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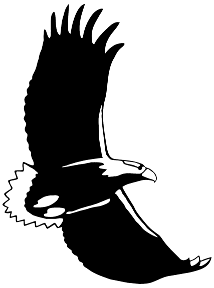

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Effects of predation pressure and nest-site selection on the breeding success of terns in a Finnish archipelago

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Studying and quantifying the breeding success of species can help to understand population trends and provide conservation guidance. Here, we studied the breeding success of Arctic Tern (*Sterna paradisaea*) and Common Tern (*Sterna hirundo*) colonies in a Natura 2000 site of the Western archipelago of Finland aiming to understand which factors related to nest-site selection and predation pressure best explain breeding success. We monitored 72 tern nests at 4 colonies and observed them during standardized monitoring sessions to record predation attacks on the tern nests. We ran generalized linear models to determine the factors which impact breeding success (hatching and fledging success). Hatching success was high across the 4 colonies with 69% of the eggs hatching, whereas fledging success was low with only 1 colony producing 14 fledglings while all other colonies had zero fledglings surviving (12% total fledging success). Regarding nest-site selection, our results demonstrate that a greater proportion of vegetation cover increases breeding success, likely through better nest concealment against predators. Nests in smaller colonies with a higher nest density and located closer to the colony center also produced more hatchlings and fledglings. Most predation likely happened during the chick stage, while our extrapolation predicted that predation accounts for at least 94% of all chick losses, indicating that predator control would aid breeding success of tern colonies in West Finland substantially.

1. Introduction

Anthropogenic stressors, including climate change, lead to drastic biodiversity change globally, including marine species and ecosystems (O'Hara *et al.* 2021). Seabirds especially are facing a combination of threats such as avian influenza wiping out entire colonies (Knief *et al.*

2023) or human encroachment (*e.g.* Carney & Sydeman 1999), introduced predators (Towns *et al.* 2011), as well as elevated populations of natural predators (Scopel & Diamond 2017). Threatened seabird species have received more attention for conservation actions, but many species of least concern are also affected by climate and anthropogenic change (Dias *et al.* 2019). Two seabird species that could be classified in the latter group having currently globally a favorable conservation status (Red List Category “Least Concern”) are the Arctic Tern (*Sterna paradisaea*, BirdLife International 2024) and the Common Tern (*Sterna hirundo*, BirdLife International 2024). Even so, they are both influenced by climate and global change (Burthe *et al.* 2014) and need thus to be monitored and studied in order to keep their populations stable through *e.g.* understanding their reproductive success and habitat selection patterns (Morris 2003, Zeale *et al.* 2012). In Finland, both species are listed as Regionally Threatened (Common Tern: Regionally Threatened 2020 – 4c Northern boreal, Forest Lapland; Arctic Tern: Regionally Threatened 2020 – 4a Northern boreal, Kuusamo district, 4b Northern boreal, North Ostrobothnia, 4c Northern boreal, Forest Lapland, 4d Northern boreal, Fjeld Lapland; Hyvärinen *et al.* 2019) and thus require special attention for this region.

Even though common monitoring programs reveal species population trends, they do not describe reasons for potential population changes which are necessary for effective conservation. Breeding success is a fast, direct, and informative indicator for species experiencing environmental change (Rönkä *et al.* 2011) such as food quality (Cairns 1988, Piatt *et al.* 2007), which can help provide insight into population threats. Many factors can influence breeding success: while it is most often used as a bioindicator of diet quality (Piatt *et al.* 2007), predation pressure is shown to be crucial, especially to ground-nesting birds (Lima 2009, Seibold *et al.* 2013) such as terns (Scopel & Diamond 2018). Nest predation can be particularly significant for certain bird colonies, such as in Greenland, where Arctic foxes strongly impact the breeding success of Arctic Terns (Burnham *et al.* 2017). In other colonies, gulls are among the most important predators of tern nests (Burger & Lesser 1978), and it has been demonstrated that controlling predator populations can benefit tern populations and hence their breeding success (Nordström *et al.* 2003, Scopel & Diamond 2017).

Overall food availability (Monaghan *et al.* 1989, Hatch & Hatch 1990, Suddaby & Ratcliffe 1997) as well as environmental conditions such as sea surface temperatures or climatic conditions (Dunn 1975, Scopel *et al.* 2018) impact reproductive success in seabirds (Pinaud & Weimerskirch 2002). The weather (*e.g.* rain and temperature) has a significant impact especially during the first week of chicks’ lives when they are more vulnerable (Scopel & Diamond 2018). Sufficient food supply is not only crucial for the chicks (Braasch *et al.* 2009) but also both parents (Suddaby & Ratcliffe 1997) to secure good breeding success. Thus, parental behavior can also influence breeding success for some species (Allen Smith *et al.* 2007, Nisbet *et al.* 2020). This may be particularly crucial for colonial breeders such as terns, where a low availability of food can lead to an increase in kleptoparasitic behavior within colonies (Schreiber & Kissling 2005) and result in breeding failures at some nests. Another important component of breeding success is the timing of egg laying. Tern pairs that lay eggs early in the breeding season have a greater chance of success compared to pairs that lay later (Arnold *et al.* 2004). In the latter case, the fitness of the parents determines the survival chances of the chicks (Arnold *et al.* 2004), which in turn is largely dependent on the age of the birds: an older bird has more experience in finding food and providing parental care compared to a young and inexperienced breeder (González-Solís *et al.* 2004).

Finally, the nest location can be a decisive factor for the breeding success of birds (Hawksley 1957, Buehler *et al.* 2017). When establishing a territory, breeding birds have to integrate several biotic and abiotic factors which may impact breeding success (Parker 1986, Ardia *et al.* 2006) and thus make nest-site selection a critical step in the habitat selection process of birds (Martin 1993). Nest concealment through vegetation around the nest, as well as nest position within the colony can lower the detectability and accessibility to predators (Donehower *et al.* 2007, Gómez-Serrano & López-López 2014, Buehler *et* *al.* 2017), such that experienced birds modify their nest-site depending on the prevailing predation pressure to maximize reproductive success (Martin 1993, Latif *et al.* 2012).

The objective of this study was to investigate the breeding success of Arctic and Common Tern colonies in a Natura 2000 site in West Finland. Natura 2000 is a network of protected areas for rare and threatened species and stretches across all 27 European Union countries. The network aims to protect Europe's most valuable and threatened species and habitats, listed under both the Birds Directive and the Habitats Directive (European Commission 2015). Most past research has focused on tern colonies in North America and the UK (*e.g.* Suddaby & Ratcliffe 1997, Arnold *et al.* 2004, Mallory 2016) or Germany (Becker 1995, González-Solís *et al.* 2004, Braasch *et al.* 2009), while few studies on Arctic Terns have examined colonies in Northern latitudes such as Greenland or Svalbard (Syrová *et al.* 2020). To date there are relatively few papers investigating breeding success of terns in the Nordic countries such as Finland. We aimed to answer the following research questions: 1) What is the breeding (hatching and fledging) success of Arctic and Common Terns in a Natura 2000 site in West Finland, 2) is there a difference in breeding success and nest-site selection between the two tern species, 3) what are the factors influencing the breeding success of both species in relation to nest-site selection, and 4) how much does predation account for breeding failure?

2. Material and methods

2.1. Study site and species

This study was conducted during June 2023 on Hällgrund and Lillberget islands, Finland (thereafter Hällgrund islands, N 63° 38’ 38” E 22° 25’ 9”). This area supports 37 species that are protected under Natura 2000 (Natura 2000 ID: FI0800133), including 35 bird species and 2 mammals. The surface of the islands is 0.03 km^2 and covered by short vegetation and a small forest patch at the northern end. The weather during the study period was fairly stable (sea water level, air pressure) and no hard wind (< 20m/s, average 4–7m/s), cold spells or heavy rain were recorded during the chick rearing period. Mean temperature in May 2023 was 7.0 °C (minimum –1.0 °C and maximum 19.3 °C) and in June 12.9 °C (minimum 1.5 °C and maximum 22.6 °C). The islands have been used by fishermen and hunters since the 18th century. Hällgrund and the surrounding archipelago belong to the Natura 2000 network and are protected according to the National Conservation Act (Anon 1993). The islands have been kept free of mink and raccoon dogs by local hunters since the 1990s (Wistbacka *et al.* 2006). An important predator on terns is the European Herring Gull (*Larus argentatus,* Burger & Lesser 1978, Hario 1994, Guillemette & Brousseau 2001). Predatory Herring Gulls are regularly expelled with a one-year delay by shooting them after detection of rings from predated tern chicks (Hario 1994) and have also selectively been culled in our study area to improve, inter alia, the breeding success of Lesser Black-Backed Gull (*Larus fuscus;* Wistbacka *et al.* 2022). During our study period there were 4 tern colonies on the two islands: 2 of them were mixed with both species present, one colony exclusively consisted of Common Terns (CT), and the other with only Arctic Terns (AT; Fig. 1). Both CT and AT are ground-nesting birds. Generally, the CT clutch size is 3 eggs (range of 1–4 eggs; Syrová *et al.* 2020) and 2 eggs for AT (1–3 with rare cases of 4; Syrová *et al.* 2020).

2.2. Nest location mapping and monitoring

An initial search and marking of tern nests with rocks and numbered wooden plates took place at the beginning of the field work (09. June 2023). We also recorded the GPS coordinates and several nest-site characteristics for each nest. Those included the total area covered by the colony (measured as the Minimum Convex Polygon (MCP) of all nest locations per colony), the distance to the colony center from each nest (measured as MCP centroid), the nest density per colony (*i.e.* number of nests/colony area), and the distance to predator nest sites (see section 3.4; see Table 1).

For the nest-site selection analysis we recorded the following habitat variables within 1 m^2 around the nest: percentage cover of

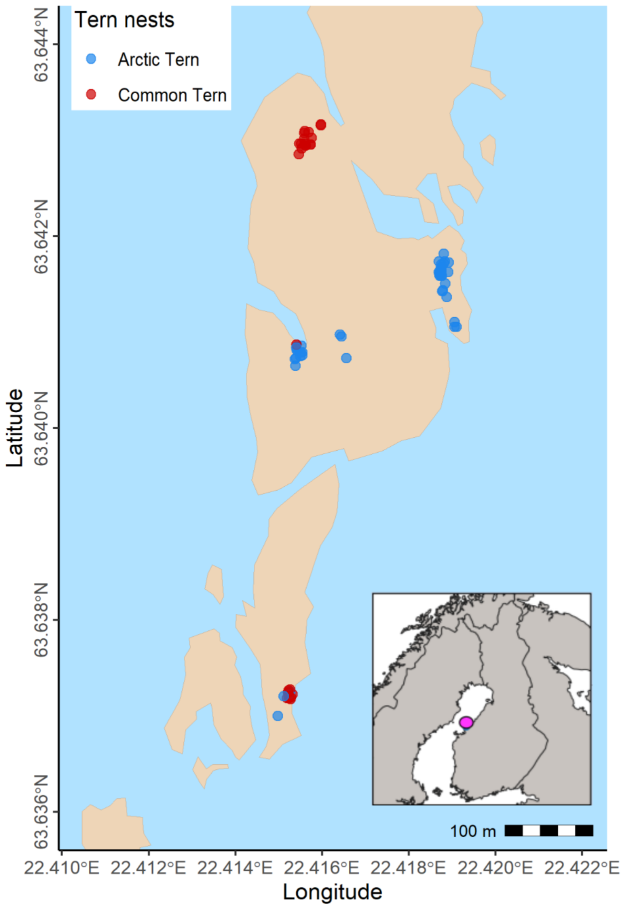

Fig. 1. Study area with Arctic and Common Tern nests. Hällgrund (North) and Lillberget (South) islands showing the 4 tern colonies with a purely Common Tern colony in the North (N = 16 nests), a mixed colony in the South (N = 15) and West (N = 16; although dominated by Arctic Terns) and a purely Arctic Tern colony in the East (N = 25). The small inset map shows the location of the study area (pink dot) on the West coast of Finland.

vegetation type (factor with 5 classes: no vegetation, bushes, forbs, grass, or moss and lichen), percentage cover of i) vegetation (regardless of the type), ii) rocks (larger than 10 cm), iii) pebbles (smaller than 10 cm and larger than sand), and iv) sand (Table 1). Those measurements were taken during the first nest visit. The vegetation around nests did not significantly change throughout the field season.

After the initial nest search and marking, every second day, the nests were visited to monitor different nest parameters: number of eggs; egg stage (*i.e.* visible cracks before hatching, cold eggs indicating egg failure); number of hatchlings. At the end of the field season, we then calculated per nest the hatching success (as the proportion of eggs that hatched), and fledgling success (as the number of chicks that reached the fledgling stage).

