åskådaren är att skrakar och skarvar inte visar några skrämselreaktioner fastän örnarna flyger på blott meterhöjd över dem – de verkar betrakta örnarna på samma sätt som de betraktar de båda trutarterna. Intressant nog har även både gråhägrar och kråkor setts kretsa över fiskeflockarna, i kråkornas fall lågt över vattnet och så långt som 100 m från land. Kråkor har också setts flyga mot land med en glänsande fisk i näbben.

ORNIS SVECICA 28: 19–38, 2018

Changes in migration and wintering patterns of Greylag Geese *Anser anser* from southernmost Sweden during three decades

Förändringar i flyttnings- och övervintringsvanor hos grågäss Anser anser *från sydligaste Sverige under trettio år*

LEIF NILSSON & HAKON KAMPE-PERSSON

Abstract

The recent increase of the Greylag Goose *Anser anser* population has caused complaints about crop damage. In response to this, the Nordic Collegium for Wildlife Research started a neck-banding program to elucidate the migration and movement patterns. During 1984–2009, 2639 Greylag Geese were marked in a breeding area in SW Scania, southernmost Sweden. Up to and including 2012, 15 296 re-sightings were reported from outside the breeding area (in addition to more than 100 000 from the breeding area). In the early years of the study, the majority of the geese migrated to winter in southernmost Spain, staging in The Netherlands. In later years, hardly any individuals migrated to Spain, the majority staying in The Netherlands with an increasing proportion wintering in southern Sweden. From 1986 to 2017, the mean latitude for re-sightings changed ten degrees to the north. About 13% of the geese changed winter quarters between two consecutive winters. Moreover, the southward migration occurred much later in the autumn and the geese returned to the breeding areas about one month earlier in spring.

Leif Nilsson, Department of Biology, Biodiversity, Ecology Building, SE-223 62 Lund, Sweden.
E-mail: leif.nilsson@biol.lu.se
Hakon Kampe-Persson, Pulmaņi, Glūdas pagasts, Jelgavas novads, LV-3040 Nākotne, Latvia.
E-mail: kampepersson@hotmail.com

Received 5 September 2017, Accepted 27 May 2018, Editor: Dennis Hasselquist

Introduction

Like most other goose populations in Europe, the Greylag Goose *Anser anser* has shown a marked increase in numbers in recent decades (Nilsson et al. 1999, Kampe-Persson 2002, 2010, Fox et al. 2010, Nilsson 2013, Fox & Madsen 2017). The populations in mainland north-western Europe (the East Atlantic Flyway population) increased from about 200 000 in the early 1990s to more than 600 000 twenty years later (Fox et al. 2010) and to 960 000 in the most recent report (Fox & Madsen 2017). This very marked increase in the population of Greylag Geese, as well as in other goose species, that started in the 1970s led to many complaints about farmland crop damages (Buij et al. 2017). Therefore, research projects including neck-banding of Greylag Geese and other species were started in many countries to increase the knowledge about the movement patterns and the migrations of different goose species. In the Nordic countries, a Greylag Goose project was initiated in 1984 (Andersson et al. 2001). The project was initially aimed for a five-year period but continued during the following years. In SW Scania, in southernmost Sweden, marking stopped after 2009 (but fieldwork continued until 2012) and in Norway marking still continues (2017).

Traditionally, the Greylag Geese in mainland north-west Europe migrated along the east Atlantic coast via staging areas in The Netherlands to winter quarters in Spain, mainly the Guadalquivir Marismas in the south-west of the country (Nilsson et al. 1999, Andersson et al. 2001). Already during the early part of the study period, changes in the migration patterns and staging habits were recorded (Nilsson et al. 1999, Andersson et al. 2001, Nilsson 2006, Nilsson 2013). This change resulted in fewer geese from southern Sweden migrating to south-western Spain. Instead new traditions were established with wintering areas in northern Spain and further north in The Netherlands. Some Greylag Geese even started to winter in Sweden.

In the present study, we analyse the data from the neck-banding project in SW Scania for the entire study period 1984–2012. A former major analysis (Andersson et al. 2001) also covered neck-banding at other sites in Sweden but these projects were terminated earlier and the re-sightings from them are not analysed in this paper.

Material and methods

Marking area

The marking (i.e., neck-banding and ringing) area for this study was situated in south-western Sweden (SW Scania, Figure 1). The main marking efforts were made at four (later two) lakes in a relatively small area in an undulating open agricultural landscape with small patches of woodland in the western lake area (Figure 1). The marking sites were all eutrophic lakes with rich reed beds *Phragmites australis* along parts of the shores. Some of the lakes have small islands suitable for breeding geese. Grasslands and at one lake a golf course offered good feeding conditions for the goose families. A description of the area is found in Nilsson & Persson (1994). The breeding population of Greylag Geese increased from 120 pairs in 1985 to a peak of 1340 pairs in 2004, and thereafter the population decreased and in 2012 there were 820 pairs the area. Various aspects of the breeding ecology and dynamics of this population have been studied (Nilsson & Persson 1992, 1994, 2001a, 2001b, Nilsson et al. 1997, 2002, Nilsson 1998). During the first years of the study, geese were also neck-banded at two lakes in the eastern lake area of Scania (Figure 1).

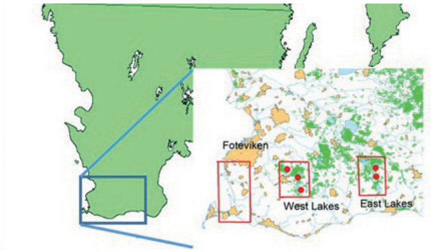


Figure 1. Map of South Sweden with the position of the main study areas inserted. Neck-banding sites are marked with red dots. The main neck-banding and ringing was undertaken in the West Lakes area, where the most intensive studies were conducted during the entire period. Some markings were made in the East Lakes area during the first years of the study. Foteviken at the coast is an important staging area for Greylag Geese from the West Lakes area and was together with the lake area regularly searched for neck-banded geese. *Karta över södra Sverige med undersökningsområdena markerade. Märklokaler har markerats med röda prickar. Huvuddelen av märkningarna ägde rum i det västra sjöområdet där mer intensiva undersökningar gjordes under hela perioden. Några märkningar genomfördes i det östra sjöområdet i början av undersökningsperioden. Foteviken vid kusten är ett viktigt område för gässen från det västra sjöområdet och genomsöktes tillsammans med sjöområdet regelbundet efter märkta gäss.*

In SW Scania, due to all other studies of the Greylag Geese, all major sites for the species were checked for the occurrence of marked individuals at least on a weekly basis during the breeding season (arrival to early summer). The same applies to the coastal staging sites in the local region (Figure 1) during late summer and early autumn when families from the study area concentrated here.

Catching and marking

In SW Scania, breeding families were caught on the breeding sites when the goslings were about six weeks old and the parents were unable to fly due to wing moult. The families were rounded up when feeding on grasslands, pastures or a golf course and driven into nets, which were mounted beforehand (Persson 1994a, 2000a, Kampe-Persson 2004). We kept the geese in large jute sacks when they awaited handling.

The geese were marked with blue neck collars of UV-resistant laminated plastic. The collars had three-digit codes engraved with the first character larger and the two following smaller and in right angel to the first one. Letters and numbers most liable to misidentification were omitted. In good light conditions, it was possible to read the codes at a distance of 500–600 m. To make it possible to follow the individuals in the study area also in the case they lost their neck-collars, a proportion of the Greylag Geese were also marked with coloured leg rings with an engraved code. All individuals were also marked with metal rings from the Swedish national ringing scheme. For further information on the Nordic marking scheme, see Andersson et al. (2001). The mean annual retention rate of neck-collars in this study was 93.1±1.6 % for males and 98.8±0.5 % for females (Persson 2000b and unpubl.)

Material

During the years 1984–2008, a total of 2 639 Greylag Geese, 685 moulting birds and 1 954 goslings, were neck-banded in the study area in SW Scania and included in the present study. Most moulting birds were breeding adults but there were also about 20 non-breeders, most of them from the local population.

When one re-sighting per country and month was counted, in all 15 296 re-sightings of the neck-banded Greylag Geese were reported from other areas than the local study area up to and including year 2012 (Table 1). In addition to the re-sightings spec-

Table 1. Number of neck-banded Greylag Goose *Anser anser* individuals from SW Scania reported from different countries together with the number of re-sightings reported (one re-sighting per country and month included). Re-sightings from the marking area and the local study area in SW Scania are not included in the table. Re-sightings reported until the end of year 2012 included. *Antalet halsmärkta grågäss från SV Skåne rapporterade från olika länder tillsammans med antalet rapporterade observationer (en observation per land och månad inkluderade). Observationer från märkningsområdet och det lokala undersökningsområdet i SV Skåne är inte medtagna i tabellen. Tabellen visar observationer rapporterade till och med 2012.*

Country	Individuals	Re-sightings
Norway	12	29
Sweden	270	675
Denmark	479	1 509
Germany	367	997
The Netherlands	1 299	7 451
Belgium	112	489
UK	8	80
France	157	272
Spain	758	3 776
Morocco	3	9
Poland	1	1
Hungary	1	1
Austria	1	1
Tunisia	5	6
Total		15 296

ified in this table, 100 050 re-sightings were obtained locally in the study area in SW Scania in connection with other studies during the same time period (Nilsson & Persson 1991, 1992, 1994, Nilsson & Kampe-Persson 2017).

Re-sightings from areas outside the study area in SW Scania were obtained through a large network of voluntary observers that checked the flocks of geese for the occurrence of neck-banded individuals. One of the authors (HKP) carried out several research projects on marked Greylag Geese in Spain during the winters 1985/1986–2001/2002, also visiting staging/wintering areas in The Netherlands, France and Portugal (Persson 1993, 1996a, 1997, Kampe-Persson 2002).

Since 2007 a website (www.geese.org) has been created on which observers can enter their readings of goose rings. On this website a lot of re-sightings, also from the past, were entered by observers through google-maps. The website encourages volunteers to report sightings, because they can check online where the bird they have observed has been ringed and which other re-sightings of the same bird that have been made.

Results

Distribution of staging and wintering Greylag Geese

The general migration pattern of the Greylag Geese marked in SW Scania in the early part of the study period has been described in Andersson et al. (2001). In the present study, we therefore concentrate on comparing the migration patterns from the later years with that of the early part of the study period to elucidate changes in migration habits.

The majority of the Greylag Geese seen outside the study area in SW Scania have been reported from The Netherlands and Spain (Figures 2–4), whereas much fewer have been reported from other countries (Table 1). During the first years of the project, up to 50% of the neck-banded individuals reported in a single year were seen in The Netherlands at least once, whereas the highest annual percentage reported from Spain was somewhat more than 35%. In both cases, the proportion of neck-banded individuals reported have decreased over the years, partly as an effect of changes in the migration pattern as discussed below, but other factors such as the intensity of search is also a factor of importance. It should be kept in mind that the goose populations increased dramatically during this time-period, so it was more difficult to find neck-banded geese with the same fieldwork effort. The Guadalquivir Marismas was intensively searched for marked geese up to 2002 but not thereafter. This can have influenced the number of marked geese reported from this wintering area in later years.

During the summer, most reports of neck-banded Greylag Geese were from the study area with some records from other parts of South Sweden (Figure 4). In the early period, a number of non-breeding Greylag Geese from SW Scania were reported from the moulting area in Oostvaardersplassen in Flevoland in The Netherlands during late May to early July, whereas only single observations were obtained from The Netherlands in these months

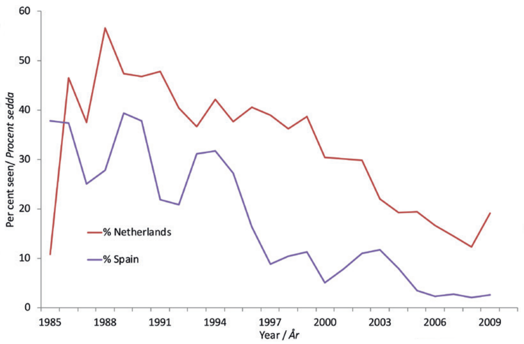


Figure 2. Annual percentages of neck-banded Greylag Geese *Anser anser* marked in SW Scania reported in a specific year, which were seen in The Netherlands and Spain that year.
Procentandelen märkta grågäss från SW Skåne rapporterade ett givet år, vilka setts i Nederländerna resp. Spanien samma år.

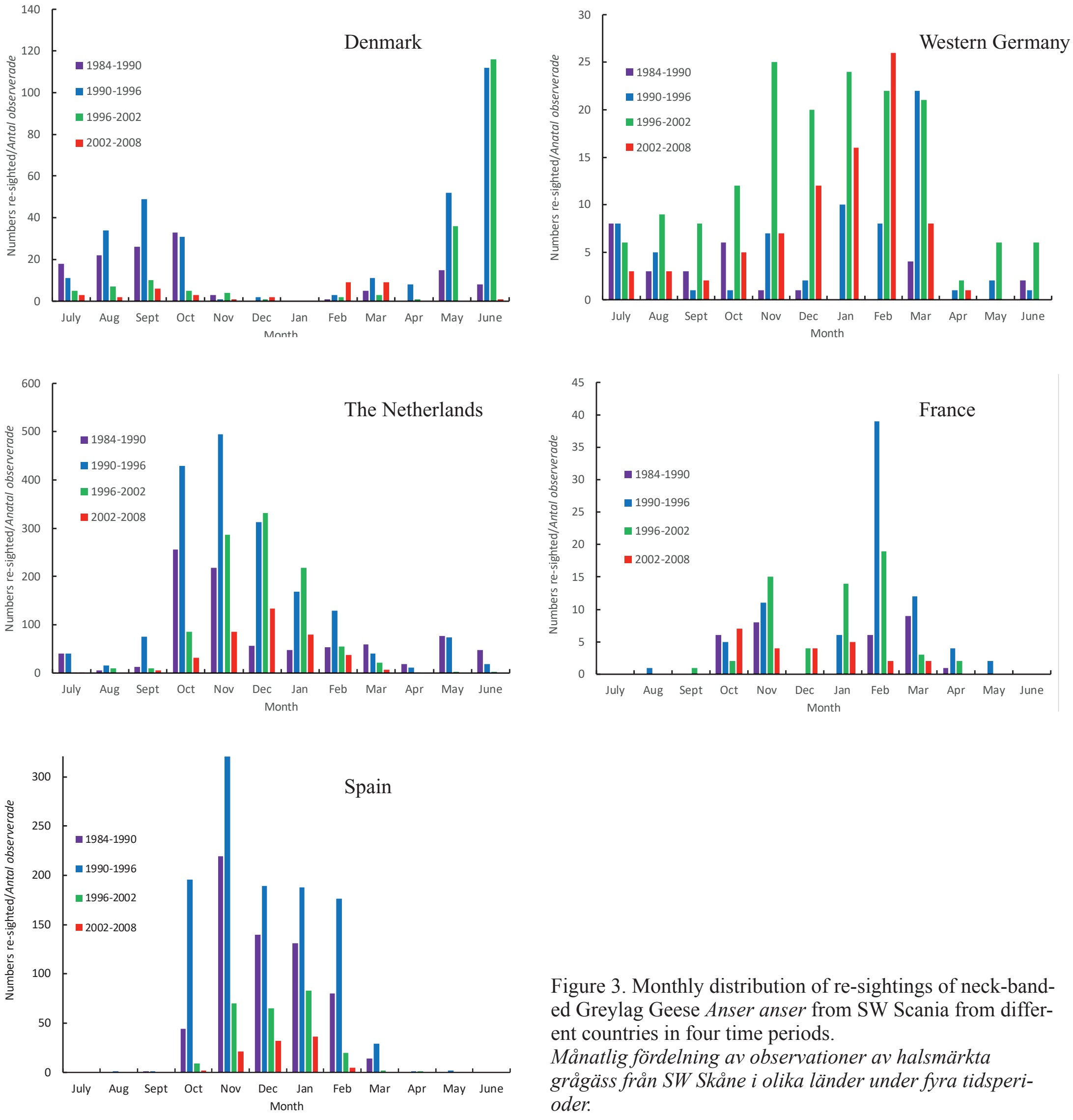


Figure 3. Monthly distribution of re-sightings of neck-banded Greylag Geese *Anser anser* from SW Scania from different countries in four time periods.
Månatlig fördelning av observationer av halsmärkta grågäss från SW Skåne i olika länder under fyra tidsperioder.

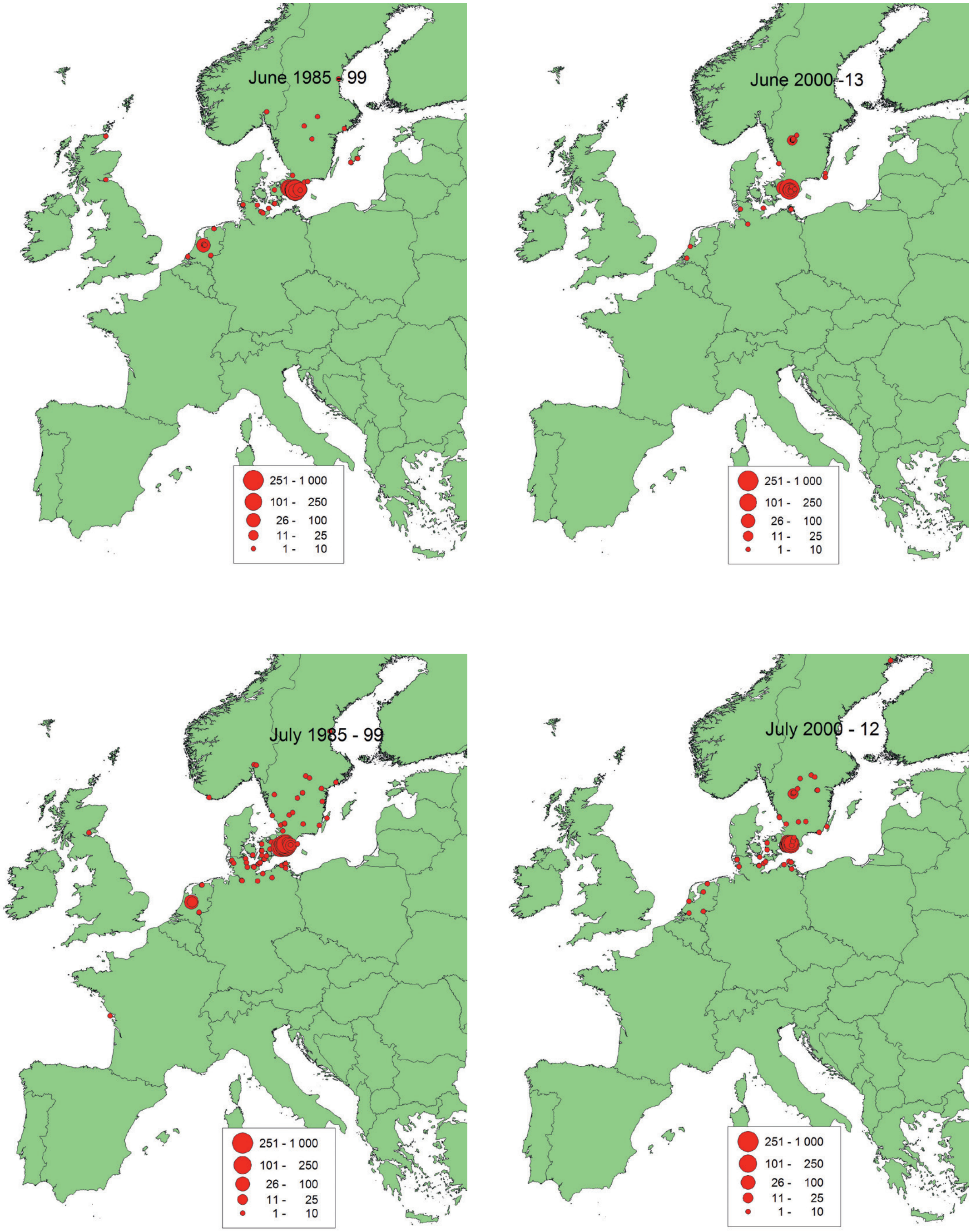


Figure 4. Monthly distribution of re-sightings of neck-banded of Greylag Geese *Anser anser* from SW Scania during 1985–1999 and 2000–2012, respectively.
Månadsfördelning av observationer av halsmärkta grågäss från SW Skåne under 1985–1999 och 2000–2012.

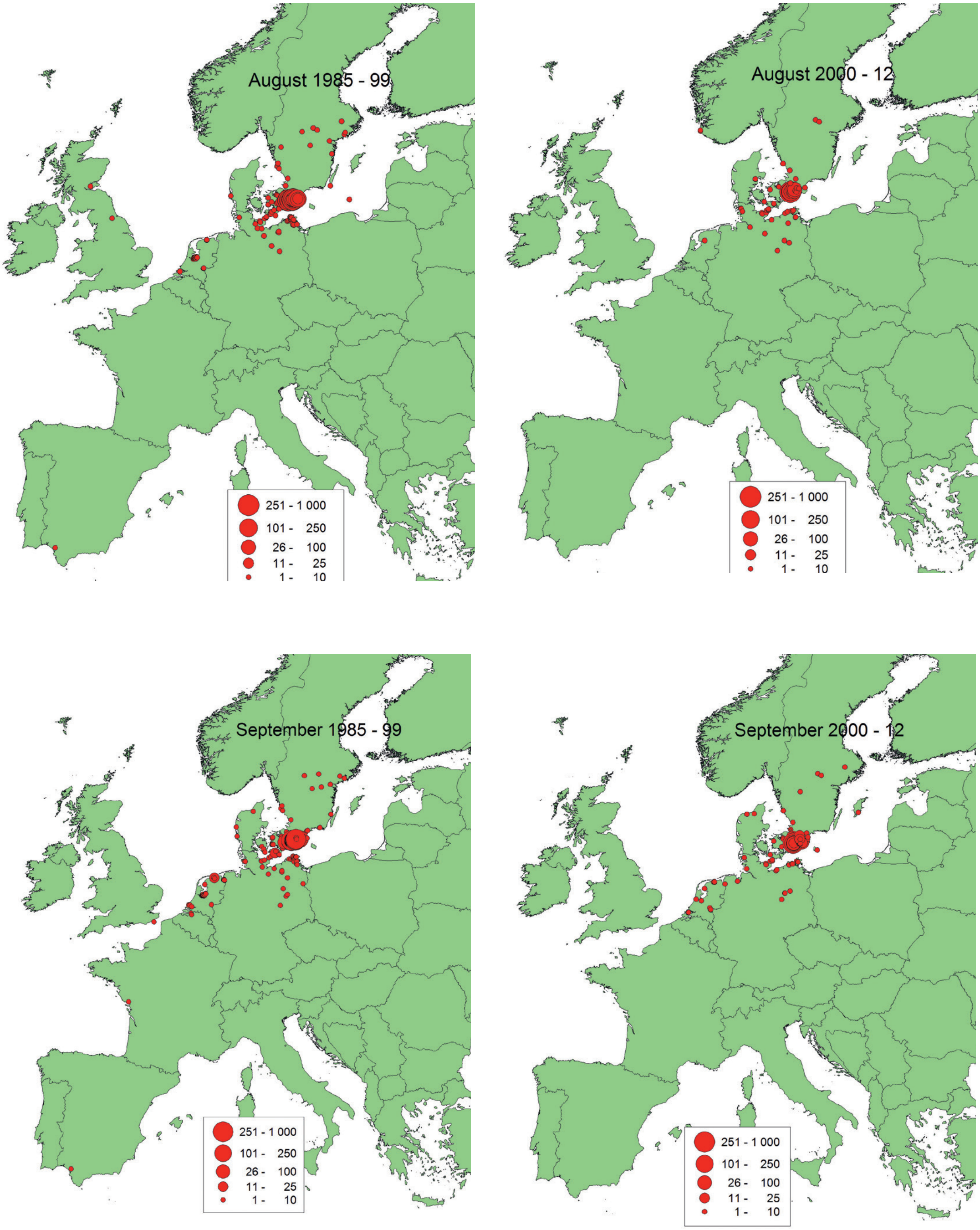


Figure 4. Monthly distribution of re-sightings of neck-banded of Greylag Geese *Anser anser* from SW Scania during 1985–1999 and 2000–2012, respectively.
Månadsfördelning av observationer av halsmärkta grågäss från SW Skåne under 1985–1999 och 2000–2012.

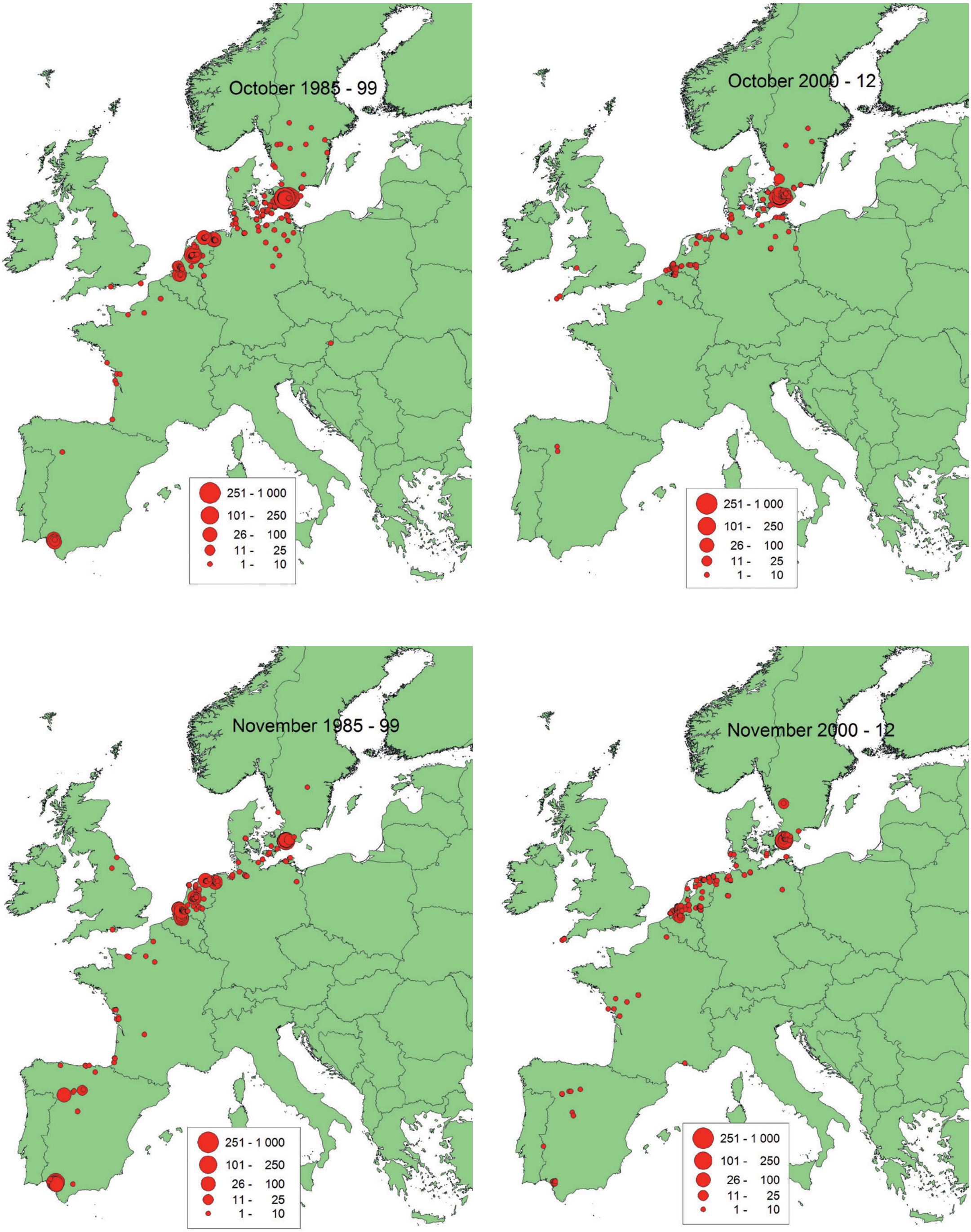


Figure 4. Monthly distribution of re-sightings of neck-banded of Greylag Geese *Anser anser* from SW Scania during 1985–1999 and 2000–2012, respectively.
Månadsfördelning av observationer av halsmärkta grågäss från SW Skåne under 1985–1999 och 2000–2012.