2.3. Predators and predation events

All colonies were observed from a distance every 1 to 3 days by 1 or 2 observers, during sessions of 30 minutes for the first week and then 120-minute observation sessions from 19 June to 30 June (survey effort was lower at the beginning as more time was needed for nest-site mapping and chick ringing activities). The observers were situated approximately 100 m from the colonies to minimize disruptions as advised by Mallory (2016). Using binoculars and scopes, we recorded the number of attempted or successful predation events per colony, visible defense attempts by adult terns, as well as other disturbances or activities in the colonies. A predation attack was marked as successful if the predator was seen flying off with an egg or chick. For the analysis we calculated the predation event rate (hereafter

Table 1. Nest site and nest position characteristics of monitored Arctic (*Sterna paradisaea*) and Common Tern (*S. hirundo*) nests at 4 colonies in western Finland, 2023. Mean and standard deviation (SD) are given for all 4 colonies together and separately (colonies North, East, West, South; see Fig. 1).

Variable	Mean ± SD Total	Mean ± SD North	Mean ± SD East	Mean ± SD West	Mean ± SD South
Local nest-site habitat (1 m^2 around nests)					
Vegetation %	48.75 ± 25.49	50.00 ± 22.51	51.80 ± 22.86	25.00 ± 18.97	67.67 ± 20.6
Rocks %	48.54 ± 28.53	50.00 ± 22.51	48.20 ± 22.86	75.00 ± 18.97	19.33 ± 24.19
Pebbles %	2.71 ± 8.18	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	13.00 ± 13.99
*Moss/lichen %	36.53 ± 24.03	48.44 ± 17.29	45.00 ± 24.02	30.00 ± 23.31	16.67 ± 16.55
*Forbs %	28.89 ± 23.26	15.00 ± 10.80	22.20 ± 21.70	46.25 ± 26.55	36.33 ± 18.75
*Grass %	30.21 ± 21.57	31.88 ± 20.16	24.80 ± 21.33	20.31 ± 16.78	48.00 ± 18.30
*Bush %	4.86 ± 11.29	5.94 ± 11.86	8.00 ± 14.65	3.44 ± 8.70	0.00 ± 0.00
Nest position in relation to colony and predatory gulls					
Distance center (m)	17.87 ± 10.77	10.79 ± 5.71	22.15 ± 11.95	26.88 ± 3.8	8.66 ± 4.47
Nest density (nr/m^2)	0.044 ± 0.03	0.05 ± 0	0.04 ± 0	0.01 ± 0	0.09 ± 0
Colony area (m^2)	682.78 ± 466.97	354.33 ± 0	707.89 ± 0	1460.27 ± 0	161.97 ± 0
Distance predator (m)	106.67 ± 51.44	51.19 ± 10.26	173.25 ± 9.94	75.30 ± 14.20	88.34 ± 2.34

** as proportion of the area that was covered by vegetation*

predation rate) based on each predation event (*i.e.* successful and attempted predation). No predation events were recorded on eggs by avian predators. However, Otters (*Lutra lutra*), which can be potential egg predators, were observed on the islands but their impact could not be quantified. As part of the island gull monitoring, the location of nesting Herring Gulls—known to be the main predator of tern nests (Donehower *et al.* 2007; also R. Wistbacka, E. Degot & K. Kaasalainen 2023 unpubl.)—were mapped. From this we then calculated the distance to predatory gull nests from each tern nest.

2.4. Statistical analyses

All analyses were performed in R studio (R version 4.2.0, R Core Team 2022) with packages performance (version 0.10.2; Lüdecke *et al.* 2021), MASS (version 7.3.56; Venables and Ripley 2002), ggplot2 (version 3.4.2; Wickham 2016), and jtools (version 2.2.0; Long 2022).

We analyzed the hatching and fledging success for both AT and CT nests together. To answer our first research question, we calculated the hatching success as the number of eggs hatched divided by the total number of eggs per nest, while for the fledging success we used the number of fledged chicks per nest. To answer our second research question, we compared breeding success, and nest-site selection variables between the two species using generalized linear models (glm) with species as explanatory variable and hatching success, number of fledglings and the nest-site variables (Table 1) as dependent variables respectively.

To answer our third research question, we analysed the 2 response variables: hatching success and number of fledglings. To model the hatching success, we ran glm with a quasibinomial error structure. For modeling the number of fledglings, we fitted negative binomial models to account for excess zeros in the data (R function ‘glm.nb’ from package MASS). For both response variables, a global model was created that contained predictors related to either the nest-site characteristics around the nest (Table 1A), or data on the nest's position within the colony (Table 1B). Prior to fitting the global models, we checked for collinearity between continuous explanatory variables and in case of Pearson correlation >0.5 we kept the variable with smaller p-value in a single predictor model (see Supplementary Material Fig. S1 and List S1). From the global models (*i.e.* after removing collinear variables), we performed a stepwise backward model selection by removing the variable with highest p-value at a time, until only (near-) significant terms were left in the models (*i.e.* $p<0.1$ for $\alpha=0.05$; see Supplementary Material List S2 for global models). We checked the model fit with regards to normality of residuals, outliers, overdispersion and homogeneity of variance (if applicable to the model type) and calculated the R^2 as a Goodness-of-Fit metric for each global as well as best model. For the quasibinomial models (hatching success), we calculated Tjur's R^2 (Tjur 2009) and for the negative binomial models (number of fledglings) we calculated Nagelkerke's R^2 (Nagelkerke 1991).

To answer our fourth research question, we calculated the expected number of predated tern chicks. We extrapolated predation rates to the entire chick rearing period using observed colony-specific and literature-based species-specific values. We used the following equation (Eq. 1) to perform the extrapolation:

$$\textit{predated chicks} = \textit{hourly attack rate} \times \textit{daily foraging hours} \times \textit{chick period} \times \textit{success rate} \qquad (1)$$

We calculated the expected average as well as minimum and maximum number of predated chicks per colony (as well as an average across the 4 colonies) using the following values for the terms in Eq. 1:

1. The hourly attack rate was based on our colony-specific observations (see results 3.4 and Supplementary Material Table S3)
2. Active foraging hours per day were based on the literature on European Herring Gulls (Van Donk *et al.* 2020) with an average of 18 hours per day. To allow for variation or uncertainty in those averages, we also used the minimum and maximum values on active hours with 12 and 24 hours per day respectively.
3. For the chick period we used an average period of 25 days across the two species (average CT: 25.5 days, AT: 24.5 days) with a minimum and maximum of 20.5 and 29.5 days respectively (Robinson 2005)
4. The success rate (*i.e.* calculated as the number of successful predations divided by the number of predation events) was based on our colony-specific observations (see results in section 3.4, and Supplementary Material Table S3).

Table 2. Breeding success of Common and Arctic Terns in Western Finland, 2023. Total number (#) of nests, average number of eggs per nest, total number of eggs, number of hatchlings, hatchling success (HS) and fledgling success (FS) rates per colony. CT = Common Tern, AT = Arctic Tern.

Colony	Species	# nests	Mean # eggs	Total # eggs	# hatched	HS %	FS %
North	CT	16	2.9	46	32	70	0
East	AT	25	1.8	45	35	78	0
West	AT + CT	16	1.9	30	14	47	0
South	CT + AT	15	2.6	39	30	77	47
	Total	72	2.3	160	111	69	12

3. Results

3.1. Breeding success and species differences

In total, we found and monitored 72 CT and AT nests during June and July 2023. There were 4 colonies in total: 3 on Hällgrund and 1 on Lillberget (Fig. 1). The average number of nests per colony was 18, with the Eastern colony being the largest with 25 nests. The average (mean ± SD) number of eggs per nest was 2.3 ± 0.6 (CT: 2.8 ± 0.42; AT: 1.9 ± 0.46), of which on average 1.5 ± 1.01 (CT: 2 ± 1.1; AT: 1.3 ± 0.8) per nest hatched, resulting in an overall hatching success of 69% (Table 2). CT had significantly more eggs per nest than AT (glm poisson, b = 0.402 ± 0.158 SE, z = 2.542, p = 0.011; Supplementary Material Fig. S2), while the hatching success did not differ between the species (glm quasibinomial, b = 0.183 ± 0.446 SE, t = 0.409, p = 0.684). Only 14 chicks reached fledgling stage, while the other 97 hatched chicks did not survive (overall fledgling success: 12%). Since most of those fledglings were CT, the number of fledglings differed significantly between species (glm.nb, b = 1.751 ± 0.756, z = 2.318, p = 0.0205; Supplementary Material Fig. S2). All 14 fledglings were from the Southern colony, while the other 3 colonies did not produce any fledglings (Table 2). More detailed descriptions of the breeding monitoring by colony can be found in the Supplementary Material (Section S2).

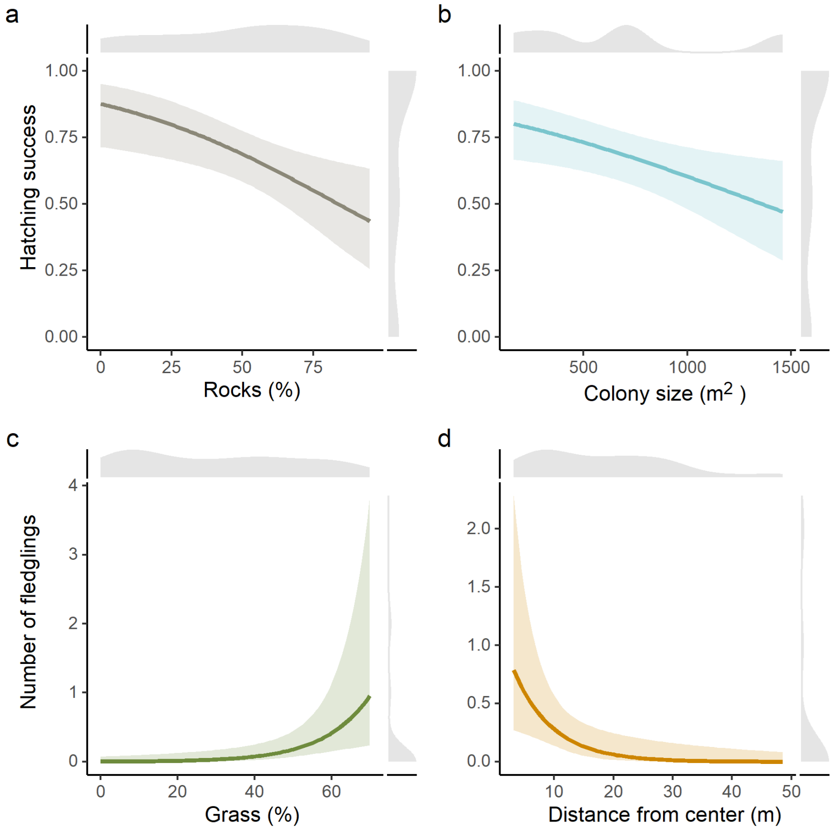

Fig. 2. Model-based regressions between the breeding success (proportion of hatched eggs per nest in a & b, and number of fledglings in c & d) and a) the percentage of rock cover within 1 m^2 around the nests, b) the colony area in m^2 measured as the MCP of all nest locations per colony, c) the percentage of grass around the nests, and d) the mean distance from the colony center to each nest. Solid lines are the model estimates, shaded areas the 95% CI and the gray shaded areas at the top and right sides of the plots are the density distributions of the raw data.

3.2. Hatching success

After removing collinear variables (Supplementary Material Fig. S1, List S1), the best model for the small-scale nest-site habitat variables included only percentage of rocks, which had a significant negative influence on the hatching success ($b = –0.666 \pm 0.243$ SE, $t = –2.735$, $p = 0.008$; Tjur’s $R^2 = 14.6$; Fig. 2a). In other words, a 1 standard deviation (SD) increase in rock cover was related to a reduction in hatching success by approximately 0.7. The other variables had non-significant effects (see Supplementary Material Table S1A for the global model output). Note that rock and vegetation cover were highly negatively collinear (Pearson coefficient = –0.96), meaning that vegetation cover has an equally strong but positive effect on hatching success.

After dropping collinear variables, the best model for the nest position variables included only the colony area, which had a significant negative effect (estimate ± SE = $– 0.544 \pm 0.216$, $t = –2.513$; $p = 0.014$; Tjur’s $R^2 = 3.0$; Fig. 2b). Colony area is strongly negatively collinear with nest density (Pearson coefficient = –0.87), so that colonies with smaller area and higher nest densities had a higher hatching success per nest. Other variables had non-significant effects in the global model (Supplementary Material Table S1B).

3.3. Number of fledglings

The best model for the small-scale nest-site habitat variables included percentages of grass, forbs and rock cover, where grass and forb cover had a significant positive effect (grass: $b = 1.818 \pm 0.658$ SE, $t = 2.763$, $p = 0.006$; Fig. 2c; forbs: $b = 1.149 \pm 0.556$ SE, $t = 2.067$, $p = 0.039$) and rocks a significant negative influence ($b = –0.700 \pm 0.352$ SE, $t = –1.991$, $p = 0.046$) on the number of fledglings per nest (Nagelkerke's $R^2 = 62.6$). Those effects suggest that a 1 SD increase in grass or forb cover is associated with an increase of approximately 1.8 or 1.1 fledglings respectively, whereas 1 SD increase in rock cover, reduces the number of fledglings by approximately 0.7. Again, note that rock and vegetation cover were highly negatively collinear (Pearson coefficient = –0.96), meaning that vegetation cover has an equally strong but opposite effect on fledgling success. Note that the percentage of bushes was dropped from the global model due to bad model performance related to generally low percentages of this variable in our data. See global model results in Supplementary Material Table S2A.