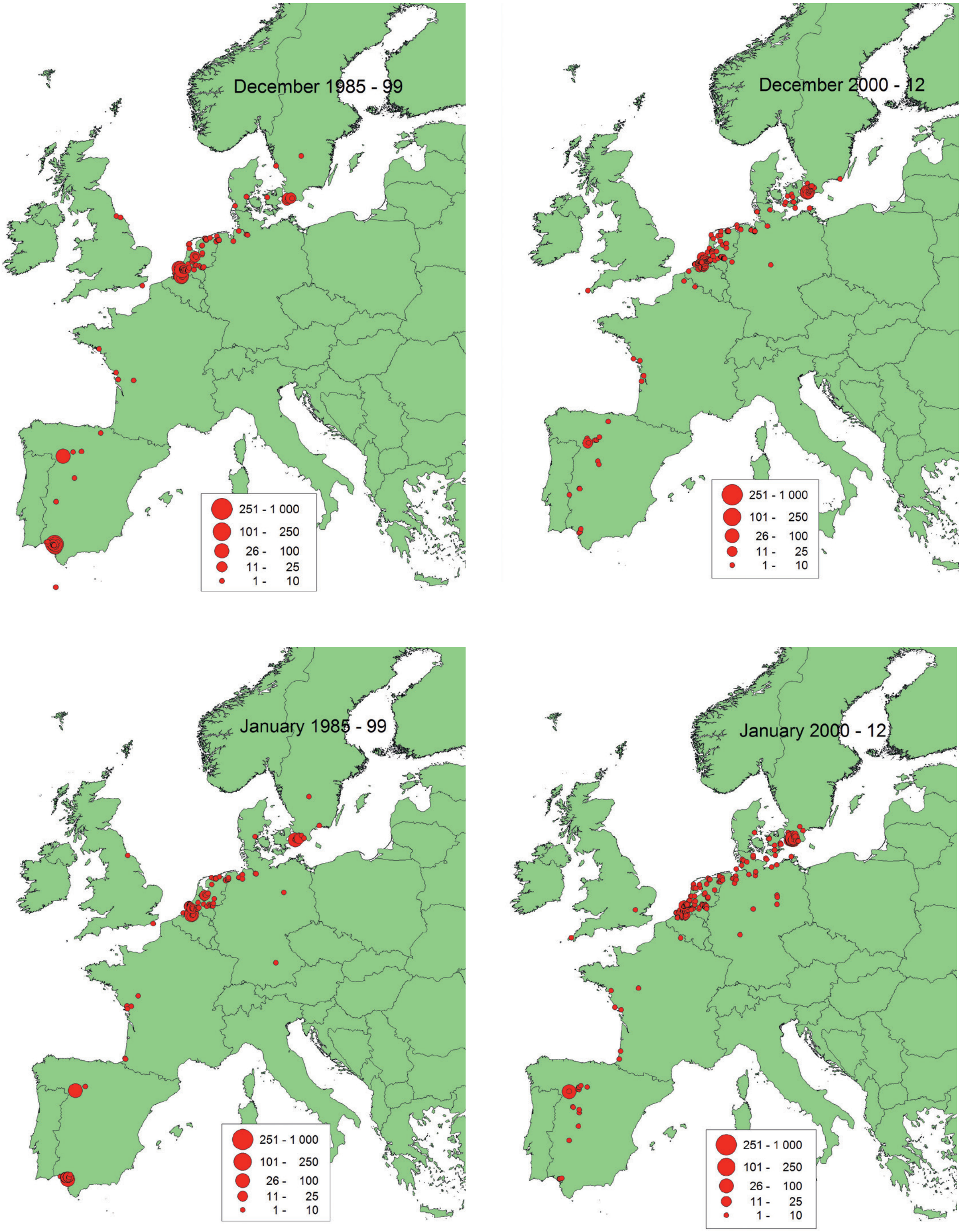


Figure 4. Monthly distribution of re-sightings of neck-banded of Greylag Geese *Anser anser* from SW Scania during 1985–1999 and 2000–2012, respectively.
Månadsfördelning av observationer av halsmärkta grågäss från SW Skåne under 1985–1999 och 2000–2012.

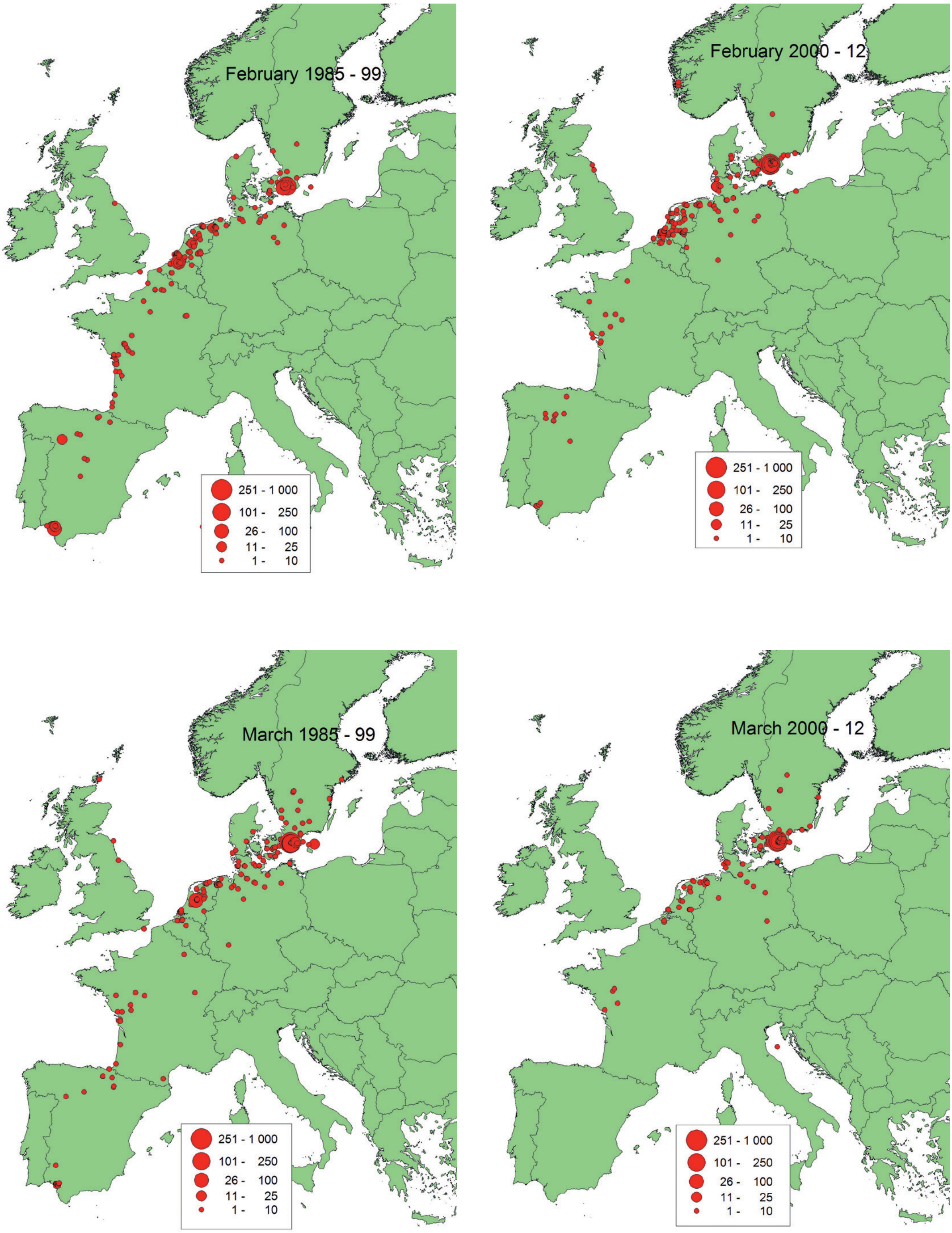


Figure 4. Monthly distribution of re-sightings of neck-banded of Greylag Geese *Anser anser* from SW Scania during 1985–1999 and 2000–2012, respectively.
Månadsfördelning av observationer av halsmärkta grågäss från SW Skåne under 1985–1999 och 2000–2012.

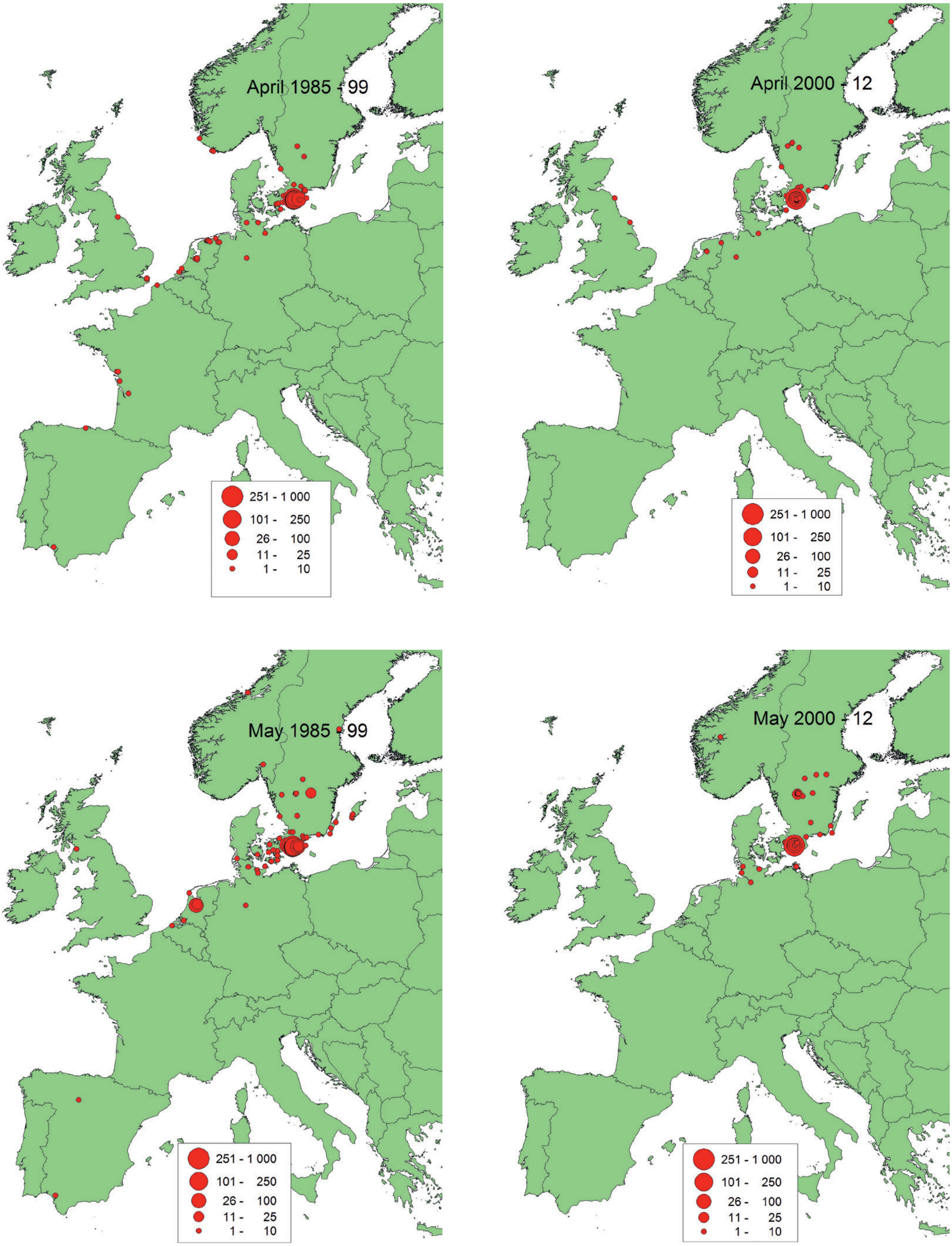
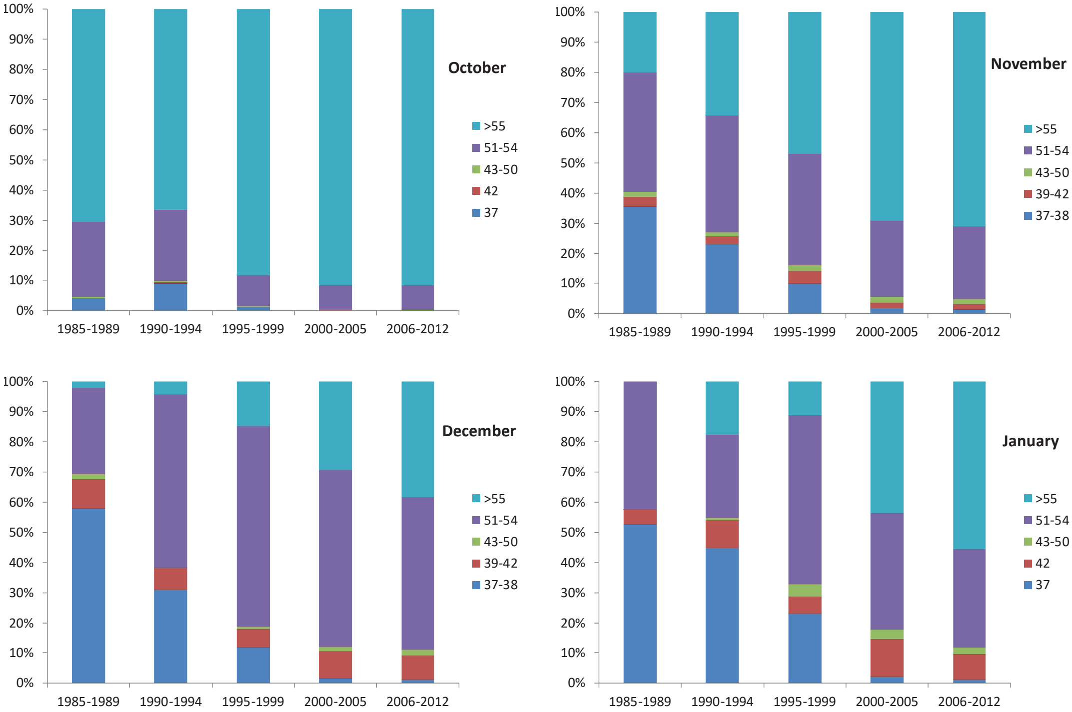


Figure 4. Monthly distribution of re-sightings of neck-banded of Greylag Geese *Anser anser* from SW Scania during 1985–1999 and 2000–2012, respectively.
Månadsfördelning av observationer av halsmärkta grågäss från SW Skåne under 1985–1999 och 2000–2012.



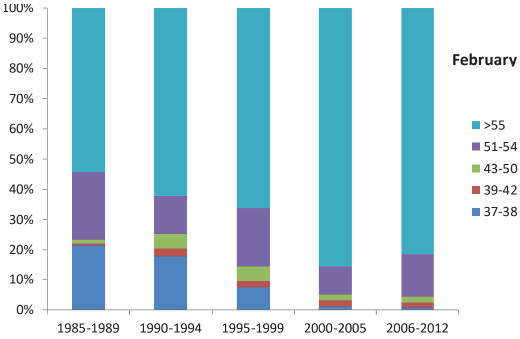


Figure 5. Latitudinal distribution (different colours denote different latitudes) of all resightings of Greylag Geese *Anser anser* neck-banded in south-western Sweden in different months during five different time periods (1985–2012).
Fördelning på latitud (olika färger) för avlästa grågäss halsmärkta i sydvästra Skåne under fem olika tidsperioder (1985–2012).

during later years (Figure 3). Numbers moulting at Oostvaardersplassen decreased already during the 1990s, when a new moulting tradition for south Swedish Greylags was established on the island of Saltholm between south Sweden and Denmark (Fox et al. 1995, Nilsson et al. 2001) and hardly any Greylag Geese from SW Scania went to Oostwaardersplassen anymore. Thus, during a period in the 1990s (due to intensive fieldwork on Saltholm in connection with the impact assessment for the bridge between Sweden and Denmark) more observations of marked Greylag Geese from SW Scania were reported from Denmark in June than from any other month (Figure 3). Unfortunately, the intensive studies on Saltholm stopped after year 2000 and there is therefore no information about geese from Scania there in later years. However, Greylag Geese still go there to moult as numbers counted on the moulting site was 46 500 in 2011 (Michael Flink pers. comm.). In later years, also a number of Greylag Geese marked in SW Scania were reported as moulting in Lake Hornborgasjön (Nilsson & Hermansson in prep.).