The best model for the nest position variables included only the distance from the colony center, which had a significant negative effect ($b = –1.631 \pm 0.636$ SE, $t = –2.562$; $p = 0.010$; Fig. 2d; Nagelkerke's $R^2 = 31.9$), indicating that nests located closer to the colony center had a higher fledgling success (Supplementary Material Table S2B). Note that colony area was dropped from the global model due to bad model performance of this variable.

3.4. Predation rate

In total 65 predation attempts (*i.e.* attempted and successful attacks) were recorded during an observation time of 43.35 hours resulting in an overall attack rate of 1.4 attacks per hour (colony North: 30 predation events, 1.85 attacks/h; colony East: 3 predation events, 0.4/h; colony West: 17 predation events, 1.47/h; colony South: 15 predation events, 1.88/h). Of the total 65 attacks only 6 (9.2%) were successful (2 in colony North, 1 in colony East, 3 in colony West and 0 in colony South; Fig. 3a; Table S3). Adult terns defended against 52% of the attacks (34 in total; 15 in colony North, 1 in colony East, 9 in colony West and 9 in colony South), which was in proportion to the rate of attacks (Pearson correlation attack and defense rate = 0.98; Fig. 3a; Table S3). European Herring Gulls enacted 88% of the attacks, with only 8 attacks potentially from other species (Mew Gull *Larus canus*, Lesser Black-backed Gull, Parasitic Jaeger *Stercorarius parasiticus,* and Ruddy Turnstone *Arenaria interpres*). All successful predations were done by European Herring Gulls and were observed on chicks only, *i.e.* no direct predation on eggs were observed. However, in total 5 eggs disappeared and 1 was found broken during our field season.

From the extrapolation calculations, we found that across the 4 colonies, the number of expected

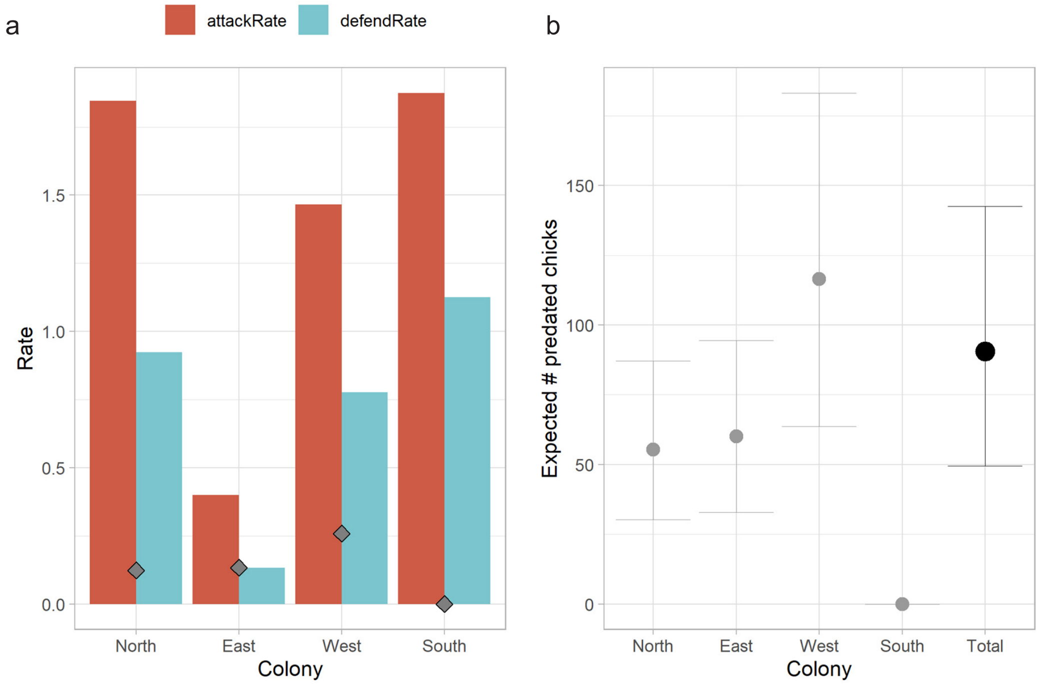

Fig. 3. a) Rates of attacks by predators (red bars) and defensive behavior by terns (blue) calculated as absolute numbers observed per hour for each colony. The gray squares indicate the rate of successful predations (number of observed successful predations per hour). b) Extrapolated expected numbers of predated tern chicks during the hatchling stage per colony and in total (*i.e.* across the 4 colonies). Points indicate average expected numbers while error bars present minimum to maximum value ranges.

predated tern chicks across the entire chick period (*i.e.* before fledging) was on average 91, *i.e.* 81% of the total 111 counted chicks (colony North: 55, *i.e.* >100%, East: 60, *i.e.* >100%, West: 116; *i.e.* >100%, South: 0; *i.e.* 0%) with a minimum of 50 (North: 30, East: 33, West: 64, South: 0) and a maximum of 143 (North: 87, East: 94, West: 183, South: 0; see Fig. 3b).

4. Discussion

In this study, we investigated the breeding success of Arctic and Common Tern colonies breeding on a Natura 2000 island in West Finland and investigated the biotic and abiotic factors influencing the breeding success. We found that the hatching success was fairly high while all except 1 colony showed a total loss during the chick stage. In terms of nest-site variables, the percentage of rock cover as well as the type of vegetation played a significant role in explaining varying hatching or fledging success, while colonies with lower nest density (*i.e.* larger colony area) and nests farther from the colony center experienced lower breeding success. Predation played a major role during the chick stage with European Herring Gulls being the main predator.

On average, the tern nests had 2.2 eggs/nest which was expected from the literature describing clutch sizes of 1–3 (AT) or 1–4 (CT) eggs per nest (Syrová *et al.* 2020). Mean hatching rate was only 1.5 eggs/nest resulting in a hatching success of 69%, which is in line with earlier findings too (Nisbet & Welton 1984, Monaghan *et al.* 1989). Worryingly, the 3 colonies located on Hällgrund experienced a total failure in fledging success while only the Southern colony recruited 14 chicks, resulting in an overall fledging success of 12% (fledged chicks per hatched egg) or 0.19 fledglings per breeding pair for the 4 colonies. This is substantially lower than figures from the earlier literature (~0.94 for AT; Monaghan *et al.* 1989 or ~1.2 for CT; Nisbet & Welton 1984) and slightly lower compared to earlier years of tern colony monitoring on Hällgrund islands (mean fledglings/pair in earlier years: 0.23, Supplementary Material Table S4 and Fig. S3). The fact that only the colony in the South produced fledglings leading to a fledging success of 47% is striking and can be related to several factors. First, this was the smallest colony in terms of occupied colony area, with a concomitant highest nest density and thus shortest distance to the colony center from the nests (Table 1). With regards to nest-site habitat, nests in the Southern colony generally had more grass and thus less rocks (Table 1) and based on field observations, the terrain of this colony's location was flatter with less cliffs and slopes as compared to the other 3 colonies. Although the predator attack rate was not different from other colonies, the number of times terns successfully defended their nests was highest and hence, no successful predations were observed (see further below). Taken together, it seems apparent that a colony with higher nest density, higher nest centrality, more vegetation and a better defense rate leads to higher breeding success (Becker 1995, Whittam 1997, Buehler *et al.* 2017).

In terms of species differences, CT recruited 11 fledglings while only 3 chicks survived to fledgling stage in AT. This can be due to differing nest-site characteristics and thus potential lower predation pressure or increased nest defense in CT (see below). Earlier studies did not find a difference in breeding success (*e.g.* Chapdelaine *et al.* 1985) or nest defense behavior (Lemmetyinen 1971) between the two tern species and thus, our reported differences might be more related to nest-site and colony conditions rather than species differences. Indeed, colonies dominated by CT (*i.e.* colony North and South) generally had nests with higher centrality (shorter distance to colony center), higher nest density and smaller colony areas than AT colonies (*i.e.* colony East and West; Table 1)—all related to higher breeding success (Austin 1940, Becker 1995). In relation to earlier reports of tern breeding success on Hällgrund islands (see Supplementary Material Table S4 and Fig. S3), AT did not seem to have lower fledgling success compared CT (Fig. S3b), and sometimes even fared better than CT or mixed tern colonies. Most of those years where AT had a higher number of fledglings recruited per pair, no predatory European Herring Gull was found in the vicinity of the AT colony which likely explains the higher breeding success (Supplementary Material Table S4).

Nest-sites were generally characterized by a mix of rocks and vegetation (Whittam & Leonard 1999), where CT nests were surrounded by higher proportions of grass and forbs and thus fewer rocks than AT nests—a pattern that has similarly been evidenced before (Robinson *et al.* 2001). Indeed, several studies discussed the preference for nest-sites with less vegetation cover by AT compared to other tern species (Hawksley 1957) and that this preference might be related to wing and tarsus length limiting the ability to move in dense vegetation (Hawksley 1957, Courtney & Blokpoel 1983). We show that nests surrounded by higher vegetation cover had up to 50% higher hatching success and nests with more grass or forbs recruited more fledglings, which can be explained by increased nest-concealment against predators (Buehler *et al.* 2017) or improved microclimatic conditions (Kim & Monaghan 2005). We also found a correlation between the colony area, nest density, and nest distance to colony center, with over 50% lower breeding (hatching and fledging) success for nests in colonies with lower nest density (and thus larger colony area) and those located closer to the colony periphery than the center. This corresponds to earlier descriptions of tern colonies, where smaller colonies (with a higher nest density) were more resilient against depredation (Austin 1940). This finding is also reflected in the Southern colony of our study, which produced fledglings and had the highest nest density and smallest colony area. A higher nest density creates more protection for nests closer to the center, at the expense of those at the periphery (Becker 1995).

We observed a fairly high number of predation events during the chick stage (N = 65), although the number of successful predations was relatively small (N = 6) and no predation on eggs were observed. Earlier results also suggest that chicks are predated more often than eggs (Becker 1995), which could partly be explained by a lower nest attendance by parents after hatching (Becker

1995, Robinson & Hamer 1998), especially so for AT (Robinson *et al.* 2001) which, as shown here, had a lower breeding success than CT. Since nests surrounded by more vegetation (especially grass and forbs) recruited more fledglings, we could infer that those nests were better protected from predators as has also been suggested earlier (Burger & Lesser 1978) and could partly explain the successful production of fledglings in the Southern colony. We did observe a significant difference in vegetation around the nests between the two species: CT preferred greater grass coverage around the nests than AT which is in line with earlier findings (*e.g.* Langham 1968).

European Herring Gulls were the main predator, as already observed previously (Becker 1995, Guillemette & Brousseau 2001). However, Sea Eagles (*Haliaeetus albicilla*) and Otters (*Lutra lutra*) were also seen on the island and could play a potential role as tern nest predators even if no observations were made. Only predation events of Sea Eagles on Herring Gulls were observed. Sea Eagles could theoretically attack terns, although such occurrences are quite rare (Sulkava *et al.* 1997), and predation by Otters on Arctic terns were also recorded earlier (Shannon & Thurgate 2014). In addition, neighboring smaller gull colonies such as Black-Headed Gulls (*Chroicocephalus ridibundus*) or Mew Gulls, or even Lesser Black-Backed Gulls, could attract predatory Gulls such as European Herring Gulls in the vicinity of tern colonies and make them secondary prey targets. Notably, many fewer Black-Headed and Mew Gulls were found around the successful Southern colony as compared to the other tern colonies, further supporting this assumption.

In total, 97 out of 111 tern chicks died, while our extrapolation of expected number of chicks predated during the entire chick period was 50–143 (average 91). This implies that, given that our assumed numbers for the terms in Eq. 1 are realistic, almost all chick losses were due to predation. But given that in our extrapolation we assumed a constant predation pressure throughout the chick period (*i.e.* no increase or decrease due to *e.g.* higher or lower food demand for nesting gulls), it might well be that less than the predicted 91 chicks were lost due to predation but also to other causes. Certainly, our extrapolated number of predated chicks are rather rough and limited to several assumptions and should thus be interpreted with this caveat in mind. There were some dead chicks found in the nests that died due to infestation by ants (N = 6), or due to unknown reasons. Furthermore, in the Northern colony a case of intraspecific killing was observed, where an incubating tern attacked and presumably killed a chick from a neighboring nest that had strayed too close. Other factors affecting chick survival can be lack or shortage of food provided by the parents (Monaghan *et al.* 1989), or adverse weather conditions (Scopel & Diamond 2018). The latter factor might not have been influential in this particular breeding season as the weather was mostly stable without rain, storms, or heavy sea level fluctuations.

Assuming that predation accounts for ~94% of chick mortality, reducing the impact of predation would likely increase the breeding success of Common, and especially Arctic Terns significantly—which has been shown in other parts of the world too (Scopel & Diamond 2017). AT seem to struggle more in repelling predatory Herring Gulls (Scopel & Diamond 2017) and given that this is the main predator in this area, predator control would likely benefit this species particularly. In addition, Arctic Terns are regionally threatened (RT) in 4 different zones (Hyvärinen *et al.* 2019), indicating that the species requires special attention in Fennoscandia in order to maintain stable populations. One solution to do so is to control the gull population on the islands as has been done successfully in the South of Finland with the American Mink (Nordström *et al.* 2003). Archipelago areas in Finland that are within Natura 2000 areas and are not affected by introduced predators (mink, raccoon dog) ought to be hot spots for breeding archipelago birds. However, on Hällgrund predatory European Herring Gulls hinder this for many species. Apart from our study species the Lesser Black-backed Gull (EN), Mew Gull (LC), Black-Headed Gull (VU), Ruddy Turnstone (EN), Common Redshank (*Tringa totanus*, NT) and the Tufted Duck (*Aythya Fuligula*, EN) are all seriously affected by Herring Gull predation (Red List status from Hyvärinen *et al.* 2019). Thus, targeted culling of predatory Herring Gulls is a method for enhancing populations of archipelago birds without affecting the population of the also vulnerable European Herring Gull (VU). Selective removal of predators has been shown to be an efficient way of reducing predation on regionally endangered Lesser Black-Backed Gull (Hyvärinen *et al.* 2019) chicks in Southern Finland (Hario 1994; Hario & Rintala 2016) and to be equally effective as large-scale random culling of European Herring Gulls (Hario *et al.* 2009). Thus, selective removal of predators would be preferable both in terms of money and effort required and also for the conservation of European Herring Gulls, which are classified as Vulnerable in Finland due to long-term population decline (Ministry of the Environment & Finnish Environment Institute 2019), although the local population in the study area has been increasing (Wistbacka 2024 unpubl.).

In conclusion, our study demonstrates that one of the most important factors impacting the breeding success of tern colonies in a Natura 2000 site is predation by European Herring Gulls. Nest-site selection and colony factors also influence hatching and fledging success and are probably indirect responses to predation pressure. To enhance the breeding success in tern populations, regulation of predators (Nordström *et al.* 2003, Scopel & Diamond 2018) or creating wood shelters around nests (Burness & Morris 1992) can be potential solutions.

Effekter av predationstryck och boplatsval på häckningsframgången hos tärnor i en finländsk skärgård

Att studera och kvantifiera arters reproduktionsframgång kan bidra till att förstå populationstrender och ge vägledning för bevarandet. Här studerade vi häckningsframgången hos silvertärna (*Sterna paradisaea*) och fisktärna (*Sterna hirundo*) i kolonier på ett Natura 2000-område i Västra Finlands skärgård för att förstå vilka faktorer relaterade till boplatsval och predationstryck som bäst förklarar häckningsframgång. Vi övervakade 72 tärnbon i 4 kolonier och observerade dem under standardiserade övervakningssessioner för att registrera predatorangrepp på tärnbon. Vi körde generaliserade linjära modeller för att bestämma vilka faktorer som påverkar häckningsframgång (antal kläckta och flygga ungar). Kläckningsframgången var hög i alla 4 kolonier med 69% av äggen som kläcktes, medan framgången för flygga ungar var låg, där endast 1 koloni producerade 14 flygfärdiga ungar medan alla andra kolonier hade noll överlevande ungar (totalt 12% blev flygga). När det gäller boplatsval visar våra resultat att en större andel vegetationsskydd ökar häckningsframgången, troligen genom bättre bo-kamouflage mot rovdjur. Bon i mindre kolonier med högre botäthet och belägna närmare kolonicentrum producerade också fler kläckta ungar och flygga ungar. De flesta predatorangrepp skedde troligtvis under ungstadiet, medan vår extrapolering förutspådde att predation står för minst 94% av alla ungförluster, vilket tyder på att rovdjurskontroll skulle kunna förbättra häckningsframgången hos tärnkolonier i Västra Finland avsevärt.

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References

Allen Smith, P., Grant Gilchrist, H. & Smith, J. N. M. 2007: Effects of Nest Habitat, Food, and Parental Behavior on Shorebird Nest Success. — The Condor 109: 15–31. https://doi.org/10.1093/condor/109.1.15

Anon 1993: Decision on starting a conservation area by the Environmental Agency of Vaasan Lääni; Nr 127A-1368 regarding an archipelago area of Torsö and Hällgrund. 8 pp.

Ardia, D. R., Pérez, J. H. & Clotfelter, E. D. 2006: Nest box orientation affects internal temperature and nest site selection by Tree Swallows. — Journal of Field

Ornithology 77: 339–344. https://doi.org/10.1111/j.1557-9263.2006.00064.x

Arnold, J. M., Hatch, J. J. & Nisbet, I. C. T. 2004: Seasonal declines in reproductive success of the common tern Sterna hirundo: timing or parental quality? — Journal of Avian Biology 35: 33–45. https://doi.org/10.1111/j.0908-8857.2004.03059.x

Austin, O. L. 1940: Some aspects of individual distribution in the Cape Cod tern colonies. — Bird-Banding 11(4): 155–169. https://doi.org/10.2307/4509635

Becker, P. H. 1995: Effects of Coloniality on Gull Predation on Common Tern (*Sterna hirundo*) Chicks. — Colonial Waterbirds 18: 11–22. https://doi.org/10.2307/1521394.

Braasch, A., Schauroth, C. & Becker, P. H. 2009: Post-fledging body mass as a determinant of subadult survival in Common Terns *Sterna hirundo*. — Journal of Ornithology 150: 401–407. https://doi.org/10.1007/s10336-008-0362-2

BirdLife International 2024: IUCN Red List for birds. — Downloaded from https://datazone.birdlife.org/species/ (Accessed 17 September 2024)

Buehler, R., Bosco, L., Arlettaz, R. & Jacot, A. 2017: Nest site preferences of the Woodlark (*Lullula arborea*) and its association with artificial nest predation. — Acta Oecologica 78: 41–46. https://doi.org/10.1016/j.actao.2016.12.004

Burger, J. & Lesser, F. 1978. Selection of Colony Sites and Nest Sites by Common Terns *Sterna Hirundo* in Ocean County, New Jersey. — Ibis 120: 433–449. https://doi.org/10.1111/j.1474-919X.1978.tb06810.x

Burness, G. P. & Morris, R. D. 1992: Shelters Decrease Gull Predation on Chicks at a Common Tern Colony. — Journal of Field Ornithology 63: 186–189.

Burnham, K. K., Burnham, J. L., Konkel, B. W. & Johnson, J. A. 2017: Significant decline observed in Arctic Tern *Sterna paradisaea* population in northwest Greenland. — Seabird 30: 39–50. https://doi.org/10.61350/sbj.30.39

Burthe, S., Wanless, S., Newell, M., Butler, A. & Daunt, F. 2014: Assessing the vulnerability of the marine bird community in the western North Sea to climate change and other anthropogenic impacts. — Marine Ecology Progress Series 507: 277–295. https://doi.org/10.3354/meps10849.

Cairns, D. K. 1988: Seabirds as Indicators of Marine Food Supplies. — Biological Oceanography 5(4): 261–271. https://doi.org/10.1080/01965581.1987.10749517

Carney, K. M. & Sydeman, W. J. 1999: A review of human disturbance effects on nesting colonial waterbirds. — Waterbirds 68–79. https://doi.org/10.2307/1521995

Chapdelaine, G., Brousseau, P., Anderson, R. & Marsan, R. 1985: Breeding ecology of common and arctic terns in the Mingan Archipelago, Quebec. — Colonial Waterbirds 8(2): 166–177. https://doi.org/10.2307/1521067

Courtney, P. & Blokpoel, H. 1983: Distribution and numbers of common terns on the lower Great Lakes during 1900-1980: a review. — Waterbirds 6: 107–120. https://doi.org/10.2307/1520977

Dias, M. P., Martin, R., Pearmain, E. J., ... & Croxall, J. P. 2019: Threats to seabirds: a global assessment. — Biological Conservation 237: 525–537. https://doi.org/10.1016/j.biocon.2019.06.033

Donehower, C. E., Bird, D. M., Hall, C. S. & Kress, S. W. 2007: Effects of gull predation and predator control on tern nesting success at Eastern Egg Rock, Maine. — Waterbirds 30(1): 29–39. https://doi.org/10.1675/1524-4695(2007)030[0029:EOGPAP]2.0.CO;2

Dunn, E. K. 1975: The role of environmental factors in the growth of tern chicks. — The Journal of Animal Ecology 44(3): 743–754. https://doi.org/10.2307/3716

European Commission: Directorate-General for Environment & Sundseth, K. 2015: The EU birds and habitats directives: For nature and people in Europe. — Publications Office. https://data.europa.eu/doi/10.2779/49288

Gómez-Serrano, M. Á. & López-López, P. 2014: Nest Site Selection by Kentish Plover Suggests a Trade-Off between Nest-Crypsis and Predator Detection Strategies. — PLOS ONE 9: e107121. https://doi.org/10.1371/journal.pone.0107121

González-Solís, J., Becker, P. H., Jover, L. & Ruiz, X. 2004: Individual changes underlie age-specific pattern of laying date and egg-size in female common terns *Sterna hirundo*. — Journal of Ornithology 145: 129–136. https://doi.org/10.1007/s10336-004-0023-z

Guillemette, M. & Brousseau, P. 2001: Does culling predatory gulls enhance the productivity of breeding common terns? — Journal of Applied Ecology 38: 1–8. https://doi.org/10.1046/j.1365-2664.2001.00564.x

Hatch, S. A. & Hatch, M. A. 1990: Components of breeding productivity in a marine bird community: key factors and concordance. — Canadian Journal of Zoology 68: 1680–1690. https://doi.org/10.1139/z90-248.

Hario, M. 1994: Reproductive performance of the nominate Lesser Black-backed Gull under the pressure of Herring Gull predation. — Ornis Fennica 71: 1–10.

Hario, M., Rintala, J. & Tanner, J. 2009: Culling project on herring gulls of the central Gulf of Finland 2004–2007. — Riista- ja kalatalous – Tutkimuksia 4/2009. Finnish Game and Fisheries Research Institute. Helsinki, Finland. (In Finnish with English abstract)

Hario, M. & Rintala, J. 2016: Population trends in herring gulls (*Larus argentatus*), great black-backed gulls *(Larus marinus*) and lesser black-backed gulls (*Larus fuscus fuscus*) in Finland. — Waterbirds 39(sp1): 10–14. http://dx.doi.org/10.1675/063.039.sp107

Hawksley, O. 1957: Ecology of a breeding population of Arctic Terns. — Bird-Banding 28(2): 57–92. https://doi.org/10.2307/4510623

Hyvärinen, E., Juslén, A., Kemppainen, E., Uddström, A. & Liukko, U.-M. (eds.) 2019: The 2019 Red List of Finnish Species. — Ympäristöministeriö & Suomen ympäristökeskus. Helsinki, Finland.

Kim, S.-Y. & Monaghan, P. 2005: Effects of vegetation on nest microclimate and breeding performance of lesser black-backed gulls (*Larus fuscus*). — Journal of Ornithology 146: 176–183. https://doi.org/10.1007/s10336-005-0077-6

Knief, U., Bregnballe, T., Alfarwi, I., ... & Courtens, W. 2024: Highly pathogenic avian influenza causes mass mortality in Sandwich tern (*Thalasseus sandvicensis*) breeding colonies across northwestern Europe. — bioRxiv (preprint). https://doi.org/10.1101/2023.05.12.540367

Langham, N. P. E. 1968: The comparative biology of terns, Sterna spp. — Doctoral dissertation, Durham University. https://etheses.dur.ac.uk/8606/ (Accessed 31 October 2024)

Latif, Q. S., Heath, S. K. & Rotenberry, J. T. 2012: How avian nest site selection responds to predation risk: testing an 'adaptive peak hypothesis.' — Journal of Animal Ecology 81: 127–138. https://doi.org/10.1111/j.1365-2656.2011.01895.x

Lemmetyinen, R. 1971: Nest defence behaviour of Common and Arctic Terns and its effects on the success achieved by predators. — Ornis Fennica 48(1): 13–24.