In late summer, after the moult, and in early autumn, the majority of the Greylag Geese remained in SW Scania close to the marking areas, but there was a shift in the local distribution with a concentration to coastal areas (Nilsson & Persson 1992, Nilsson 2013, Nilsson & Kampe-Persson 2017). Smaller numbers stayed in Denmark, The Netherlands and northern Germany during this time of the year (Figures 3–5). Re-sightings from The Netherlands in late summer were restricted to the early part of the study period, when Greylag Geese from Scania still moulted at Oostwaardersplassen. Most German re-sightings during August and September were from Mecklenburg-Vorpommern.

October and November was the main migration period for the Greylag Geese from SW Scania during the early years and a large proportion of the neck-banded birds was reported from The Netherlands. In these months, marked differences were found between the different time periods. During the early part of the study an appreciable proportion of the geese were already reaching south-western Spain in October and the staging and wintering areas in The Netherlands and Spain dominated over the areas in the north, for example Sweden, in November. In the later years, the majority of the Greylag Geese remained in Sweden during this time of the year. Small numbers were found in The Netherlands in October but hardly any reached Spain in that month. The picture was similar for November in the late period with much fewer south Swedish Greylag Geese reaching Spain compared to in the earlier years.

December and January are typical winter months and Greylag Geese were found all along the flyway from SW Scania to southern Spain. When comparing the two time-periods for these months it has been a clear shift in the distribution, especially during January. Within Spain, two areas were important during the first time-period, the Guadalquivir Marismas in the south-west and Villafáfila in the north, whereas very few geese were found in the former area in January during 2000–2012. Moreover, Greylag Geese from SW Scania were reported from a number of new sites in Spain during the latter period. It is also clear that more Greylag Geese were on migration northwards in January during the latter time-period compared to the first period. Re-sightings from South Sweden were more common in later years. Over the study period, there was a northward change of the mean latitude for January re-sightings of marked Greylag Geese from Scania (Figure 6).

In February, Greylag Geese were found along the entire flyway and spring migration northwards was apparent even during the early period. The northern distribution bias was more apparent during the second period (2000–2012). Similar patterns were seen in March, when very few Greylag Geese were still found south of The Netherlands in 2000–2017.

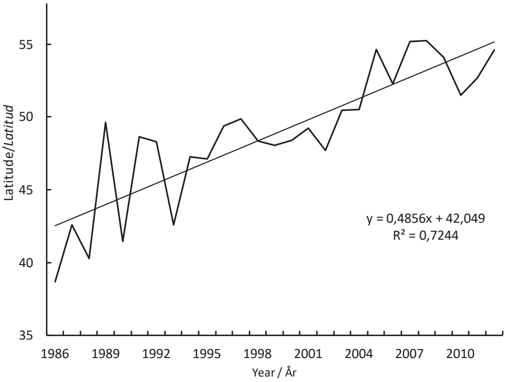


Figure 6. Mean latitude for January observations of neck banded Greylag Geese *Anser anser* from SW Scania in 1986–2017.
Medel-latitud för januariobservationer av halsmärkta grågäss från SW Skåne 1986–2017.

In April, most reports were from the breeding areas with some individuals lingering around in the north, fewer were found south of Sweden in the second period than during the first period (1985–1994). In May, the moult migration to Oostvaardersplassen in The Netherlands was apparent in the first time-period, whereas no geese were reported from this area in May during the second period.

Outside the main flyway from south-west Sweden, only few reports have been obtained of marked Greylag Geese from other areas. As is seen from the maps small numbers have been seen regularly in Britain and there are a few observations further to the east in Europe. A few individuals from south-west Sweden established a breeding population in Britain, probably somewhere in Scotland and migrating to wintering areas in England (cf. Insley 1997).

The maps (Figure 4) clearly show that marked changes in the migration pattern and wintering areas of the Greylag Geese from south-west Scania have occurred over the years of the study. These changes became still clearer when the distribution of the re-sightings was analysed according to latitudinal distribution (Figure 5). The differences are most prominent for December and January, when almost all re-sightings were from The Netherlands and Spain during the first period (1985–1999), with no re-sightings reported from the marking area.

In the second period, an increasing proportion of the birds were found wintering in Sweden. In the same time period, the numbers wintering in Spain decreased markedly. Over the period 1986–2012, the mean latitude for January re-sightings changed about ten degrees northwards, the trend being highly significant (Figure 6). This change towards more northerly wintering areas continued during the entire study period.

When the study started only few Greylag Geese were found in SW Scania during the January counts. In the same way there were no winter observations of neck-banded Greylag Geese from Scania during the first years of the study. Beginning in 1991, small numbers of marked Greylag Geese remained in SW Scania in most winters, staying mainly close to the coast at Foteviken. Suddenly, in 2005, this number increased and 25% of all marked Greylag Geese seen that year were seen in Scania during the winter (Figure 5a-c), with more that 30% of the neck-banded geese staying in the winter of 2009.

Over the years, 13% of the re-sighted Greylag Geese changed winter quarter between two consecutive winters (Table 2). The highest frequency of change was seen for the two Spanish winter areas (14% and 15%, respectively), whereas only 8% of those wintering in SW Netherlands changed winter area between two consecutive seasons. Clearly, the number of changes shown in Table 2 are biased to the low side as all geese were not reported in the winter in all years (not being seen). In addition to the 29 changes recorded between two consecutive years a further 27 changes were noted for geese that were not recorded in consecutive winters. The majority of the changes were from a southern winter area to a more northern winter area (Table 3) but there were six geese changing from the Netherlands to Spain. There is, however, a possibility that some of these birds were late migrants staging in the Netherlands not being seen later the same year in Spain.

Phenology of migration

The monthly distribution of reported re-sightings of neck-banded Greylag Geese from different countries gives a good picture of the phenology of the migration for the species through the main staging and wintering areas (Figures 3, 4). For Denmark, the picture was markedly dominated by the number of Greylag Geese reported from the moulting site at Saltholm in May–June during a number of years in the 1990s. Very few observations were reported from Denmark during November–February, but generally, the number of reported re-sightings from Denmark was quite small. Apparently, most Greylag Geese just passed over Denmark on their migration south.

The picture for Western Germany is quite different from the Danish one. During the first years, few Swedish Greylag Geese were reported from Germany outside the migration periods, but in the latter

Area	Number of individuals			Per cent changing
	No Change	Change	Total	
Guadalquivir delta	45	8	53	15
Villafafila	23	0	23	0
N Spain excl. Villafafila	12	2	14	14
France	2	3	5	+
SW Netherlands	96	8	104	8
Flevoland	8	1	9	+
N Netherlands	5	3	8	+
NW Germany	0	4	4	+
SW Scania	5	0	5	+
Total	196	29	225	13

Table 2. Number of neck-banded Greylag Geese *Anser anser* from SW Scania changing winter quarters between years for individuals where the winter quarter was established in two consecutive years.
Antal halsmärkta grågäss från SV Skåne som bytt vinterkvarter mellan år, för gäss där vinterkvarteret fastställts två på varandra följande år.

Table 3. Shifts of winter quarters by neck-banded Greylag Geese *Anser anser* from SW Scania separated between those seen on different winter areas in two consecutive years (Table 2) and those seen on the second winter quarter later (=year of change unknown).
Byte av vinterkvarter för halsmärkta grågäss från SV Skåne, separat för dem som setts två på varandra följande år (Tabell 2) och dem som setts i det nya vinterområdet senare (år för bytet okänt).

Winter area 1	Winter-area 2	Second Winter	Later Winter	Total
Gualdalquivir	SW Netherlands	6	7	13
Gualdalquivir	Villafafila	0	5	5
Gualdalquivir	France	1	0	1
Gualdalquivir	SW Scania	1	1	2
N Spain	SW Netherlands	2	2	4
N Spain	NW Germany	0	1	1
France	Villafafila	1	0	1
France	SW Netherlands	2	0	2
SW Netherlands	SW Scania	5	9	14
Netherlands	Spain	5	1	6
N Netherlands	SW Netherlands	1	0	1
N Netherlands	NW Germany	1	0	1
N Netherlands	SW Scania	10	1	1
NW Germany	SW Netherlands	3	0	3
NW Germany	SW Scania	1	0	1
Total		29	27	56

part of the study period, a number of observations of marked Swedish Greylag Geese were reported from the winter months and early spring. There are some reports of moulting Swedish Greylag Geese from the German west coast in May–June.

As mentioned before, the largest number of re-sightings of Scanian Greylag Geese were reported from The Netherlands. During the early years, the highest numbers were reported from the autumn period, with much smaller number of re-sightings reported from the other months. Over the years, there was a change in the pattern with the highest counts reported from October 1984–1990, in November in 1990–1996 and in December for the last two periods (1996–2008).

France was mainly a passage country for the Greylag Geese from SW Scania (Figure 2). Very few observations were reported before October. Peak number of observations were noted in November and February (during the first period March). Few geese from Scania stayed in France over the winter. For further details on the occurrence of Greylag Geese in France, see Nilsson et al. (2013). The majority of the Greylag Geese from SW Scania migrating to Spain apparently made a direct flight from the Netherlands to Spain (Persson 1993, 1994b). We assume that it was the extremely high hunting pressure in France (Persson 1999) made the geese reluctant to stage there

Spain is the southernmost wintering area for the Greylag Geese from SW Scania even if a few individuals have been recorded in Morocco. During the first two periods (1984–1996), many Greylag Geese were seen in Spain but especially in the last period (2002–2008; Figure 3), the number of observations was small. The data from Spain is a little biased as one of the authors (HKP) made intensive field work in the area up to 2002. The data from Spain clearly show a change in the wintering phenology. In the first part of the study Greylag Geese from SW Scania arrived in October, but later the arrival was in November.

In The Netherlands, there is a great interest in reading and reporting neck-bands and other marks on birds and this therefore offers a very good opportunity to follow changes in the timing of the

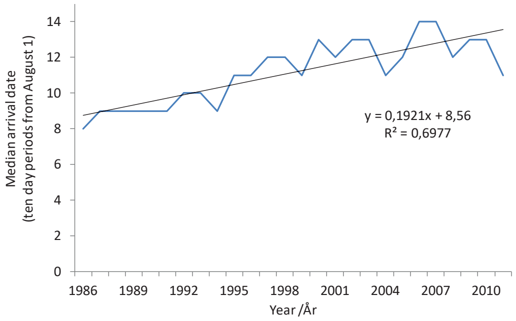


Figure 7. Median arrival dates in autumn in The Netherlands in different years during ten-day periods from August 1st for Greylag Geese *Anser anser* marked in SW Scania.
Median för första observation under hösten i Nederländerna i tiodagarsperioder från 1 augusti för grågäss märkta i SW Skåne.

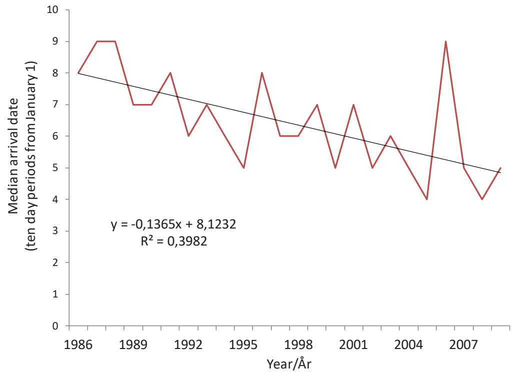


Figure 8. Median arrival dates in spring in SW Scania, South Sweden in different years during ten-day periods from January 1st for Greylag Geese *Anser anser* marked in the area in earlier years.
Median för första observation under våren i sydvästra Skåne under olika år i tiodagarsperioder från 1 januari för grågäss märkta i området under tidigare år.

Greylag Goose migration as a very large proportion of the geese stay here for longer or shorter periods during the autumn migration. Thus, calculating annual median dates for the first observation of neck-banded Greylag Geese in The Netherlands give a good indication of changes in the time-table of autumn migration, which is much better than comparing last-sightings of the birds in the staging areas in Scania. During autumn, the Greylag Geese in Scania are dispersed over a large area for feeding during the day and it is difficult to establish with certainty when they leave the region on migration. Between 1987 and 2011 there has been a significant trend towards a later arrival of the marked birds in The Netherlands (Figure 7), the median arrival date for the last few years being about one month later (early November) compared to the start of the study (early October).

The timing of spring arrival of the Greylag Geese from SW Scania has also changed significantly during the study period (Figure 8), and the median arrival date back to Scania during the last few years is now ca. one month earlier than at the beginning of the study. For Greylag Geese known from winter re-sightings to winter in Spain, about 20% were back in the breeding areas in Scania in February during 1986–1990 compared to more than 40% in 2001–2005 (Figure 9).

Discussion

The reason why only few birds used Denmark as a staging area in the autumn, just passing over the country on the migration to the staging areas in The Netherlands, may be that the distance is short and easy to complete in a few hours. In the same way, few of the marked Scanian Greylag Geese used France as a staging area on the migration from The Netherlands to the wintering areas in Spain (Nilsson et al. 2013). The distance from The Netherlands to south-western Spain was usually covered by a non-stop flight (Persson 1993, 1994b).

The changes in the migration and wintering habits of the Greylag Geese from south-west Scania shown in the analysis of neck-banded individuals in this contribution are also reflected in the results from the ordinary goose counts (Nilsson 2013).

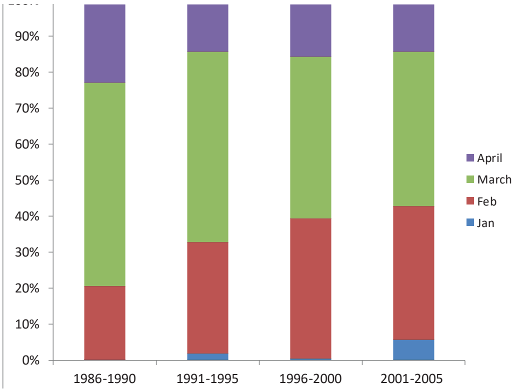


Figure 9. Monthly distribution of first spring observations of neck-banded individuals during different time periods in the breeding area in SW Scania, South Sweden, for Greylag Geese *Anser anser* wintering in Spain.
Månadsfördelning av första vårobservationer av halsmärkta individer under olika tidsperioder i häckningsområdet i SW Skåne för grågäss som övervintrat i Spanien.

Before year 2000, hardly any Greylag Geese stayed in Scania over the winter. However, after 2000 the numbers wintering in southern Sweden increased markedly with a peak count in 2008 of about 50 000 Greylag Geese. This is about 25% of the total count of the species in the special survey in September the preceding autumn (Nilsson 2013, Nilsson & Haas 2016). The departure of the geese of the neck-banded population leaving the country was later during the study period. Thus, both October and November counts increased over the years and a larger proportion of the Greylag Geese counted in September stayed in October and November. This increase in the number of geese staying longer in the autumn was noted before the start of the wintering tradition of Greylag Geese in Sweden (Nilsson 2013). On the European scale, these changes in winter distribution of Greylag Geese have been discussed by Ramo et al. (2015).

This type of northern range shift has been reported for other goose species both from Sweden and from other countries. In Spain, the Tundra Bean Goose *Anser fabalis rossicus* declined from perhaps 200 000 birds in the 1930s to none in the mid-1990s (Persson & Urdiales 1995). Whether this was due to deterioration of conditions in Spain, or improvements at wintering areas closer to breeding areas (or a combination of both) is not known. In North America, there are several examples of how improved conditions along the migration routes have shifted the winter distribution northwards in both the Canada Goose *Branta canadensis* and the Snow Goose *Anser caerulescens* (for references, see Elmberg et al. 2014).

In Sweden, the Taiga Bean Goose *Anser fabalis fabalis* breeding in the north has also changed migration and wintering habits (Nilsson 1984, 2011, 2013, Nilsson & Persson 1984) staging further north in Sweden during autumn and to a large extent wintering in south Sweden and/or Denmark and not migrating to The Netherlands and Western Germany any more. The timing of migration has also changed and the Taiga Bean Geese arrive earlier to the spring staging areas in northern Sweden nowadays compared to in the late seventies (Nilsson & Persson 1984, Nilsson unpublished). In one of the most important staging and wintering areas for this taxon, NE Scania, the geese nowadays arrive much later in autumn and leave much earlier in spring than some decades ago (Kampe-Persson 2014).

The changes in winter distribution and migration pattern in the Greylag Goose have been quite fast occurring over a short time period. This is, however, not unique for the Greylag Goose but has been found in several other goose species, showing the large flexibility in the migration behaviour of geese. In Sweden, the number of autumn staging Barnacle Geese *Branta leucopsis* has increased markedly in the last few years. Actually, there has been a change in the entire migration strategy for the Russian population of the species related to changes in the availability of staging sites in the Baltic (Eichhorn et al. 2009). Other fast changes in the migration pattern seen in Sweden is the occurrence of larger numbers of Tundra Bean Geese in recent years (Nilsson 2013, Kampe-Persson 2014) and a higher number of staging Pink-footed Geese *Anser brachyrhynchus* in south-central Sweden in autumn and spring (Nilsson 2013).

Several duck species have also changed the winter distribution northwards. In Sweden, Nilsson & Haas (2016) found such changes in the winter distribution of several species as an effect of milder winters. Lehikoinen et al. (2013) and Pavon-Jordan et al. (2015) found similar changes when comparing duck census data from a number of countries.

Besides climate change, changes in the availability of suitable crops for feeding can be a factor contributing to the changes in winter distribution and migration habits for the geese. For the Greylag Geese, the later migration from Sweden coincided with changes in the feeding habits of the geese in Scania (Nilsson & Persson 1998, Nilsson & Kampe-Persson 2013), as the geese starting to utilize fields with leftover sugar beet in the autumn. The agricultural landscape of South Sweden nowadays offers the geese a succession of good feeding opportunities over the entire season. This change in the availability of food in combination with milder winters and less snow cover creates better possibilities for the geese to stay in South Sweden over the winter. Changes in agriculture and suitable crops for feeding was probably also an important factor behind the change in autumn staging habits for the Taiga Bean Geese in Sweden.

Changes in the migration habits of the Greylag Geese from SW Scania over the years were not only found in the regular migrations to and from the wintering areas. Young, non-breeding geese migrate to traditional moulting sites in early summer (Salomonsen 1968). In the early years of the study, the Greylag Geese from Scania migrated to Flevoland in The Netherlands for moulting (Andersson et al. 2001) but as the population of Greylag Geese in Western Europe increased and the moulting site in Flevoland reached its carrying capacity (Zijlstra et al. 1991), Greylag Geese from South Sweden started to change their moult migration. Eventually, a large proportion of Greylag Geese from Scania were found moulting on the neighbouring island of Saltholm in the Øresund between Sweden and Denmark (Fox et al. 1995, Nilsson et al. 2001). When the moulting tradition for Scanian Greylag Geese started on Saltholm is not known because the systematic work on the island only started in 1994, when a number of marked geese were found here.

Acknowledgements

The Nordic Greylag Goose project started in 1984 with grants from the Nordic Collegium for Wildlife Research. Later work on the Greylag Goose in Sweden was supported by grants from the Swedish Environmental Protection Agency, Carl Trygger's Foundation for Scientific Research, the Swedish Association and the Øresund Bridge Consortium (as a part of an impact assessment study).

We also express our sincere thanks to all those thousands of bird-watchers which over the years have checked the goose flocks all over Europe, reporting hundreds of thousands of re-sightings to us and recently to the data-base www.geese.org. Without this massive support from voluntary observers the study could never have been done.

References

Andersson, Å., Follestad, A., Nilsson, L. & Persson, H. 2001. Migration patterns of Nordic Greylag Geese *Anser anser*. *Ornis Svecica* 11: 19–58.

Buij, R., Melman, T.C.P., Loonen, M.J.J.E. & Fox, A.D. 2017. Balancing ecosystem function, services and disservices from expanding goose populations. *Ambio* 46 Suppl. 2: S301-S318.

Calderón, J., Mañez, M. & García, L. 1991. A note on wintering Greylag Geese *Anser anser* of the Guadalquivir Marismas. *Ardea* 79: 269–270.

Eichhorn, G., Drent, R.H., Stahl, J., Leito, A. & Alerstam, T. 2009. Skipping the Baltic: the emergence of a dichotomy of alternative spring migration strategies in Russian barnacle geese. *Journal of Animal Ecology* 78: 63–72.

Elmberg,J. Hessel, R., Fox, A.D. & Dalby, L. 2014. Interpreting seasoal range shifts in migratory birds: a critical assessment of "short-stopping" and a suggested terminology. *Journal of Onrithology* 155:571-579.

Fox, T., Ebbinge, B.S., Mitchell, C., Heinicke, T., Aarvak, T., Colhoun, K., Clausen, P., Dereliev, S., Faragó, S., Koffijberg, K., Kruckenberg, H., Loonen, M.J.J.E., Madsen, J., Mooij, J., Musil, P., Nilsson, L. Pihl, S. & van der Jeugd, H. 2010. Current estimates of goose population sizes in Western Europe, a gap analysis and assessment of trends. *Ornis Svecica* 20: 115–127.

Fox, A.D., Kahlert, J., Ettrup, H., Nilsson, L. & Hounisen, J.P. 1995. Moulting Greylag Geese *Anser anser* on the Danish island of Saltholm; numbers, phenology, status and origins. *Wildfowl* 46: 16–30.

Fox, A.D. & Madsen, J. 2017. Threatened to super-abundance: The unexpected international implications of successful goose conservation. *Ambio* 46(Suppl. 2): S179–S187.

Kampe-Persson, H. 2002. *Anser anser* Greylag Goose. *BWP Update* 4: 181–216.

Kampe-Persson, H. 2004. Halsringmärkning av häckande grågäss i Skåne 1984–2004. *Ringinform* 27: 34–36.

Kampe-Persson, H. 2010. Naturalised geese in Europe. *Ornis Svecica* 20: 155–173.

Kampe-Persson, H. 2014. Staging and wintering Taiga Bean Geese *Anser fabalis fabalis* in north-east Scania, south Sweden. *Ornis Svecica* 24: 56–78.

Lehikoinen, A., Jaatinen, K., Vähätalo, A.V., Clausen. P., Crowe, O., Deceuninck, B., Hearn, R., Holt, C.A., Hornman, M., Kewller, V., Langedoen, T., Tomankova, I., Wahl, J. & Fox, A.D. 2013. Rapid climate driven shifts in wintering distributions of three common waterbird species. *Global Change Biology* 19: 2071–2081.

Nilsson, L. 1984. Migrations of Fennoscandian Bean Geese *Anser fabalis. Swedish Wildlife Research* 13: 83–106.

Nilsson, L. 1998. The Greylag Goose *Anser anser* as a model species for the study of waterfowl breeding ecology. *Acta Zoologica Lituanica, Ornithologia* 8: 20–28.

Nilsson, L. 2006. Changes in migration patterns and wintering areas of south Swedish Greylag Geese *Anser anser*. Pp 514–516 in *Waterbirds around the World* (Boere, G.C., Galbraith, C.A. & Stroud, D.A., eds.). The Stationary Office. Edinburgh, UK.

Nilsson, L. 2011. The migrations of Finnish Bean Geese *Anser fabalis* in 1978–2011. *Ornis Svecica* 21: 157–166.

Nilsson, L. 2013. Censuses of staging and wintering goose populations in Sweden 1977/78–2011/12. *Ornis Svecica* 23: 3–45.

Nilsson, L., Follestad, M.A., Koffijberg, K., Kuijken, E., Madsen, J., Mooij, J., Mouronval, J.B., Persson, H., Schricke, V. & Voslamber, B. 1999b. Greylag Goose *Anser anser*: Northwest Europe. Pp 182–201 in *Goose populations of the Western Palearctic. A review of status and distribution* (Madsen, J., Cracknell, G. & Fox, A.D., eds). Wetlands International Publ. No. 48, Wetlands International, Wageningen, The Netherlands. National Environmental Research Institute, Rønde, Denmark.

Nilsson, L., Green, M. & Persson, H. 2002. Field choice in spring and breeding performance of Greylag Geese *Anser anser* in southern Sweden. *Wildfowl* 53: 7–25.

Nilsson, L. & Haas, F. 2016. Distribution and numbers of wintering waterbirds in Sweden in 2015 and changes during the last fifty years. *Ornis Svecica* 26: 3–54.

Nilsson, L. Kahlert, J. & Persson, H. 2001. Moult and moult migration of Greylag Geese *Anser anser* from a population in Scania, south Sweden. *Bird Study* 48: 129–138.

Nilsson, L. & Kampe-Persson, H. 2013. Field choice of autumn staging and wintering geese in southwestern Sweden 1977/78–2011/12. *Ornis Svecica* 23: 46–60.

Nilsson, L. & Kampe-Persson, H. 2017. Local movements of Greylag Geese *Anser anser* in South Sweden during the non-breeding season. *Ornis Svecica* 27: 13–22.

Nilsson, L. & Persson, H. 1984. Non-breeding distribution, numbers and ecology of Bean Goose, *Anser fabalis*, in Sweden. *Swedish Wildlife Research* 13: 107–170.

Nilsson, L. & Persson, H. 1991. Selection and exploitation of feeding areas by staging and wintering geese in southernmost Sweden. *Ornis Svecica* 1: 81–92.

Nilsson, L. & Persson, H. 1992. Feeding areas and local movement patterns of post-breeding Greylag Geese *Anser anser* in South Sweden. *Ornis Svecica* 2: 77–90.

Nilsson, L. & Persson, H. 1994. Factors affecting the breeding performance of a marked Greylag Goose *Anser anser* population in south Sweden. *Wildfowl* 45: 33–48.

Nilsson, L. & Persson, H. 1996. The influence of the choice of winter quarters on the survival and breeding performance of grelag geese (*Anser anser*). *Gibier Faune Sauvage*, *Game Wildlife* 13: 557–571.

Nilsson, L. & Persson, H. 1998. Field choice of staging Greylag Geese *Anser anser* in relation to changes in agriculture in South Sweden. *Ornis Svecica* 8: 27–39.

Nilsson, L. & Persson, H. 2001a. Change of mate in a Greylag Goose *Anser anser* population: effects of timing on reproductive success. *Wildfowl* 52: 31–40.

Nilsson, L. & Persson, H. 2001b. Natal and breeding dispersal in the Baltic Greylag Goose *Anser anser*. *Wildfowl* 52: 21–30.

Nilsson, L., Persson, H. & Voslamber, B. 1997. Factors affecting survival of young Greylag Geese and their recruitment into the breeding population. *Wildfowl* 48: 72–87.

Pavon-Jordan, D., Fox, A.D., Clausen, P., Dagys, M., Deceuninck, B., Devos, K., Hearn, R.D., Holt, C.A., Hornman, M., Keller, V., Langedoen, T., Lawickii, L., Lorentsen, S.H., Luigujoe, L., Meissner, W., Musil, P., Nilsson, L., Paquet, J.-Y., Stipniece, A., Stroud, D.A., Wahl, J., Zenaqtello, M. & Lehikoinen, A. 2015. Climate-driven changes in winter abundance of a migratory waterbird in relation to EU protected areas. *Diversity and Distributions* (2015): 1–12.

Persson, H. 1993. Arrival patterns of Greylag Geese *Anser anser* in the Guadalquivir Marismas. *Wildfowl* 44: 19–23.

Persson, H. 1994a. Neck-banding of Greylag Geese *Anser anser* in Scania, 1984–1993. *Anser* 33: 101–106. (in Swedish with English summary).

Persson, H. 1994b. Autumn migration in the Greylag Goose *Anser anser*; non-stop flight from the Netherlands to Coto de Doñana? *Limosa* 67: 79-80. (in Dutch with English summary).

Persson, H. 1996a. Survival rates and breeding success in a marked Greylag Goose *Anser anser* population, wintering in the Guadalquivir Marismas. *Revista Florestal* 9: 189–199.

Persson, H. 1997. Gestión de las poblaciones de gansos en el Paleártico Occidental. Pp. 1–17 in *Las Salinas de Villafáfila: "Humedal estratégico europeo para aves"*. Colegio Oficial de Veterinarios de Zamora – A.D.R.I. "Palomares", Zamora.

Persson, H. 1999. La chasse á l'Oie cendrée *Anser anser* en France… ou de l'exploitation excessive d'une resource naturelle. *Alauda* 67: 223–230.

Persson, H. 2000a. Neck-collaring of Greylag Geese *Anser anser* in Scania, 1984–2000. *Anser* 39: 167–172. (in Swedish with English summary).

Persson, H. 2000b. Neck collar retention in a Greylag Goose *Anser anser* population. *Ornis Svecica* 10: 155–160.

Persson, H. & Urdiales, C. 1995. The disappearance of the Tundra Bean Goose *Anser fabalis rossicus* from the Iberian Peninsula. *IWRB Goose Research Group Bulletin* 6: 17–19.

Ramo, C., Amat, J.A., Nilsson, L., Schricke, V., Rodriguez-Alonso, M., Gomez-Crespo, E., Jubete, F., Navedo, J.S., Masero, J.A., Palacios, J., Boos, M. & Green, A.J. 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(10): e0140181.

Salomonsen, F. 1968. The moult migration. *Wildfowl* 19: 5–24.