Lima, S. L. 2009: Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. — Biological Reviews 84: 485–513. https://doi.org/10.1111/j.1469-185X.2009.00085.x

Long, J. A. 2022: jtools: Analysis and Presentation of Social Scientific Data. https://doi.org/10.21105/joss.06610

Lüdecke, D., Ben-Shachar, M., Patil, S. I., Waggoner, P. & Makowski, D. 2021: performance: An R Package for Assessment, Comparison and Testing of Statistical Models. — Journal of Open Source Software 6: 3139. https://doi.org/10.21105/joss.03139

Mallory, M. L. 2016: Reactions of ground-nesting marine birds to human disturbance in the Canadian Arctic. — Arctic Science 2: 67–77. https://doi.org/10.1139/as-2015-0029

Martin, T. E. 1993: Nest Predation and Nest Sites: New perspectives on old patterns. — BioScience 43: 523–532. https://doi.org/10.2307/1311947

Ministry of the Environment & Finnish Environment Institute 2019: The 2019 Red List of Finnish Species: data download (version 1). — Downloaded from https://punainenkirja.laji.fi/publications (Accessed 27 March 2024)

Monaghan, P., Uttley, J. D., Burns, M. D., Thaine, C. & Blackwood, J. 1989: The Relationship Between Food Supply, Reproductive Effort and Breeding Success in Arctic Terns *Sterna paradisaea*. — Journal of Animal Ecology 58: 261–274. https://doi.org/10.2307/4999

Morris, D. W. 2003: How can we apply theories of habitat selection to wildlife conservation and management? — Wildlife Research 30: 303–319. https://doi.org/10.1071/wr02028

Nagelkerke, N. J. 1991: A note on a general definition of the coefficient of determination. — biometrika 78(3): 691–692. https://doi.org/10.1093/biomet/78.3.691

Nisbet, I. C. T. & Welton, M. J. 1984: Seasonal Variations in Breeding Success of Common Terns: Consequences of Predation. — The Condor 86: 53–60. https://doi.org/10.2307/1367345

Nisbet, I. C., Iles, D., Kaneb, A., Mostello, C. S. & Jenouvrier, S. 2020: Breeding performance of Common Terns (*Sterna hirundo*) does not decline among older age classes. — The Auk 137(3): ukaa022. https://doi.org/10.1093/auk/ukaa022

Nordström, M., Högmander, J., Laine, J., Nummelin, J., Laanetu, N. & Korpimäki, E. 2003: Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. — Biological Conservation 109: 359–368. https://doi.org/10.1016/S0006-3207(02)00162-3

O'Hara, C. C., Frazier, M. & Halpern, B. S. 2021: At-risk marine biodiversity faces extensive, expanding, and intensifying human impacts. — Science 372: 84–87. https://doi.org/10.1126/science.abe6731

Parker, K. C. 1986 Partitioning of Foraging Space and Nest Sites in a Desert Shrubland Bird Community. — The American Midland Naturalist 115: 255–267. https://doi.org/10.2307/2425862

Piatt, J. F., Harding, A. M., Shultz, M., Speckman, S. G., Van Pelt, T. I., Drew, G. S., Kettle & A. B. 2007: Seabirds as indicators of marine food supplies: Cairns revisited. — Marine Ecology Progress Series 352: 221–234. https://doi.org/10.3354/meps07078

Pinaud, D. & Weimerskirch, H. 2002: Ultimate and proximate factors affecting the breeding performance of a marine top-predator. — Oikos 99: 141–150. https://doi.org/10.1034/j.1600-0706.2002.990114.x

R Core Team 2022: R: A Language and Environment for Statistical Computing. — Version 4.2.0. R Foundation for Statistical Computing. Vienna, Austria.

Robinson, J. A. & Hamer, K. C. 1998: Predation of Arctic Tern chicks by rabbits in northeast England. — Seabird: 41–43.

Robinson, J. A., Hamer, K. C. & Chivers, L. S. 2001: Contrasting Brood Sizes in Common and Arctic Terns: The Roles of Food Provisioning Rates and Parental Brooding. — The Condor 103: 108–117. https://doi.org/10.1093/condor/103.1.108

Robinson, R.A. 2005: BirdFacts: profiles of birds occurring in Britain & Ireland (v1.24, June 2009). — BTO Research Report 407. BTO, Thetford. http://www.bto.org/birdfacts (Accessed 31 October 2024)

Rönkä, M., Saari, L., Hario, M., Hänninen, J. & Lehikoinen, E. 2011: Breeding success and breeding population trends of waterfowl: implications for monitoring. — Wildlife Biology 17: 225–239. https://doi.org/10.2981/09-064

Schreiber, J. & Kissling, D. W. 2005: Factors affecting the breeding success of Arctic Terns *Sterna paradisaea* in a colony at Kaldbaksbotnur, Faroe Islands. — Atlantic Seabirds 7: 97–105.

Scopel, L. C. & Diamond, A. W. 2017: The case for lethal control of gulls on seabird colonies. — The Journal of Wildlife Management 81(4): 572–580. https://doi.org/10.1002/jwmg.21233

Scopel, L. C. & Diamond, A. W. 2018: Predation and food–weather interactions drive colony collapse in a managed metapopulation of Arctic Terns (*Sterna paradisaea*). — Canadian Journal of Zoology 96(1): 13–22. https://doi.org/10.1139/cjz-2016-0281

Scopel, L. C., Diamond, A. W., Kress, S. W., Hards, A. R. & Shannon, P. 2018: Seabird diets as bioindicators of Atlantic herring recruitment and stock size: a new tool for ecosystem-based fisheries management. — Canadian Journal of Fisheries and Aquatic Sciences 75: 1215–1229. https://doi.org/10.1139/cjfas-2017-0140

Seibold, S., Hempel, A., Piehl, S., Bässler, C., Brandl, R., Rösner, S. & Müller, J. 2013: Forest vegetation structure has more influence on predation risk of artificial ground nests than human activities. — Basic and Applied Ecology 14: 687–693. https://doi.org/10.1016/j.baae.2013.09.003

Shannon, T. & Thurgate, H. 2014: Strangford Lough-Seabird Predation Report 2014. — Northern Ireland Seabird Report 2014. Downloaded from https://www.bto.org/sites/default/files/u41/NI-Seabird-Report-2014-web-version.pdf) (Accessed 12 September 2024)

Suddaby, D. & Ratcliffe, N. 1997: The Effects of Fluctuating Food Availability on Breeding Arctic Terns (*Sterna paradisaea*). — The Auk 114: 524–530. https://doi.org/10.2307/4089260

Sulkava, S., Tornberg, R. & Koivusaari, J. (1997): Diet of the White-tailed Eagle *Haliaeetus albicilia* in Finland. — Ornis Fennica 74(2): 65–78.

Syrová, M., Hromádková, T., Pavel, V. & Veselý, P. 2020: Responses of nesting Arctic terns (*Sterna paradisaea*) to disturbance by humans. — Polar Biology 43: 399–407. https://doi.org/10.1007/s00300-020-02641-2

Tjur, T. 2009: Coefficients of determination in logistic regression models—A new proposal: The coefficient of discrimination. — The American Statistician 63(4): 366–372. https://doi.org/10.1198/tast.2009.08210

Towns, D. R., Byrd, G. V., Jones, H. P., Rauzon, M. J., Russell, J. C. & Wilcox, C. 2011: Impacts of introduced predators on seabirds. — In Seabird Islands: Ecology, Invasion, and Restoration (ed. Mulder, C. P. H., Anderson, W. B., Towns, D. R. & Bellingham, P. J.): 56–90. New York. https://doi.org/10.1093/acprof:osobl/9780199735693.003.0003

Van Donk, S., Shamoun-Baranes, J., Bouten, W., Van Der Meer, J. & Camphuysen, K. C. J. 2020: Individual differences in foraging site fidelity are not related to time-activity budgets in Herring Gulls. — Ibis 162: 429–445. https://doi.org/10.1111/ibi.12697

Venables, W. & Ripley, B. 2002: Modern Applied Statistics with S. — Springer, New York. https://doi.org/10.1007/978-0-387-21706-2

Whittam, R. 1997: The effects of predation on the breeding biology and behaviour of roseate, Arctic, and common terns nesting on Country Island, Nova Scotia. — Thesis, Dalhousie University. Halifax, NS, Canada.

Whittam, R. M. & Leonard, M. L. 1999: Predation and breeding success in roseate terns (*Sterna dougallii*). — Canadian Journal of Zoology 77: 851–856. https://doi.org/10.1139/z99-047

Wickham, H. 2016: ggplot2. — Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-24277-4

Wistbacka, R. Wistbacka, P., Wistbacka K. O., Bäck A. & Sandvik, E. 2006: Inventering av fågelfaunan i Torsö skärgård 2006. — Arbetsrapport. Working report on the avifauna of Torsö. (In Swedish)

Wistbacka, R., Liljeqvist, F., Wistbacka, P., Höglund, J., Sundelin, A., Back, R. & Hultèn, T. 2022: Studie av förekomst och häckningsframgång hos silltrut (*Larus f. fuscus*) i Jakobstadsnejden sommaren 2022 (Study on impact of Herring gull predation on *Larus fuscus* and other species on Hällgrund). — Arbetsrapport, Working report. (In Swedish)

Zeale, M. R. K., Davidson-Watts, I. & Jones, G. 2012: Home range use and habitat selection by barbastelle bats (*Barbastella barbastellus*): implications for conservation. — Journal of Mammalogy 93: 1110–1118. https://doi.org/10.1644/11-MAMM-A-366.1

Online supplementary material

Supplementary material available in the online version of the article (https://doi.org/10.51812/of.145291) includes extended data analysis description, detailed description of colony monitoring, and extended results with Figures S1–S3, Lists S1–S2, and Tables S1–S4.

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Survival estimates of GPS-tagged adult Golden Eagles (*Aquila chrysaetos*) breeding in Finland

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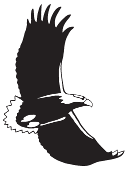

Adult survival estimates are important for assessing population status and viability and for investigating the role of different anthropogenic effects on their variation. Currently, the rapidly increasing wind power poses a new and severe threat to survival of large raptors. Between 2011–2024, we monitored 26 Golden Eagles (*Aquila chrysaetos*) using Global Positioning System tracking devices in Finland, on territories where wind-power plants are currently absent and eagles are not subject to increased mortality from wind power plant collisions. Using the accumulated tracking data, we constructed individual capture histories on a monthly basis and adult survival rates using known-fate models in program MARK. We also review published adult survival estimates of Golden Eagles reported throughout their range for relative comparison. Monthly adult survival in our study area was 0.9933 (0.9854–0.9970) which translates to annual survival of 0.924 (0.838–0.965). We found eight studies reporting survival estimates, which ranged from 0.860 to 0.975 with a mean of 0.928. Thus, adult survival rates of Golden Eagles breeding in northern Finland, that are not affected by wind power plants, are high as expected for a viable population and very close to the mean estimated from other Golden Eagle populations. Maintaining high adult survival rates will be key to Golden Eagle population stability with expanding wind energy development in Finland.

1. Introduction

Information about demographic rates is important for assessing the causes of population declines (*e.g.* Green 2002, Pakanen & Kylmänen 2023) and for assessing the potential impacts of human caused mortality due to persecution or environmental change on population viability (Whitfield *et al.* 2004, Carrete *et al.* 2009, Gauld *et al.* 2022). For example, recent developments in wind energy have increased potential negative impacts on wildlife (Santangeli *et al.* 2018), especially birds and bats that may suffer increased mortality due to collisions with wind turbines (Hunt *et al.* 2017, Katzner *et al.* 2017, Monti *et al.* 2023, Serratosa *et al.* 2024). Assessing overall contribution of wind energy-related impacts to wildlife requires baseline survival rates from natural conditions.

Large raptors have been suffering from anthropogenic effects such as persecution and poisoning in the last century (*e.g.* Whitfield *et al.* 2004), but recently these large species with reduced flight maneuverability are known to be affected by wind turbines, mostly through direct mortality and secondarily through habitat alteration and loss (Watson *et al.* 2018, Gauld *et al.* 2022). Golden Eagles (*Aquila chrysaetos*) are of conservation concern and are among the highest profile wildlife species killed at renewable-energy facilities in United States (Katzner *et al.* 2017). Information about adult survival is especially important from populations of these long-lived species in which surviving adults form the largest contribution to the population growth rates out of all demographic rates, and therefore increased adult mortality will have strong impacts on future population growth (Tack *et al.* 2017).

Unfortunately, survival estimates for medium to large sized raptors are rare because acquiring standard live-recapture data requires systems where the adults can be recaptured safely (Tolvanen *et al.* 2017), resighted using cameras (see *e.g.* Santangeli *et al.* 2020, Väli *et al.* 2021) or individuals identified through DNA (*e.g.* Nebel *et al.* 2023). However, these are often unfeasible leaving the estimation of large raptor survival to radio telemetry (Hunt *et al.* 2017), age ratio (Hernández-Matías *et al.* 2011) or dead recovery data (Millsap *et al.* 2022). Telemetry offers an option for estimating survival of large species, such as Golden Eagles, that may not suffer from transmitter-related impacts (*e.g.* Sergio *et al.* 2015, Crandall *et al.* 2019). Global Positioning System (GPS) transmitters specifically have been successfully used to study movements, habitat use and survival of eagles with no apparent ill effects (Harmata 2016, Nygård *et al.* 2016, Tikkanen *et al.* 2018a, 2018b).

Onshore wind power has increased enormously in Finland over the last decade, and it is predicted to grow from the current (the end of June 2024) over 7 GW (Renewables Finland 2024) potentially to 79 GW by 2045 (Fingrid 2023). In the future, the wind energy facilities will extend to the distribution of breeding Golden Eagles (Balotari-Chiebao *et al.* 2021). The predicted increase in risk requires collection of baseline information to fully assess impacts to Golden Eagles and help identify successful mitigation measures if needed (Allison *et al.* 2017). One important demographic component to maintaining population stability is adult survival. Currently, there is a lack of information on Golden Eagle adult survival in Finland, which could be used to inform demographic models in the future and to evaluate the potential impacts of future wind power plans. To help inform this information gap, we use GPS-tracking data from 26 adult Golden Eagles breeding in northern Finland to estimate adult survival probabilities. We also review scientific literature to assess the state of Golden Eagle adult survival from different areas across Finland.

2. Material and methods

2.1. Tracking data

We trapped 30 territorial adult Golden Eagles (17 males, 13 females) from carcass feeding sites using remote-controlled bow nets. Trapping was done during winter months from 2011 to 2023 at territories across the range of breeding Golden Eagles in Finland (Fig. 1). Survival of Golden Eagles followed on these territories was not affected by wind-power plants as wind power projects were absent from their home ranges. For individuals that died during the study, the distances from nest sites to the closest wind power project were at least 12 km, which exceeds Golden Eagle home ranges (mean distance to center of Minimum Convex Polygon 11.7 km, Tikkanen *et al.* 2018a). For individuals that are still followed, four home ranges contained wind turbines (the shortest distances to active nests were 3.5–9.1 km during monitoring).

We determined sex on the basis of mass and wing length tail feather coloration (Forsman 1980, Watson 2010). Seventeen individuals had been ringed as a chick before the GPS study began. At the start of GPS data collection, their age was on average 12 years (range 5–26 years calculated from those ringed as young, whose age is known).

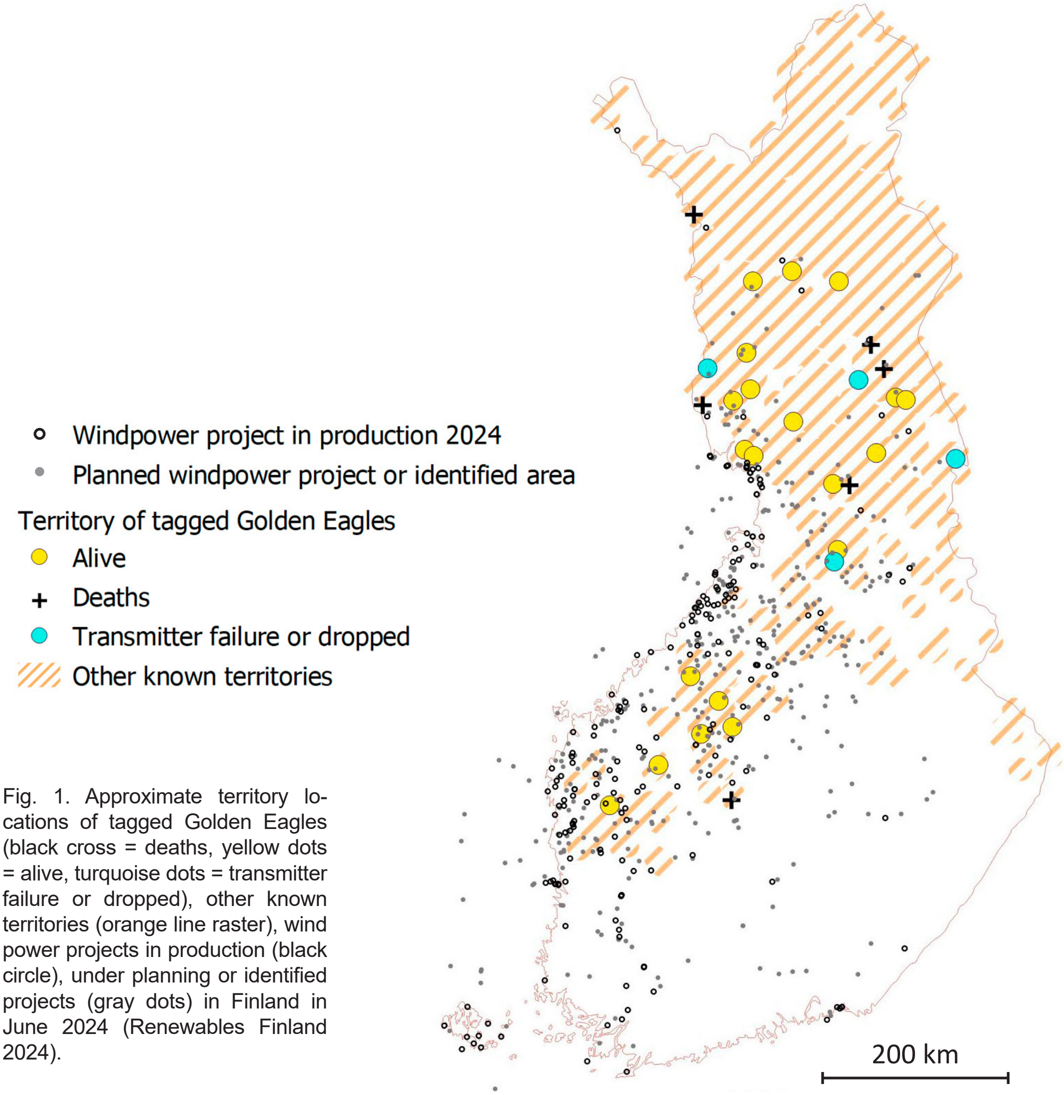

Fig. 1. Approximate territory locations of tagged Golden Eagles (black cross = deaths, yellow dots = alive, turquoise dots = transmitter failure or dropped), other known territories (orange line raster), wind power projects in production (black circle), under planning or identified projects (gray dots) in Finland in June 2024 (Renewables Finland 2024).

We ringed all previously unringed individuals with steel rings. All individuals were fitted with solar powered GPS transmitters (Cellular tracking ES-400-40-BKP; OrniTrack-50 - solar powered GPS-GSM tracker; Microwave telemetry Solar 50g PTT; Solar Argos GPS PTT-100 telemetry transmitter Microwave Telemetry, Inc.) using Teflon harnesses (not designed to fall off, see also Tikkanen *et al.* 2018a) with permission from the Centre for Economic Development, Transport and the Environment. The weights of these tracking devices were 50–70 g, which is at the maximum 2% of Golden Eagle mass as the smallest individual weighed 3.5 kg. These devices should therefore be a safe tracking method (Costantini & Møller 2013).

We followed tagged Golden Eagles until death, the device was shed, transmitter malfunction, or the study period was over in January 2024. The transmitters sent location data every 1 min – 1 hour in daylight depending on the programming of the transmitters. Those data were used to track the fate of each tracked individual eagle. Movement of individuals were followed closely so that deaths could be identified (Crandall *et al.* 2019). If the location remained stationary for

2 or more days, we visited (within 7 days at the latest) the site to determine if the Golden Eagle had died or if the tracking device had dropped (Crandall *et al.* 2019). If the Golden Eagle had died, we attempted to determine cause of death. If the tracking device stopped sending locations and was nowhere to be found at the latest location, the transmitter was concluded to have malfunctioned (Nygård *et al.* 2016).

2.2. Data analysis

We analyzed the data with program MARK using known fate models (White & Burnham 1999). We used the tracking information to construct individual capture histories that detailed for each month whether the individual stayed alive (10) or died (11), which allowed us to examine monthly survival. If the tracking device had dropped or failed and there was uncertainty in the fate of the individual, we removed the individual from the analysis (four individuals). If there were sighting information indicating that the bird was alive, we censored the history after the last month which the individual survived when the transmitter was still functioning (one individual). The dataset used in the final analysis included 908 monthly observations from 26 individuals (14 males and 12 females). We fit an intercept only model to derive an estimate of monthly survival. We derived an annual survival estimate by raising the monthly survival to the power of 12 (monthly survival^{12}).

2.3. Review of adult survival rates

We used information available in previous reviews of large raptors (Newton 2016, Tack *et al.* 2017) and the Golden Eagle (Watson 2010), and searched for published adult survival estimates for the Golden Eagle using Google Scholar with search words "Golden Eagle" or "*Aquila chrysaetos*" and "survival" or "mortality" with words indicating methods "capture-recapture", "dead recovery", "CJS-model", "age ratio", "GPS", "known fate". We had no spatial or temporal restrictions in the search. See Appendix 1 for a prisma figure outlining the review process.

3. Results

Individuals were followed from two to 94 months. Out of 26 individuals, 19 were still alive and tracked at the end of January 2024 (Table 1). Six individuals died during the study. Causes of death were starvation (n = 1) and unknown (n = 5). One of these individuals was found injured (probably in a collision with a power line) and would have died without treatment at an animal hospital. After treatment, the bird was released without GPS tracking. One transmitter had dropped. Four transmitters stopped working. Of these, one individual was resighted after the transmitter failure and confirmed to be alive (identified by a ring). This individual was censored after the last observation received from the GPS-device. The remaining three birds and the one that dropped its transmitter were removed from the data before the survival analysis. Monthly survival estimated from the intercept model was 0.9933 (0.9854–0.9970), which translates to annual survival of 0.924 (0.838–0.965).

3.1. Review

We found eight publications that reported nine survival estimates for adult Golden Eagles with varying methods (Table 2). Millsap *et al.* (2022) used joint dead recovery (3,128 individuals) and satellite tagging data (512 individuals) collected from western parts of the United States together with an integrated population model (Schaub & Kéry 2021) to model impacts of survival and other demographic rates on population growth rates. Another study from Sweden estimated adult survival using accumulated dead recovery data from Golden Eagles ringed as chicks from 1990 to 2015 (Daouti 2017). Daouti (2017) used the Seber parametrization (Seber 1970) assuming that juveniles and adults have equal recovery probabilities.

Hunt *et al.* (2017) followed 257 Golden Eagles from four life-stages (132 juveniles, 64 subadults, 21 floaters and 41 adult) in California United States using radio telemetry. Using information on cause-specific mortality, they were able to separate different sources of mortality.

Table 1. Information about GPS-tagged Golden Eagles.

Bird ID	County	Transmitter	Sex	Year	Months	End status
#1	Perho	OrniTrack-50 - solar powered GPS-GSM tracker	Male	2021	25	Alive
#2	Ylitornio	Microwave telemetry Solar 50g PTT	Male	2016	33	Dead
#3	Muonio	Microwave telemetry Solar 50g PTT	Male	2011	30	Dead
#4	Salla	Microwave telemetry Solar 50g PTT	Male	2051	25	Dead
#5	Kyyjärvi	Cellular tracking ES-400-40-BKP	Female	2018	52	Dead
#6	Pudasjärvi	OrniTrack-50 - solar powered GPS-GSM tracker	Female	2022	17	Dead
#7	Salla	Cellular tracking ES-400-40-BKP	Male	2016	28	Dead
#8	Kemijärvi	Microwave telemetry Solar 50g PTT	Male	2013	7	Transmitter dropped
#9	Sodankylä	Microwave telemetry Solar 50g PTT	Male	2014	77	Transmitter failure; seen alive
#10	Rovaniemi	Cellular tracking ES-400-40-BKP	Female	2019	59	Alive
#11	Lestijärvi	Cellular tracking ES-400-40-BKP	Female	2019	58	Alive
#12	Utajärvi	OrniTrack-50 - solar powered GPS-GSM tracker	Male	2021	34	Alive
#13	Utajärvi	OrniTrack-50 - solar powered GPS-GSM tracker	Male	2021	3	Transmitter failure
#14	Kuusamo	Microwave telemetry Solar 50g PTT	Female	2013	25	Transmitter failure
#15	Kaustinen	Microwave telemetry Solar 50g PTT	Male	2016	94	Alive
#16	Pello	Microwave telemetry Solar 50g PTT	Male	2017	17	Transmitter failure
#17	Sodankylä	Cellular tracking ES-400-40-BKP	Female	2018	62	Alive
#18	Kuusamo	Cellular tracking ES-400-40-BKP	Male	2020	39	Alive
#19	Posio	Cellular tracking ES-400-40-BKP	Female	2020	38	Alive
#20	Ranua	OrniTrack-50 - solar powered GPS-GSM tracker	Female	2020	38	Alive
#21	Pudasjärvi	OrniTrack-50 - solar powered GPS-GSM tracker	Female	2018	70	Alive
#22	Kittilä	OrniTrack-50 - solar powered GPS-GSM tracker	Female	2021	26	Alive
#23	Simo	OrniTrack-50 - solar powered GPS-GSM tracker	Female	2022	26	Alive
#24	Kauhajoki	OrniTrack-50 - solar powered GPS-GSM tracker	Male	2022	25	Alive
#25	Seinäjoki	OrniTrack-50 - solar powered GPS-GSM tracker	Female	2022	13	Alive
#26	Alajärvi	OrniTrack-50 - solar powered GPS-GSM tracker	Male	2023	2	Alive
#27	Simo	OrniTrack-50 - solar powered GPS-GSM tracker	Male	2023	3	Alive
#28	Ylitornio	OrniTrack-50 - solar powered GPS-GSM tracker	Female	2021	27	Alive
#29	Taivalkoski	OrniTrack-50 - solar powered GPS-GSM tracker	Male	2023	11	Alive
#30	Ylitornio	OrniTrack-50 - solar powered GPS-GSM tracker	Male	2023	3	Alive

Table 2. Published adult survival rates for Golden Eagles with confidence intervals or standard errors (SE) in parenthesis.