Sammanfattning

I likhet med de flesta andra gåsbestånd i Europa har grågåsen visat en markant beståndsökning under senare decennier (Nilsson 2013) och den nordvästeuropeiska populationen beräknas nu till ca 960 000 individ (Fox & Madsen 2017). Som en följd av de markanta ökningarna av gåsbestånden kom många klagomål rörande gåsskador (Buij et al. 2017). Detta ledde i sin tur till att flera forskningsprogram rörande gäss startade runt om i Europa. I de nordiska länderna startade ett grågåsprojekt med bl.a. halsmärkning av grågäss 1984 (Andersson et al. 2001). Projektet var ursprungligen planerat för en femårsperiod, men i SW Skåne fortsatte märkningarna till 2009 (och kontroller efter märkta gäss till och med 2012) och i Norge till och med 2017.

Traditionellt flyttade grågässen från nordvästeuropas fastland längs Atlantkusten söderut via rastplatser i främst Nederländerna till vinterområden i Spanien, huvudsakligen Guadalquivirs delta i den sydvästra delen av landet (Nilsson et al. 1999, Andersson et al. 2001). Under de år vi studerade grågässens flyttningsvanor noterades betydande förändringar med färre övervintrande grågäss från sydligaste Sverige i södra Spanien och en ökad övervintring längre norrut främst i Nederländerna (Nilsson 2006).

I denna uppsats analyserar vi hela det insamlande materialet från halsmärkningarna i SW Skåne för 1985-2012 för att belysa förändringar i grågässens flyttningsvanor och val av övervintringslokaler. Vi uppdaterar därmed den tidigare analysen som publicerades av Andersson et al. (2001).

Material och metoder

Den sydsvenska delen av undersökningarna koncentrerades till två sjöområden i södra Skåne (Figur 1). Huvuddelen av märkningarna skedde i det västra sjöområdet främst koncentrerade till två sjöar; Klosterviken och Yddingen. Under de första åren märktes också en del grågäss i det östra sjöområdet. Förutom flyttningsundersökningarna genomfördes ett flertal andra studier av olika aspekter på grågåsens ekologi i det västra sjöområdet (Nilsson

& Persson 1992, 1994, 2001a, 2001b, Nilsson et al. 1997, 2002, Nilsson 1998).

Fångst ägde rum på häckningsområdena när ungarna var ca. sex veckor gamla och då föräldrarna fortfarande var flygodugliga på grund av ruggning. Gässen drevs in i nätfållor för att kunna märkas. Gässen märktes med halsringar av UV-beständig plast, vilka hade en ingraverad kod med tre tecken. Alla gäss märktes dessutom med en RC-ring. Vissa av dem fick också en plastring med graverad kod på det andra benet.

Totalt märktes 685 vuxna gäss och 1954 ungar i området under projektet. Fram till och med 2012 erhölls 15 296 rapporter om avlästa gäss utanför märkområdet. Därtill kommer 100 050 avläsningar från undersökningsområdet i södra Skåne.

Resultat

De tidiga resultaten från det nordiska grågåsprojektet har tidigare presenterats av Andersson et al. (2001). I denna uppsats koncentrerar vi oss därför på att jämföra flyttningsmönstret hos grågässen i början och i slutet av undersökningsperioden för att belysa de stora förändringar som skett under de år undersökningarna pågått.

Merparten av de märkta grågäss som setts utanför undersökningsområdet har rapporterats från Nederländerna och Spanien (Figur 2 – 4) med betydligt färre observationer av märkta gäss från andra länder (Tabell 1). Under de första åren av projektet rapporterades upp till 50% av de individer som sågs ett givet år från Nederländerna, medan andelen för Spanien var något lägre, ca 35% (Figur 2). Genom åren har denna andel minskat dels beroende på ökande gåsbestånd och dels på grund av gässens ändrade flyttningsvanor.

Den månatliga utbredningen av rastande och övervintrande grågäss under den tidiga och sena delen av undersökningsperioden illustreras i en serie kartor (Figur 4), medan gässens tidsmässiga uppträdande under olika perioder i viktiga länder illustreras i en serie diagram (Figur 3). Under sommaren kommer flertalet avläsningar från Sverige, men under den tidiga delen av studien rapporterades flera avläsningar också från Nederländerna under sommaren, då många gäss flög till Flevoland för att rugga. I takt med att gässen blev vanligare minskade antalet ruggare som flög till Flevoland och en ny ruggningsplats etablerades på Saltholm i Öresund. Under senare delen av 1990-talet gjordes däremot ett större antal avläsningar under ruggningsperioden på Saltholm i Öresund, men dessa undersökningar upphörde år 2000.

Oktober och november var de huvudsakliga flyttningsmånaderna för de skånska grågässen och många rapporter om märkta gäss erhölls från speciellt Nederländerna, men under de tidiga åren nådde en del märkta gäss i Spanien redan i oktober. Genom åren skedde en senareläggning av flyttningen söderut och de senaste åren nådde få gäss Spanien under hösten. Gässen har också stannat längre norrut under den senare delen av undersökningsperioden (Figur 5).

December och januari är typiska vintermånader för grågässen och observationer har erhållits längs hela flyttningsstråket från Sydsverige ner till södra Spanien. Under vintern har en mycket markant förskjutning norrut skett i grågässens vinterutbredning (Figur 5, 6). Medel-latituden för januariobservationerna av märkta grågäss visade en stadigt ökande trend och försköts under undersökningsperioden ca 10 grader norrut (Figur 6). För ett betydande antal individer har vinterkvarteret kunnat fastställas under två på varandra följande år (Tabell 2). Totalt bytte minst 13% av gässen vinterkvarter mellan två år, nästan i samtliga fall innebar detta att de övervintrade längre norrut (Tabell 3).

Genom åren har grågässen också kommit att stanna allt längre tid i södra Sverige. Det är alltid svårt att säkert fastställa när de märkta gässen lämnar ett område, men det är däremot lättare att fastställa när de första observationerna görs. I Nederländerna är ett mycket stort antal ornitologer intresserade av att läsa av färgringar och som nämnts har vi en hög frekvens av avlästa halsringar därifrån. Under de år undersökningarna pågått har medianen för första observationen av halsmärkta gäss från Skåne i Nederländerna inträffat ungefär en månad senare (Figur 7). På motsvarande sätt anländer gässen allt tidigare till häckningsområdena i Skåne (Figur 8) och median ankomsten för de märkta var ungefär en månad tidigare i slutet av studieperioden. Även bland de grågäss som flyttade ända till vinterområden i södra Spanien var flera individer tillbaka i häckningsområdena i februari. Under åren 1986-1990 var denna andel 20%, medan motsvarande andel för åren 2001-2005 var 40% (Figur 9).

Diskussion

Grågässen från södra Skåne flyttar söderut längs Europas västkust, ett stråk som utnyttjas också av gäss från andra delar av landet (Andersson et al. 2011, Nilsson in prep. Nilsson & Hermansson in prep.). Endast få gäss från området rapporterades från andra dela av Europa, till exempel de Brittiska öarna, dit några individer från den skånska populationen uppenbarligen rekryterats till den lokala häckande populationen. Analysen av de märkta gässen visar också klart på de betydande förändringar som skett i gässens flyttningsvanor och val av övervintringsområden, vilka förskjutits norrut under de nästan trettio år studien pågått.

Förändringarna i flyttnings- och övervintringsvanor framträder också tydligt i resultaten från de nationella och internationella gåsinventeringarna (Nilsson 2013, Ramo et al. 2015). När gåsinventeringarna startade i Sverige sågs knappt några grågäss i Sverige i januari, medan upp till 50 000 räknats under senare år, vilket motsvarar ca 25% av beståndet föregående höst.

Liknande förändringar i rast och övervintringsvanor har rapporterats från flera andra gåsarter både i Sverige och från andra länder. Sädgåsen har visat betydande förändringar i sina rastnings- och övervintringsvanor. Sålunda övervintrade stora antal tundrasädgäss under 1930-talet i Spanien, medan de helt saknas där sedan 1990-talet (Persson & Urdiales 1995). För taigasädgåsen har vi sett liknande förändringar i Sverige, där de numera knappast finns i Skåne tidigt om hösten (Nilsson 1984, 2011, 2013, Nilsson & Persson 1984). Snabba och stora förändringar i uppträdandet har också noterats i Sverige för den vitkindade gåsen (Eichhorn et al. 2009) samt för tundrasädgåsen och spetsbergsgåsen (Nilsson 2013).

Många olika faktorer kan ha orsakat dessa betydande förändringar i gässens flyttningsvanor och vinterutbredning. Förändringar i klimatet är en faktor man lätt kommer att tänka på, men därutöver har stora förändringar skett i jordbruket genom åren samtidigt som de mildare och snöfattiga vintrarna gör att gässen lättare kommer åt födan. Man måste också beakta att gässen ökat markant i antal (Fox & Madsen 2017), vilket kan ha lett till ökad konkurrens.

ORNIS SVECICA 28: 39–47, 2018

Lifetime reproductive success of Greylag Geese *Anser anser* breeding in south Sweden

Livslång häckningsframgång för grågäss Anser anser *häckande i* södra Sverige.

LEIF NILSSON & HAKON KAMPE-PERSSON

Abstract

During 1984–2009, 664 adults and 1,944 goslings of Greylag Geese *Anser anser* were neck-banded in south-west Scania, Sweden. After hatching the area was carefully searched for marked geese, giving more than 100,000 re-sightings. Of those marked as goslings 71% survived the first year, 52% the second year, and the oldest bird recorded was 25 years. About 50% of the survivors were recruited into the breeding population when two to three years old. Of 1,187 geese that survived for at least two years, 25% produced at least one brood of small young, and 18% at least one fledged young. The maximum lifetime number of broods with fledged young was nine, but 50% of the geese known to have bred successfully produced only one brood of fledged young. Ten percent of the geese seen with small goslings produced 47% of all fledged young. The maximum number of fledged young for a goose of known age was 32 (age 15 years), but two geese marked as adults and followed for 16 and 17 years produced 40 fledglings each.

Leif Nilsson, Department of Biology, Biodiversity, University of Lund, Ecology Building, SE-223 62 Lund, Sweden. E-mail: leif.nilsson@biol.lu.se
Hakon Kampe-Persson, Pulmaņi, Glūdas pagasts, Jelgavas novads, LV-3040, kampepersson@hotmail.com

Received 12 March 2018, Accepted 26 April 2018, Editor: Sören Svensson

Introduction

That only a small proportion of individuals is responsible for the recruitment of young into the next generation has been recorded for a range of avian species, either because the others die before reaching breeding age or do not manage to produce young successfully (Newton 1989). This applies both to smaller short-lived passerines and to larger and long-lived birds such as waterfowl (Cooke et al. 1995, Blums & Clark 2004, Rees 2006, Black et al. 2014, Weegman et al. 2016). In geese, these aspects have been studied in arctic-breeding geese including the Barnacle Goose *Branta leucopsis* (Black et al. 2014), Lesser Snow Goose *Anser caerulescens caerulescens* (Cooke et al. 1995) and Greenland White-fronted Goose *Anser albifrons flavirostris* (Weegman et al. 2016), but no corresponding studies have been published for geese breeding in temperate regions. During recent decades, the Barnacle Goose has established populations in temperate regions such as the islands in the Baltic Sea and in the Dutch delta. Large scale studies of the species have been undertaken on both Svalbard and Gotland but a detailed study comparing the lifetime reproductive output between the two populations is still lacking (Black et al. 2014).

Information about the breeding performance of individual Greylag Geese *Anser anser*, a temperate breeding goose species, was collected as a part of a large-scale neck-banding program, originally started by the Nordic Council for Wildlife Research (NKV) to illustrate the migration patterns of different populations in the Nordic countries (Andersson et al. 2001). In addition to the study of migration, intensive studies of different aspects of breeding ecology and population dynamics were carried out in a study area in south-west Scania, south Sweden. Neck banding started in the area in 1984 and continued through 2009, with observations of neck-banded geese running through 2013. For general information about the breeding performance of Greylag Geese in the study area see Nilsson (2016) and Nilsson & Persson (1994), and references cited there.

In the present paper, we use the data from this individually marked population of Greylag Geese to calculate the reproductive output for individual geese over their lifetime, measured as the total number of fledged young produced.

Study area

The current analysis is based on the Greylag Geese that were breeding and neck-banded in south-west Scania, southernmost Sweden (Figure 1), mainly in the lakes Yddingen, Fjällfotasjön, Börringesjön and Klosterviken.

During late summer and early autumn, regular searches after neck-banded Greylag Geese were undertaken in a larger area to establish the fledging success for families leaving the breeding area early. Searches were also made in the Foteviken area at the coast (Figure 1), where geese gather on the vast shore meadows in late summer. For a general description of this wider area, see Nilsson & Persson (1992, 1998).

The Greylag Goose started to breed in the study area during the late 1960s. When the study started in 1984, 120 pairs were breeding. There was a more or less steady increase to a peak of 1,340 pairs in 2004, after which the population decreased to between 775 and 985 pairs in 2009–2013 (Nilsson 2016).

Methods

We based our estimates of the breeding success on observations of pairs where at least one in the pair was marked with a neck-band. The families concentrate on certain feeding areas close to the breeding lake where it is easy to obtain an overview of the newly hatched families. The families occur mostly as discrete units easy to follow. The brood rearing areas were checked several times a week after the first appearance of small broods until the last broods fledged.

As most geese breed in arctic and other distant areas the method we used cannot be used for establishing breeding results in these populations, so the productivity has to be established on the basis of age ratio counts and observations of yearlings returning to the wintering areas with their parents (Black et al. 2014, Weegman et al. 2016). Goose families do not break up until late winter or just before spring migration so this method does also work for temperate breeding geese but our method gives more precise results. We can establish the production of both small and fledged young, whereas the other methods only give information of the number of fledged young that survive their first autumn migration.

We caught families of Greylag Geese during early summer, about three weeks before the goslings started to fly, and when the parents still were in the moulting phase and unable to fly, by driving them into nets mounted on the shore meadows at the different lakes and on the golf course at Lake Yddingen (Persson 1994, Andersson et al. 2001). Marking started in 1984 and the last few geese were marked in 2009. Sightings of marked individuals continued to be collected until spring 2013. In total, 664 adults and 1,944 goslings were neck-banded in the study area. These birds yielded a total of 100,500 re-sightings from the local area in south-west Scania and 15,200 re-sightings outside the local area.

Besides a neckband, each bird was fitted with a metal ring from the Swedish ringing office on one of the legs and from 1998 a numbered plastic ring on the other leg. In this way, it was possible to put on a new neckband (with a new code) if the bird was recaptured. As there are some neckband losses, where the bird was not recaptured, there will be a risk of bias when considering long-lived individual's life-time production of young. The values presented here are therefore to be regarded as minima.

In early spring, we searched intensively all potential feeding areas for Greylag Geese to count the number of pairs before they dispersed for nest building and to identify all marked individuals. During the entire spring and early summer, the area was checked at least twice a week for neck-banded individuals, often simultaneous with the pair counts, to establish survival, arrival of the marked geese, pair bonds, and the production of small and fledged young. When the young hatched, intensive surveys of all feeding areas around all lakes were performed at least three times a week. Families with neck-banded adults were checked for fledglings also in the summer. Once a week these searches also extended to staging areas at the coast (Figure 1).

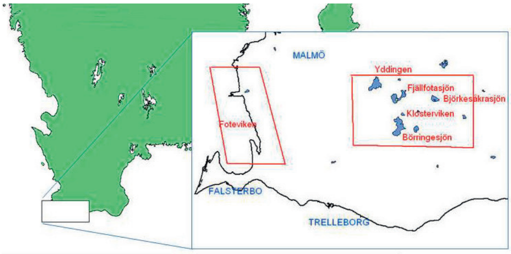


Figure 1. Map of southernmost Sweden showing the geographical position of the study area.
Karta över sydligaste Sverige med undersökningsområdet markerat.

The proportion of the geese attempting to breed is not known as most of the geese placed their nests where it was impossible to check for nests. Instead, we define recruitment into the local breeding population as the first time a bird marked as gosling was seen with small young. A few parents might have been overlooked if they lost all young before reaching the brood-rearing areas. This risk is considered to be small as the main brood-rearing areas were checked on nearly a daily basis during the main hatching period.

Early brood amalgamation taking place before the family was seen for the first time could normally not be accounted for, as it was usually impossible to identify adopted goslings (Persson 2002). Nine broods that were too large to have been hatched by one female (>12 young) were recorded, and seven of these still numbered more than 12 young at fledging. The geese with apparently amalgamated broods were not included in the calculations of the total production of fledged young.

When calculating the lifetime production of fledged young for geese of known age, we used only geese marked as goslings before the year 1999, which were later recruited into the breeding population, to avoid bias from the very few individuals surviving over the end of the study period. Only geese seen in the study area every year were included in the analysis.

Results

Survival and recruitment into the breeding population

Of the 1,944 Greylag Geese neck-banded as goslings, a minimum of 74% (1438 individuals) survived their first year and 61% (1187 individuals) survived to at least two years old, i. e. the age of the earliest recruits. The maximum age recorded for a bird marked as gosling included in the analysis here was 18 years, although one bird with an incomplete breeding record reached the age of 25 years (Figure 2).

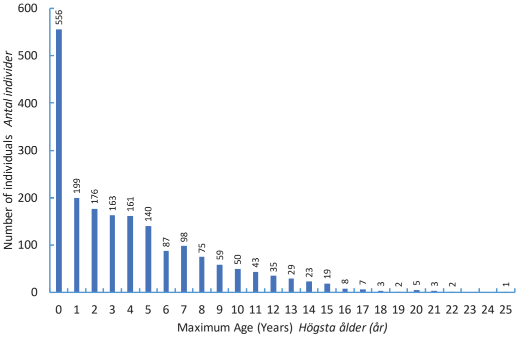


Figure 2. Number of Greylag Geese *Anser anser* marked as goslings that reached different recorded maximum ages.
Antal grågäss märkta som ungar som noterats ha nått olika högsta ålder.

For the 664 Greylag Geese marked as breeding adults, it was not possible to establish their life span as they were at least 2–3 years old at marking. The maximum number of years a bird marked as adult was available for observation in this study was 22, which gives a minimum age of at least 24–25 years.

Only 15% of the birds marked as goslings were ever seen with young (Figure 3). Of all birds marked as goslings and surviving for at least two years (1189 individuals), 26% were at least once found with a brood of small young. About 27% of these lost their young before fledging and only 18% of all birds marked as goslings and surviving to the age of at least two years were ever seen with any fledged young.

Of the 309 birds (102 males, 207 females) marked as goslings that were monitored each year until they joined the local breeding population, 18% (18 males, 38 females) were found to have bred for the first time at age 2 years and about 50% (33 males, 82 females) when aged 3 years (Figure 4). Some birds did however start breeding much later; the oldest individuals were seen with small young for the first time at eight years of age. There were no differences between the sexes in the age of first breeding. The difference in male and female sample sizes may be partly attributable to a higher rate of neckband losses for males (Persson 2000) but also to male dispersal away from the natal area (Nilsson & Persson 2001a).

Total production of fledged young

The maximum number of fledged broods produced by a Greylag Goose of known age was nine, but 50% of 160 Greylag Geese that bred successfully (i.e. raised young to fledging) only produced one brood of fledged young (Figure 5). The proportion of parents marked as goslings producing fledged young increased by age: 56% (38 of 88) for ages 2–5 years, 74% (91 of 122) for ages 6–10 years, and 100% (6 of 6) for ages >10 years.

Most individuals recruited into the breeding population (seen at least once with small young) had a lifetime production of young that was zero (32%) or only between one and nine (54%) (Figure 6). But there are some exceptions, and one Greylag Goose managed to raise 32 young to fledging. The most productive 10% (15 to 32 young in Figure 7) accounted for 47% of all fledged young. There is not unexpectedly an effect of age here and the six oldest birds (>10 years old) were all productive

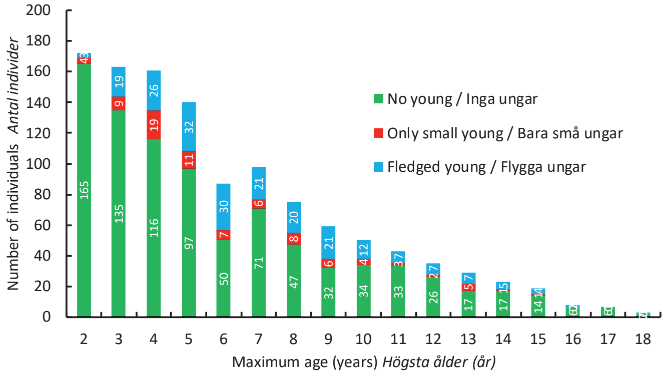


Figure 3. Number of Greylag Geese *Anser anser* that had been observed with young at least once or never when having reached different maximum ages (at least two years). All had been marked as goslings.
Antal grågäss som setts med unge minst en gång eller aldrig när de nått olika högsta ålder (minst 2 år). Alla hade märkts som ungar.

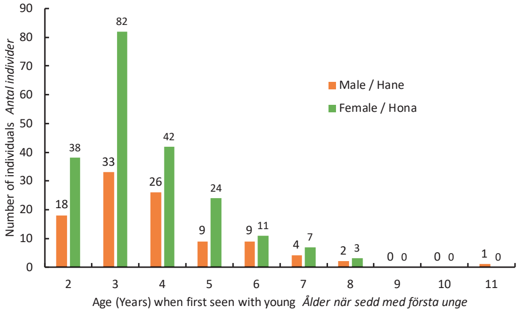


Figure 4. Number of Greylag Geese *Anser anser* observed with young for the first time at different age, all marked as goslings.
Antal grågäss som setts med ungar för första gången vid olika ålder, alla märkta som ungar.

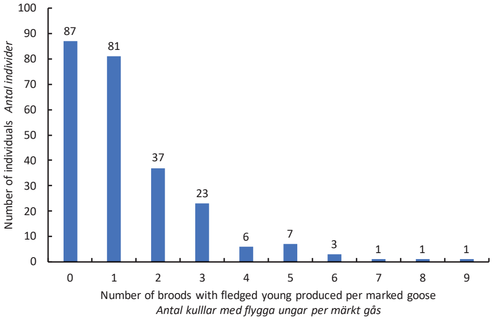


Figure 5. Number of Greylag Geese *Anser anser* that produced different number of broods with fledged young. All marked as goslings.
Antal grågäss som producerade olika antal kullar med flygga ungar. Alla märkta som ungar.

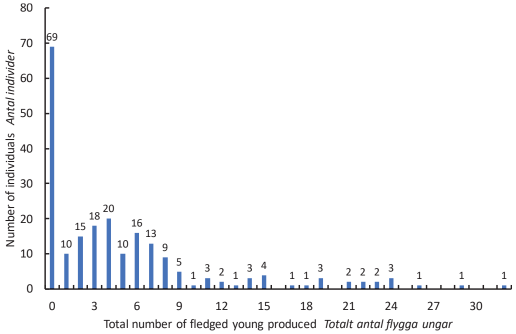


Figure 6. Number of Greylag Geese *Anser anser*, marked as goslings and recruited into the breeding population (seen with small young), with different lifetime production of fledged young.
Antal grågäss, märkta som ungar och rekryterade in i den häckande populationen (sedda med små ungar), med olika livslång produktion av flygga ungar.

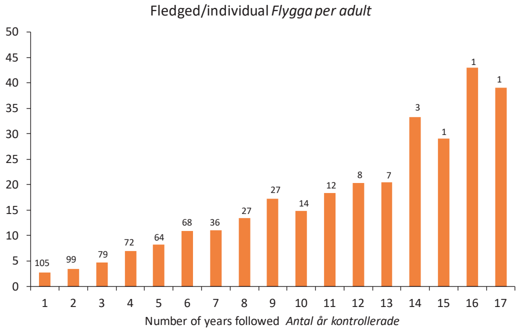


Figure 7. Mean number of fledged young produced by Greylag Geese *Anser anser* marked as breeding adults (i.e. age not known) in relation to the number of years observed. Values above columns give sample size, number of individuals.
Medeltal flygga ungar producerade av grågäss märkta som häckande vuxna (dvs. ålder okänd) i relation till antalet år de kunnat följas. Antalet individ markerat över staplarna.

producing on average 18 fledged young each. 88 individuals with a maximum life span of 2–5 years produced an average of 2.7 young, whereas 122 individuals reaching a maximum life of 6–10 years had an average production of fledged young of 6.1.

For Greylag Geese marked as breeding adults, it is not possible to give a true measure of the total production of fledged young, as these birds might have been breeding a number of years before they were marked. For these birds, there was a steady increase in the mean number of fledglings produced with the number of years the birds were under observation (Figure 7). Two successful individuals, followed for 16 and 17 years respectively, each managed to produce at least 40 fledged young. Overall, as for the geese of known age, those marked as breeding adults mostly had a quite low total production of fledged young over the time they could be followed.

Factors affecting the lifetime production of young

Longevity was the most important factor determining the lifetime production of young. The correlation between lifespan and lifetime production of young was highly significant, even though there was a large spread for parents reaching the same age (Figure 8, linear regression r = 0.47, P < 0.001, n = 216). In the same way there was a significant correlation between the length of life and the number of breeding attempts (linear regression, r = 0.57, P < 0.001, n = 186).

In an earlier analysis (Nilsson et al. 1997), the weight at marking, about three weeks before they fledged, was found to have a marked influence on the survival and recruitment rate (and age) of the Greylag Geese, with almost all recruits having above median weight at marking. Here, we use the weight close to fledging as a proxy for the condition of the fledgling. We compared these weights at marking with the future total production of fledged young for the same individuals and found a small but significant effect (Figure 9, R = 0.21, P < 0.01, n =161).

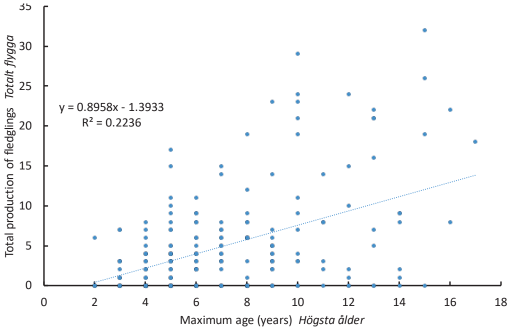


Figure 8. Total production of fledglings in relation to the age of the parent Greylag Geese *Anser anser* marked as goslings. Linear regression R=0.47, P<0.001, n=216.
Total production av flygga ungar i relation till föräldrarnas ålder för grågäss märkta som ungar. Linjär regression R=0,47, P<0,001, n=216.

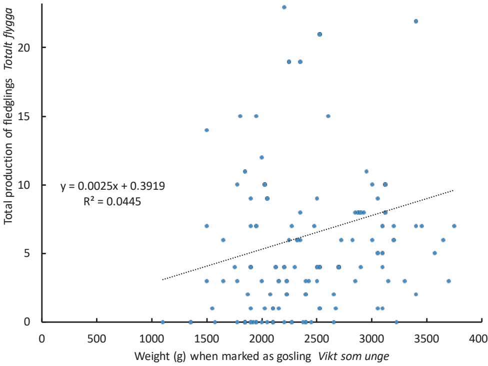


Figure 9. Life-time production of fledged young by Greylag Geese *Anser anser* marked as goslings in relation to the weight at marking of the parents (as a proxy to their condition). Linear regression R= 0.21, P<0.01, n=161.
Totalproduktion av flygga ungar för grågäss märkta som ungar i relation till föräldrarnas vikt vid märkning (som mått på deras kondition). Lineär regression R= 0.21, P<0.01, n=161.

The choice of winter quarter has earlier been found to have an effect on the survival and breeding performance of individual Greylag Geese (Nilsson & Persson 1996). This effect was also found in the current study. Geese wintering in Doñana in southernmost Spain had a lower breeding output (5.2 young per bird; n=86) than geese wintering at Villafáfila in northern Spain (10.6; n = 17) or in the Dutch delta (8.6; n = 94).

Experience was found to influence lifetime production of young. 44% of the Greylag Geese of known age producing fledged young in their first breeding attempt also managed to produce a brood of fledged young in the following year.

Effects on production of young in the second generation

For 27 Greylag Geese marked as goslings it was possible to establish the total production of their young. No correlation was found between the total production of fledged young of the parents and of their offspring (linear regression r = 0.05, N.S., n = 27).

Discussion

Only a small proportion of the Greylag Geese in the study population in south Sweden managed to produce any fledged young but on the other hand, a small number of the Greylag Geese in the population fledged a larger number of young. The same was the case in the Svalbard Barnacle Goose, where only 17% of the marked birds arrived in the winter quarters in Scotland with a brood of fledged young (Prop & de Vries 1993, Black et al. 2014). Unfortunately, there are no similar data available from the temperate breeding populations of the species. A similarly low proportion of Lesser Snow Geese Cooke et al. (1995), and Greenland White-fronted Goose (Weegman et al. 2016) returned to the winter quarters with fledged young. Bewick's Swans *Cygnus columbianus bewickii* also breed in the arctic and like the geese, many pairs had a low success rate (Rees 2006).

Local conditions and individual characteristics were important for the recruitment of Greylag Geese into the breeding population in south Sweden (Nilsson et al. 1997), heavier goslings recruiting into the breeding population at an earlier age than lighter ones. Young Greylag Geese were first found to recruit at an age of two years, but the vast majority of the recruits was older. Similar results were found for the Greater Snow Geese *Anser caerulescens atlantica* and Barnacle Geese, which are able to breed at an age of two years but generally recruited into the breeding population at their third or fourth year (Reed et al. 2003, Black et al. 2014). In the studied population of Greenland White-fronted Geese, the recruitment age was generally higher, and varied with the local conditions experienced before the first breeding attempt (Weegman et al. 2016).