Survival	Method	Years	Country	Reference
0.860 (SE 0.132)	Satellite tracking	2011–2015	USA	Harmata 2016
0.890 (0.820–0.940)	Dead recovery data	1990–2015	Sweden	Daouti 2017
0.935 (0.892–0.979)	Radio telemetry	1994–1999	USA	Hunt *et al.* 2017
0.925	Disappearance of individuals		Germany	Bezzel & Fünfstück 1994 (in Watson 2010)
0.924 (0.838–0.965)	Satellite tracking	2011–2024	Finland	This study
0.930 (0.814–0.976)	Satellite tracking	2010–2017	Montana, USA	Crandall *et al.* 2019
0.940 (0.900–0.980)	Dead recovery data & satellite tracking	1997–2016	USA	Millsap *et al.* 2022
0.942 (0.923–0.955)	Age ratios	1982–1992	Scotland	Whitfield *et al.* 2004
0.958 (0.935–0.982)	Age ratios	1982–1992	Scotland	Whitfield *et al.* 2004
0.975	Disappearance of individuals		Scotland	Crane & Nellist 1999 (in Watson 2010)

They used known fate models to estimate adult survival with all causes of mortality (0.905), when wind power caused mortalities were censored (0.920) and when all human caused mortalities were censored (0.935).

Two studies used satellite telemetry to follow Golden Eagles in Montana, United States. Crandall *et al.* (2019) followed 16 adults using satellite transmitters that were mounted using a Teflon ribbon with a cross-chest breakaway harness. They used a multistate model with three states (alive, dead and unknown) to estimate adult survival. Harmata (2016) estimated adult survival by following 25 Golden Eagles equipped with tail-mounted satellite transmitters.

Whitfield *et al.* (2004) estimated two adult survival rates for populations in Scotland by comparing age groups. They generated survival estimates where persecution did not affect the results. One estimate was derived for the whole of Scotland (with multiple areas called zones included) using a regression model where the number of subadults for every 100 adults was explained by the density of poisoning incidents. The persecution free survival estimate was taken from the intercept as 0.942. In one completely persecution free zone (Western Seaboard), the estimate was 0.958. Watson (2010) reported studies from Germany (0.925) and Scotland (0.975) where estimates were drawn by using the disappearance of individuals from their territories as a cue for mortality.

Adult survival rates from all the published estimates ranged from 0.860 to 0.975 with a mean of 0.928 when using estimates that do not include human caused mortalities such as persecution or wind turbine collisions (Table 2).

4. Discussion

Using data from GPS-tagged individuals, we estimated annual survival probability of breeding Golden Eagles in Finland to be 0.924. In our review, we found only eight studies reporting adult survival estimates for Golden Eagles. These studies used varying methods, including three studies that did not use marking or tagging of individuals as a source of survival estimation indicating that there are a limited number of robust adult survival estimates available for Golden Eagles. Estimates from previous studies ranged from 0.860 to 0.975 and the mean Golden Eagle survival across all studies was on average 0.928. Thus, our estimate for the Finnish Golden Eagle population is close to this mean. This level of adult survival is within expected levels of a healthy population in Scotland (Whitfield *et al.* 2004).

Our study is among the first to examine adult survival of Golden Eagles in Northern Europe. A previous study from Sweden estimated mean annual survival (0.890) using dead recoveries (Daouti 2017). This study did not control for age differences in the recovery parameter, which may have affected the results if the assumption of equal recovery rates between juveniles and adults was not met by the data. Another study from Finland examined turnover rates from breeding Golden Eagles using chick DNA as a source of information (Kylmänen *et al.* 2023). Given our survival estimate, annual mortality of Golden Eagles is 0.076. Hence, the turnover rate (0.23) estimated by Kylmänen *et al.* (2023) likely reflects additional factors such as site fidelity.

Juvenile survival rates among Golden Eagles are clearly lower than those of adults (*e.g.* McIntyre *et al.* 2006: 1. year survival 0.19–0.34; Nygård *et al.* 2016: 1. year survival 0.58, 2. year survival 0.50; Millsap *et al.* 2022: 1. year survival 0.73, 2. year survival 0.87; Hunt *et al.* 2017: 1. year survival 0.84; Murphy *et al.* 2017: 1. year survival 0.79). Despite that this strong spatial variation may be caused by methodological differences between the above studies, large differences in juvenile survival warrant studies examining it also in Finland.

Our approach, the use of GPS-tracking data to estimate survival of adult Golden Eagles in Finland, facilitates estimation of adult survival from territories that are not yet subject to potential impacts from wind turbine collisions. Given the known importance of adult survival to Golden Eagle population stability, our relatively high estimated annual adult survival is likely a primary contributor to the observed population growth rate in Finland based on territories (1.02 SE 0.01; Tikkanen *et al.* unpublished). Therefore, this population may be vulnerable to increased mortality from expanding wind energy development. Further modelling efforts to quantify effects of future lost Golden Eagle habitat (Tikkanen *et al.* 2018a) from expanding wind energy development and collision risk models (Band *et al.* 2007) joined with subsequent modelling of their impacts on population viability (Wiens *et al.* 2017) are needed in order to guide responsible siting of wind power plants in Finland.

GPS-merkittyjen pesivien aikuisten maakotkien (*Aquila chrysaetos*) selviytymisarviot Suomessa

Aikuislintujen selviytymisarviot ovat tärkeitä arvioitaessa populaation tilaa ja elinkelpoisuutta sekä tutkittaessa ihmisen aiheuttamien vaikutusten roolia arvioiden vaihtelussa. Tällä hetkellä nopeasti lisääntyvä tuulivoima muodostaa uuden ja vakavan uhan suurten petolintujen selviytymiselle.

Vuosina 2011–2024 seurasimme 26 maakotkaa (*Aquila chrysaetos*) Suomessa käyttämällä satelliittipaikannusjärjestelmän seurantalaitteita alueilla, joilla ei ole tuulivoimaloita, eikä kotkien kuolleisuus ole lisääntynyt törmäysten vuoksi. Kerättyjen seurantatietojen avulla rakensimme yksilöllisiä havaintosarjoja kuukausitasolla ja arvioimme aikuisten selviytymisprosentit käyttämällä tunnetun kohtalon malleja MARK-ohjelmassa. Tarkastelimme myös julkaistuja aikuisten maakotkien selviytymisarvioita niiden levinneisyysalueella vertailevaa analyysia varten.

Tutkimusalueellamme kuukausittainen aikuisten selviytymisprosentti oli 0.993 (0.985–0.997), mikä tarkoittaa vuosittaista selviytymisprosenttia 0.924 (0.838–0.965). Löysimme kahdeksan tutkimusta, jotka raportoivat selviytymisarvioita, ja niiden vaihteluväli oli 0.860–0.975, keskiarvon ollessa 0.928. Näin ollen Pohjois-Suomessa pesivien maakotkien, jotka eivät ole tuulivoimaloiden vaikutuksen alaisia, aikuisten selviytymisprosentit ovat korkeat, kuten elinkelpoisessa populaatiossa odotetaan, ja hyvin lähellä muiden maakotkakantojen keskiarvoa. Korkeiden aikuisten selviytymisprosenttien ylläpitäminen on avainasemassa maakotkien populaation vakauden säilyttämisessä, kun tuulivoimarakentaminen Suomessa lisääntyy.

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References

Allison, T.D., Cochrane, J.F., Lonsdorf, E. & Sanders-Reed, C. 2017: A review of options for mitigating take of Golden eagles at wind energy facilities. — Journal of Raptor Research 51: 319–333. https://doi.org/10.3356/JRR-16-76.1

Balotari-Chiebao, F., Valkama, J. & Byholm, P. 2021: Assessing the vulnerability of breeding bird populations to onshore wind-energy developments in Finland. — Ornis Fennica 98: 59–73. https://doi.org/10.51812/of.133981

Band, W., Madders, M. & Whitfield, D.P. 2007: Developing field and analytical methods to assess avian collision risk at wind farms. — In Birds and Wind Farms: Risk Assessment and Mitigation (ed. de Lucas, M., Janss, G.F.E. & Ferrer, M.): 259–275. Quercus, Madrid.

Bezzel, E. & Fünfstück, H.J. 1994: Breeding biology and population dynamics of the golden eagle (*Aquila chrysaetos*) in the Werdenfelser Land, Southern Bavaria. — Acta Ornithoecologica 3: 5–32. (In German)

Carrete, M., Sánchez-Zapata, J.A., Benítez, J.R., Lobón, M. & Donázar, J.A. 2009: Large scale risk-assessment of wind-farms on population viability of a globally endangered long-lived raptor. — Biological Conservation 142: 2954–2961. https://doi.org/10.1016/j.biocon.2009.07.027

Costantini, D. & Møller, A.P. 2013: A meta-analysis of the effects of geolocator application on birds. — Current Zoology 59: 697–706. https://doi.org/10.1093/czoolo/59.6.697

Crandall, R.H., Craighead, D.J., Bedrosian, B. & Slabe, V.A. 2019: Survival estimates and cause of mortality of golden eagles in South-Central Montana. — Journal of Raptor Research 53: 38–45.

Crane, K. & Nellist, K. 1999: Island Eagles. 20 years observing eagles on the Isle of Skye. — Cartwheeling Press, Skye.

Daouti, E.L. 2017: Breeding dynamics of a Golden Eagle (*Aquila chrysaetos*) population in the boreal forest of Sweden. — Master thesis. University of Umeå. Retrieved from https://stud.epsilon.slu.se/10023/

Gauld, J. G., Silva, J. P., Atkinson, P. W., ... & Franco, A. M. 2022: Hotspots in the grid: Avian sensitivity and vulnerability to collision risk from energy infrastructure interactions in Europe and North Africa. — Journal of Applied Ecology 59: 1496–1512. https://doi.org/10.1111/1365-2664.14160

Green, R.E. 2002: Diagnosing causes of population declines and selecting remedial actions. — In Conserving Bird Biodiversity (ed. Norris, K. & Pain, D.J.): 139–156. Cambridge University Press, Cambridge

Fingrid 2023: Fingrid's electricity system vision 2023. — Retrieved from https://www.fingrid.fi/globalassets/dokumentit/en/news/electricity-market/2023/fingrid_electricity_system_vision_2023.pdf

Forsman, D. 1980: Suomen päiväpetolinnut – haukkojen ja kotkien määritysopas. — Lintutieto Oy. (In Finnish)

Harmata, A.R. 2016: Retention, effect, and utility of tailmounted satellite-tracked transmitters on Golden Eagles. — Journal of Raptor Research 50: 265–275.

Hernández-Matías, A., Real, J. & Pradel, R. 2011: Quick methods for evaluating survival of age-characterizable long-lived territorial birds. — The Journal of Wildlife Management 75: 856–866. https://doi.org/10.1002/jwmg.102

Hunt, G.W, Wiens, J.D., Law, P.R., Fuller, M.R., Hunt, T.L., Driscoll, D.E. & Jackman, R.E. 2017: Quantifying the demographic cost of human-related mortality to a raptor population. — PLoS ONE 12(2): e0172232. https://doi.org/10.1371/journal.pone.0172232

Katzner, T.E., Nelson, D.M., Braham, M.A., Doyle, J.M., Fernandez, N.B., Duerr, A.E., Bloom, P.H., Fitzpatrick, M.C., Miller, T.A., Culver, R.C.E., Braswell, L. & DeWoody, J.A. 2017: Golden Eagle fatalities and the continental-scale consequences of local wind-energy generation. — Conservation Biology 31: 406–415. https://doi.org/10.1111/cobi.12836

Kylmänen, A., Karabanina, E., Ollila, T., Ponnikas, S. & Kvist, L. 2023: Turnover and natal dispersal in the Finnish Golden eagle (*Aquila chrysaetos*) population. — Diversity 15: 567. https://doi.org/10.3390/d1504056

McIntyre, C. L., Collopy, M.W. &Lindberg M.S. 2006: Survival probability and mortality of migratory juvenile Golden Eagles from interior Alaska. — Journal of Wildlife Management 70: 717–22.