In the Greylag Goose breeding in south Sweden, earlier studies established the importance of several factors on the breeding results, such as choice of winter quarters and breeding lake, amount of precipitation in the winter quarters, arrival time in spring, amount of rainfall during the first days after hatching and disease (Nilsson & Persson 1994, 1996, Persson 1996, Nilsson et al. 1997). Change of mate could also influence the result causing a lower productivity (Nilsson & Persson 2001b).

Moreover, young with a higher weight at fledging had a higher survival, recruited earlier into the breeding population and had a better breeding output than lighter individuals (Nilsson et al. 1997). In this way, the conditions in the breeding areas (lakes) will influence the reproductive results of the breeding Greylags.

The size of the Greylag Geese at fledging still had a significant but small effect on their lifetime reproductive success (this study). Similarly, larger Barnacle Geese were found to be more successful than smaller individuals (Black et al. 2014). Better breeding results of larger individuals have also been reported for Lesser Snow Geese and Brent Geese *Branta bernicla* (Ankney & McInnes 1978, Alisauskas & Ankney 1990, Sedinger et al. 1995).

In general, factors in the breeding areas had a relatively small effect on the life-time reproduction. Differences in the breeding environment explained about 4.5 % of the variation of the life-time reproduction success of breeding Barnacle Geese in the Svalbard population (Black et al. 2014), whereas 84 % could be attributed to individual characteristics. Similar results were found for the Greenland White-fronted Goose, Weegman et al. (2016).

The choice of winter quarters was also found to have a significant influence on the lifetime reproduction of fledged young of Greylag Geese, individuals wintering in the Dutch delta having a higher lifetime production than those migrating all the way to the former traditional wintering area in southwestern Spain. For those wintering in southwest Spain, there was a strong correlation between the amount of precipitation in autumn in the Guadalquivir Marismas and the breeding output the following season (Persson 1996). Thus, the geese show a similar carry-over effect from the winter conditions to the breeding results as has been established for swans (Nilsson 1979, Brazil 2003, Rees 2006).

Food quality during brood-rearing and predation can have an impact on the breeding output. In an earlier study in the same area, fledging rate was related to the amount of grazed pastures or similar areas that the families had access to during the brood-rearing period (Nilsson et al. 1997). The lowest survival rate was found at the lake lacking such pastures, whereas the highest rates were found at lakes with a rich supply of grazed pastures. During the study period, the supply of grazed pastures in the study area has decreased, as grazing pressure by livestock in many pastures has diminished or ceased.

Geese select nest sites to avoid predators. Islets are preferred when available as hatching success is higher on natural islets than in reed beds (Witkowski 1983). On islets, they are often colonial, with nests as close as one meter (for references, see Kampe-Persson 2002). Another way of avoiding predators is to place the nest in a tree, in an old raptor nest or in a hollow (Kampe-Persson 2007).

In the early years of our study, the Red Fox *Vulpes vulpes* was virtually absent from the study area but later; the species re-populated the study area. Besides killing goslings, the foxes restricted the available brood-rearing area by forcing goose families to feed closer to water. On Vega (Norway), White-tailed Eagles *Halieatus albicilla* killed at least five percent of brooding females on the nest in the early 1990s (Follestad 1994). During the latter part of the study period, White-tailed Eagles spread to the study area. Some geese were killed on their nests and some other geese may have been flushed from the nest by the eagles exposing them to crow predation, which in some years was important (cf. Nilsson et al. 1997).

From what have been said in the last few paragraphs there are indications that the conditions for the production of young was better for the Greylag Geese during the early part of the study. During the study period, the breeding population in the area increased dramatically and Nilsson (2016) found evidence for density-dependent effects. These effects will explain why two birds marked as adults produced at least 40 fledged young each, while none of the birds of known age produced more than 32 fledged young. The latter group of geese was not available until a few years later, when the conditions for the geese may have started to deteriorate.

Acknowledgements

The Greylag Goose project started as a joint Nordic program supported by the Nordic Council for Wildlife Research (NKV). Over the years, the project was supported by different grants from the Swedish Environmental Protection Agency and the Swedish Sportsmen's Association ("Jägartjugan"). During some years, neck-banding was supported by the Øresund Bridge Company as a part of one of their control programs. The second author was responsible for the catching and marking operations during the first 24 years, with the help of a large number of voluntary "goose-catchers".

References

Alisauskas, R.T. & Ankney, C.D. 1990. Body size and fecundity in lesser snow geese. *Auk* 107: 440–443.

Andersson, Å., Follestad, A., Nilsson, L. & Persson, H. 2001. Migration patterns of Nordic Greylag Geese *Anser anser*. *Ornis Svecica* 11: 19–58.

Ankney , C.D. & MacInnes, D.C. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. *Auk* 95: 459–471.

Black, J.M., Prop, J. & Larsson, K. 2014. *The Barnacle Goose*. T & AD Poyser, London.

Blums, P. & Clark, R.G. 2004. Correlates of lifetime reproductive success in three species of European ducks. *Oecologia* 140: 61–67.

Brazil, M. 2003.The *Whooper Swan*. T & AD Poyser, London.

Cooke, F., Rockwell, R.F. & Lank, D.B. 1995. *The Snow Geese of La Pérouse Bay*. Oxford University Press, Oxford, UK.

Follestad, A. 1994. Background for a management plan for geese in Norway. *Nina Utredningar* 65: 1–78. (Norwegian with English summary).

Kampe-Persson, H. 2002. *Anser anser* Greylag Goose. *BWP Update* 4: 181–216.

Kampe-Persson, H. 2007. Tree-nesting – a new trend among Swedish Greylag Geese? *Ornis Svecica* 17: 187–189. (Swedish with English summary).

Newton, I. 1989. *Lifetime Reproduction in Birds*. Academic Press, London.

Nilsson, L. 1979. Variation in the production of young in swans wintering in Sweden. *Wildfowl* 30: 129–134.

Nilsson, L. 2016. Possible density-dependence in an expanding population of Greylag Goose *Anser anser* in south Sweden. *Wildfowl* 66: 98–111.

Nilsson, L. & Persson, H. 1992. Feeding areas and local movement patterns of post-breeding Greylag Geese *Anser anser* in South Sweden. *Ornis Svecica* 2: 77–90.

Nilsson, L. & Persson, H. 1994. Factors affecting the breeding performance of a marked Greylag Goose *Anser anser* population in south Sweden. *Wildfowl* 45: 33–48.

Nilsson, L. & Persson, H. 1996. The influence of the choice of winter quarters on the survival and breeding performance of Greylag Geese (*Anser anser*). *In* M. Birkan, J. van Vessem, P. Havet, J. Madsen, B. Trolliet & M. Moser (eds.), Proceedings of the Anatidae 2000 Conference, Strasbourg, France, 5–9 December 1994. *Gibier Faune Sauvage, Game Wildlife* 13: 557–571.

Nilsson, L. & Persson, H. 1998. Field choice of staging Greylag Geese *Anser anser* in relation to changes in agriculture in South Sweden. *Ornis Svecica* 8: 27–39.

Nilsson, L. & Persson, H. 2001a. Natal and breeding dispersal in the Baltic Greylag Goose *Anser anser*. *Wildfowl* 52: 21–30.

Nilsson, L. & Persson, H. 2001b. Change of mate in a Greylag Goose *Anser anser* population: effects of timing on reproductive success. *Wildfowl* 52: 31–40.

Nilsson, L., Persson, H. & Voslamber, B. 1997. Factors affecting survival of young Greylag Geese and their recruitment into the breeding population. *Wildfowl* 48: 72–87.

Persson, H. 1994. Neck-banding of Greylag Geese *Anser anser* in Scania, 1984–1993. *Anser* 33: 101–106. (Swedish with English summary).

Persson, H. 1996. Survival rates and breeding success in a marked Greylag Goose *Anser anser* population, wintering in the Guadalquivir Marismas. *Revista Florestal* 9: 189–199.

Persson, H. 2000. Neck collar retention in a Greylag Goose *Anser anser* population. *Ornis Svecica* 10: 155–160.

Persson, H. 2002. Brood amalgamation in the Greylag Goose *Anser anser*. *Ornis Svecica* 12: 96–99. (Swedish with English summary).

Pistorius, P.A., Follestad, A., Nilsson, L. & Taylor, F.E. 2007.

A demographic comparison of two Nordic populations of Greylag Geese *Anser anser*. *Ibis* 149: 553–563.

Prop, J. & de Vries, J. 1993. Impact of snow and food conditions on the reproductive performance of barnacle geese *Branta leucopsis*. *Ornis Scandinavica* 24: 110–121.

Reed,E.T., Gauthier,G. Pradel,R. & Lebreton,J.D. 2003. Age and environmental conditions affect recruitment in GreaterSnow Geese. *Ecology* 84: 219–230.

Rees, E. 2006. *Bewick's Swan*. T & AD Poyser, London.

Sedinger, J.S., Flint, P.L. & Lindberg, M.S. 1995. Environmental influence on life-history traits: growth, survival and fecundity in black brant (*Branta bernicla*). *Ecology* 76: 2404–2414.

Weegman, M.D., Bearhop, S., Hilton, G.M., Walsh, A. & Fox, A.D. 2016. Conditions during adulthood affect cohort-specific reproductive success in an Arctic nesting goose population. *PeerJ*. DOI:10.7717/peerj.2044.

Witkowski, J. 1983. Population studies of the grey-lag goose *Anser anser* breeding in the Barycz valley, Poland. *Acta Ornithologica* 19: 179–216.

Sammanfattning

Det är ett välkänt fenomen att endast en mindre del av individerna i en fågelpopulation står för rekryteringen av nya häckande individer till populationen (Newton 1989), något som är känt både för kortlivade tättingar och mer långlivade fåglar som olika andfågelarter (Cooke et al. 1995, Blums & Clark 2004, Rees 2006, Black et al. 2014, Weegman et al. 2016). Bland gäss har detta fenomen främst studerats för arktiska gäss såsom vitkindad gås (Black et al. 2014), snögås (Cooke et al. 1995) samt grönländsk bläsgås (Weegman et al 2016). Däremot saknas motsvarande undersökningar för gäss häckande i tempererade områden såsom grågås.

Information om häckningsresultat för olika grågåsindivider samlades in inom ramen för ett långvarigt nordiskt grågåsprojekt, vilket startade 1984 (Andersson et al. 2001). Projektet avsåg primärt att studera flyttningsvanorna hos de nordiska grågässen, men i det sydvästsvenska undersökningsområdet genomfördes också en serie studier av olika aspekter på grågåsens häckningsekologi, lokala rörelser och populationsdynamik (se bl.a. Nilsson 2016 samt Nilsson & Persson 1994).

I föreliggande uppsats utnyttjar vi de insamlade data för att fastställa den totala produktionen av ungar under de olika individernas livstid för grågäss av känd ålder.

Undersökningsområde

Undersökningarna koncentrerades till SW Skåne (Figur 1). Fångst av grågäss för halsmärkning ägde huvudsakligen rum vid sjöarna Yddingen, Klosterviken, Fjällfotasjön och Börringesjön. Kontroller efter märkta gäss utfördes inom ett större område. Särskilt under höstarna kontrollerades gässen vid Öresundskusten, speciellt Foteviken, vilket utgör ett viktigt område för grågässen vid denna tid på året.

För en närmare beskrivning av undersökningsområdet hänvisas till tidigare uppsatser (särskilt Nilsson & Persson 1994).

När undersökningarna startade 1984 häckade totalt 120 par grågäss i området, efter att ha börjat häcka här under senare delen av 1960-talet. Därefter ökade antalet häckande par till en topp på 1340 par 2004, varefter det minskade till mellan 775 och 985 för åren 2009–2013 (Nilsson 2016).

Metodik

Grågåsfamiljer fångades ungefär tre veckor innan ungarna blev flygga genom att driva dem in i nät som monterats på strandängarna och på golfbanan vid Yddingen (Persson 1994, Andersson et al. 2001). Märkningarna startade 1984 och de sista märktes 2009. Kontrollerna efter märkta i området fortsatte därefter till våren 2013. Området genomsöktes under säsongen regelbundet flera gånger per vecka för att fastställa häckningsresultatet och närvaron av de märkta gässen.

Totalt märktes 664 adulta och 1944 ungar med halsband i det sydvästskånska undersökningsområdet. Märkningarna resulterade i ca 100 500 lokala avläsningar, vartill kommer 15 200 avläsningar från andra områden.

För att beräkna den totala ungproduktionen för olika gäss har vi endast använt gäss märkta som ungar och sålunda av känd ålder. I våra analyser har vi endast tagit med gäss märkta före 1999 för att inte få en skev åldersfördelning i materialet.

Resultat

Av de 1944 grågåsungarna överlevde 74% det första året, medan överlevnaden till två år var 61%. Den äldsta gåsen med komplett serie nådde en ålder av 18 år, men en gås med ofullständig serie nådde en ålder av 25 år (Figur 2). Bland gäss märkta som vuxna häckare (okänd ålder) kunde vi följa en individ under 22 år, vilket innebär att den blev minst 24 år.

Endast 24% av de gäss som överlevde till två års ålder (1189 individer)sågs åtminstone vid ett tillfälle med en kull små ungar. En del av gässen förlorade ungarna tidigt och andelen som producerade minst en flygg kull var 18% (Figur 3). 18% av gässen häckade vid en ålder på två år, medan 50%

hade rekryterats vid tre års ålder (Figur 4). Vissa började häcka först betydligt senare, en vid åtta års ålder.

Det högsta antalet kullar med flygga ungar som noterades var nio, men ca 50% av de grågäss som lyckades med sin häckning producerade endast en flygg kull (Figur 5). Andelen som lyckats ökade inte oväntat med åldern (Figur 6). De flesta gäss som lyckades producera flygga ungar fick ganska få ungar (Figur 7), men en gås producerade 32 flygga ungar. 10% av gässen stod för 47% av den samlade ungproduktionen bland de studerade gässen. Gäss som märkts som vuxna (okänd ålder) visade också ett ökat antal flygga ungar med ökat antals studerade häckningssäsonger (Figur 9) och en gås som följdes 17 säsonger producerade under dessa år 40 flygga ungar.

Den totala produktionen av flygga ungar var inte oväntat beroende av förälderns ålder (Figur 10). Som tidigare påvisats (Nilsson et al 1997) var de ungar som vägde mest innan de blev flygga mer framgångsrika i överlevnad och rekrytering till den häckande populationen. De fick också en högre produktion av flygga ungar under sin häckningsperiod. Valet av vinterkvarter påverkade också den totala ungproduktionen (Figur 12). Erfarenhet var också viktig för att lyckas, 44% av de gäss som producerade en flygg kull ett givet år lyckades även med detta följande år.

Diskussion

Som framgått av resultatredovisningen bidrog endast en mindre del av grågässen till rekryteringen av nya häckfåglar, vilket också påvisats för andra gäss. Andelen framgångsrika individer var dock något högre hos grågåsen än hos vitkindade gäss från Svalbard och grönländska bläsgäss. Hos båda dessa arter förklarade livslängden en mindre del av den totala produktionen av ungar, medan olika individuella faktorer hade större betydelse liksom fallet hos grågåsen.