Millsap, B.A., Zimmerman, G.S., Kendall, W.L., ... & Watson, J.W. 2022: Age-specific survival rates, causes of death, and allowable take of Golden Eagles in the Western United States. — Ecological Applications 32(3): e2544. https://doi.org/10.1002/eap.2544

Monti, F, Serroni, P, Rotondaro, F., Sangiuliano, A., Sforzi, A., Opramolla, G., Pascazi, A., Spacca, S., La Civita, F. & Posillico, M. 2023: Survival of a small reintroduced griffon vulture population in the Apennines: Insights from Global Positioning System tracking. — Avian Biology Research 16: 3–13. doi:10.1177/17581559221137309

Murphy, R. K. , Dunk J. R., Woodbridge B., Stahlecker D. W., LaPlante D. W., Millsap B. A. & Jacobson K. V. 2017: First-year dispersal of Golden Eagles from natal areas in the southwestern United States and implications for second-year settling. — Journal of Raptor Research 51: 216–33. https://doi.org/10.3356/JRR-16-80.1

Nebel, C., Ekblad, C., Balotari-Chiebao, F., Penttinen, I., Stjernberg, T. & Laaksonen, T. 2023: Early-life diet specificity is associated with long-lasting differences in apparent survival in a generalist predator. — Journal of Animal Ecology 92: 850–862. https://doi.org/10.1111/1365-2656.13894

Newton, I., McGrady, M.J. & Oli, M.K. 2016: A review of survival estimates for raptors and owls. — Ibis 158: 227–248. https://doi.org/10.1111/ibi.12355

Nygård, T., Jacobsen, K.-O., Johnsen, T.-V. & Systad, G.H. 2016: Dispersal and Survival of Juvenile Golden Eagles (*Aquila chrysaetos*) from Finnmark, Northern Norway. — Journal of Raptor Research 50: 144–160. https://doi.org/10.3356/rapt-50-02-144-160.1

Pakanen, V.-M. & Kylmänen, R. 2023: High adult survival in a northern Eurasian Curlew (*Numenius arquata*) population. — Ornis Fennica 100: 112–122. https://doi.org/10.51812/of.126810

Renewables Finland 2024: Retrieved from https://suomenuusiutuvat.fi/en/ (Accessed June 2024)

Santangeli, A., Butchart, S. H., Pogson, M., Hastings, A., Smith, P., Girardello, M. & Moilanen, A. 2018: Mapping the global potential exposure of soaring birds to terrestrial wind energy expansion. — Ornis Fennica 95: 1–14. Retrieved from https://ornisfennica.journal.fi/article/view/133925

Santangeli, A., Pakanen, V.-M., Bridgeford, P., Boorman, M., Kolberg, H. & Sanz-Aguilar, A. 2020: The relative contribution of camera traps and citizen data for estimating survival of an endangered vulture in an arid South African landscape. — Biological Conservation 246: 108593. https://doi.org/10.1016/j.biocon.2020.108593

Seber, G.A.F. 1970: Estimating time-specific survival and reporting rates for adult birds from band returns. — Biometrika 57: 313–318.

Sergio, F., Tavecchia, G., Tanferna, A., López Jiménez, L., Blas, J., De Stephanis, R., Marchant, T.A., Kumar, N. & Hiraldo, F. 2015: No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning and condition of its offspring. — Journal of Applied Ecology 52: 1665–1675. https://doi.org/10.1111/1365-2664.12520

Serratosa J, Oppel S, Rotics S, ... & Jones VR 2024: Tracking data highlight the importance of human-induced mortality for large migratory birds at a flyway scale. — Biological Conservation 293: 110525. https://doi.org/10.1016/j.biocon.2024.110525

Schaub, M. & Kéry, M. 2021: Integrated population models: Theory and ecological applications with R and JAGS. — Elsevier Science.

Tack, J.D., Noon, B.R., Bowen, Z.H., Strybos, L. & Fedy, B.C. 2017: No substitute for survival: perturbation analyses using a Golden Eagle population model reveal limits to managing for take. — Journal of Raptor Research 51: 258–272. https://doi.org/10.3356/JRR-16-32.1

Tikkanen, H., Rytkönen, S., Karlin, O.-P., Ollila, T., Pakanen, V.-M., Tuohimaa, H. & Orell, M. 2018a: Modelling Golden Eagle habitat selection and flight activity in their home ranges for safer wind farm planning. — Environmental Impact Assessment Review 71: 120–131. https://doi.org/10.1016/j.eiar.2018.04.006

Tikkanen, H., Balotari-Chiebao, F., Laaksonen, T., Pakanen, V.-M. & Rytkönen, S. 2018b: Habitat selection of flying pre-breeding White-tailed Eagles (*Haliaeetus albicilla*): implications for land use and wind farm planning. — Ornis Fennica 95: 137–150. https://doi.org/10.51812/of.133937

Tolvanen, J., Pakanen, V.-M., Valkama, J. & Tornberg, R. 2017: Apparent survival, territory turnover and site fidelity rates in Northern Goshawk *Accipiter gentilis* populations close to northern range limit. — Bird Study 64: 168–177. https://doi.org/10.1080/00063657.2017.1309351

Väli, Ü., Kalvāns, A. & Tuvi, J. 2021: Apparent survival and dispersal in a recovered Osprey population: effects of age, sex and social status. — Journal of Ornithology 162: 1025–1034. https://doi.org/10.1007/s10336-021-01908-7

Watson, J. 2010: The Golden Eagle (2nd edition). — Yale University Press, New Haven.

Watson, R.T., Kolar, P.S., Ferrer, M., Nygård, T., Johnston, N., Hunt, W.G., Smit-Robinson, H.A., Farmer, C.J., Huso, M. & Katzner, T.E. 2018: Raptor interactions with wind energy: case studies from around the world. — Journal of Raptor Research 52: 1–18. https://doi.org/10.3356/JRR-16-100.1

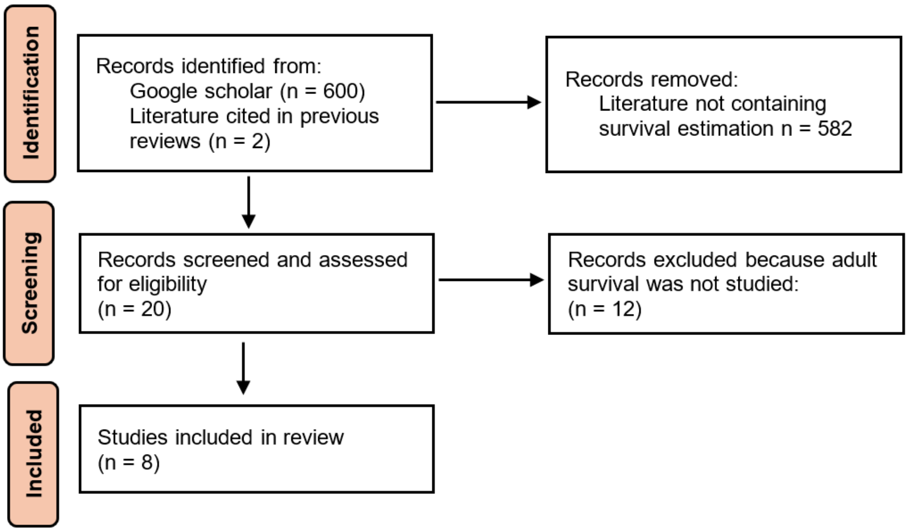
White, G.C. & Burnham, K.P. 1999: Program MARK: survival estimation from populations of marked animals. — Bird Study 46: 120–139.

Whitfield, D.P., Fielding, A.H., Mcleod, D.R.A. & Haworth, P.F. 2004: Modelling the effects of persecution on the population dynamics of Golden Eagles in Scotland. — Biological Conservation 119: 319–333. https://doi.org/10.1016/j.biocon.2003.11.015

Wiens, J.D., Schumaker, N.H., Inman, R.D., Esque, T.C., Longshore, K.M. & Nussear, K.E. 2017: Spatial demographic models to inform conservation planning of Golden Eagles in renewable energy landscapes. — Journal of Raptor Research 51: 234–257. https://doi.org/10.3356/JRR-16-77.1

Appendix 1

A prisma figure for steps of the review. We used two sources. First, we searched for records on published adult survival estimates for the Golden Eagle from Google scholar with search words “Golden Eagle” or “*Aquila chrysaetos*” and “survival” or “mortality” with words indicating methods “capture-recapture”, “dead recovery”, “CJS-model”, “age ratio”, “GPS”, “known fate”. From these, we examined the first 600 hits and removed those not including survival estimation. The second source of information was previous reviews of large raptors (Newton 2016, Tack *et al.* 2017) and the Golden Eagle (Watson 2010), which provided 2 records not included in the Google scholar search.



References

Newton, I., McGrady, M.J. & Oli, M.K. 2016: A review of survival estimates for raptors and owls. — Ibis 158: 227-248. https://doi.org/10.1111/ibi.12355

Tack, J.D., Noon, B.R., Bowen, Z.H., Strybos, L. & Fedy, B.C. 2017: No substitute for survival: perturbation analyses using a Golden Eagle population model reveal limits to managing for take. — Journal of Raptor Research 51: 258–272. https://doi.org/10.3356/JRR-16-32.1

Watson, J. 2010: The Golden Eagle (2nd edition). — Yale University Press, New Haven.

Ornis Fennica 101: 101–115. 2024

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

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

1. Introduction

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

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

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

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

Paludan (1965) described the Danish summering population of Greylag Geese at that time as a winter migrant to Marismas de Guadalquivir (Coto Doñana, 36°58'N, 06°24'W) in southern Spain, an area which was "by far the most important winter quarter for West and Central European Greylag Geese". Bønløkke *et al.* (2006) also described the main wintering quarters for Danish Greylag Geese as southern Spain, but also mentioned that the centre of gravity of the wintering quarters had shifted northwards since the 1950s, a pattern also seen among Greylag Geese from south Sweden (Nilsson & Kampe-Persson 2018). This was recently confirmed by Clausen *et al.* (2023), who showed that the proportion of Danish-ringed Greylag Geese recovered in Spain in winter decreased from *ca.* 75% in the 1950s to almost none in the 2010s, while those recovered in Denmark increased from almost none to *ca.* 50% over the same period, most marked since the early 1990s (Kampp & Preuss 2005).

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

2. Material and methods

2.1. Sites and captures

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

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

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

2.2. Rings and tags

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

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

2.3. Data

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

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

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

2.4. Migratory patterns

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

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

3. Results

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

3.1. Migratory patterns

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

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

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

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

3.2. Monthly movements

3.2.1. Geese ringed on Djursland

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

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

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

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

3.2.2. Geese ringed at Zealand

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

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

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

3.3. Migrants to Spain

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

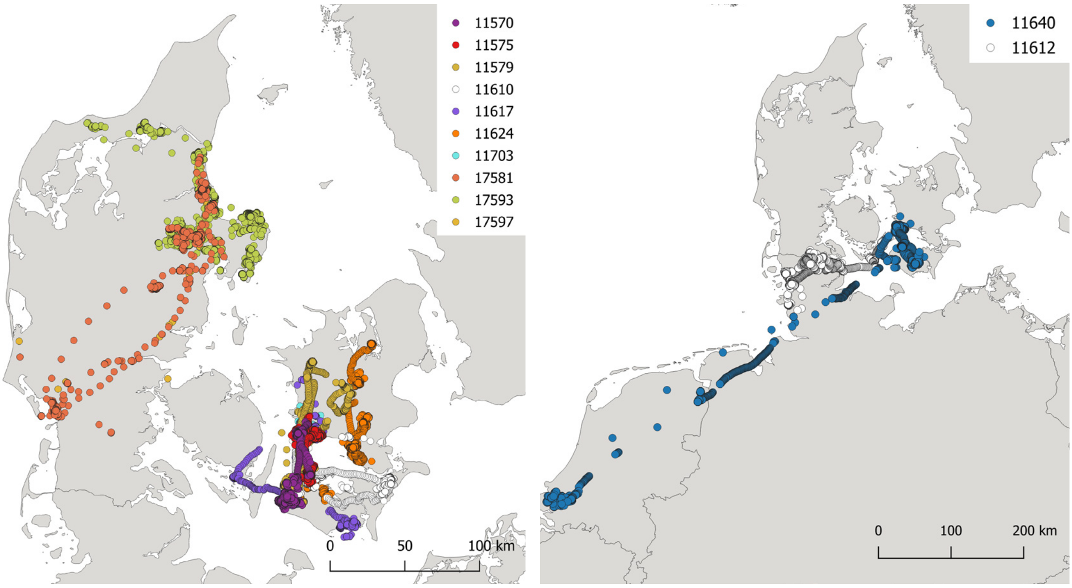

Fig. 1. Movements of Greylag Geese (*Anser anser*) during the first year after being tagged. Left: All sedentary individuals (staying in Denmark throughout the annual cycle): Three tagged in Vasen, Clausholm, Jutland, Denmark in 2021 and seven tagged at Zealand (Agersø and Skjoldnæsholm Engsø) in 2022.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

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

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

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

3.4. Active migration

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

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

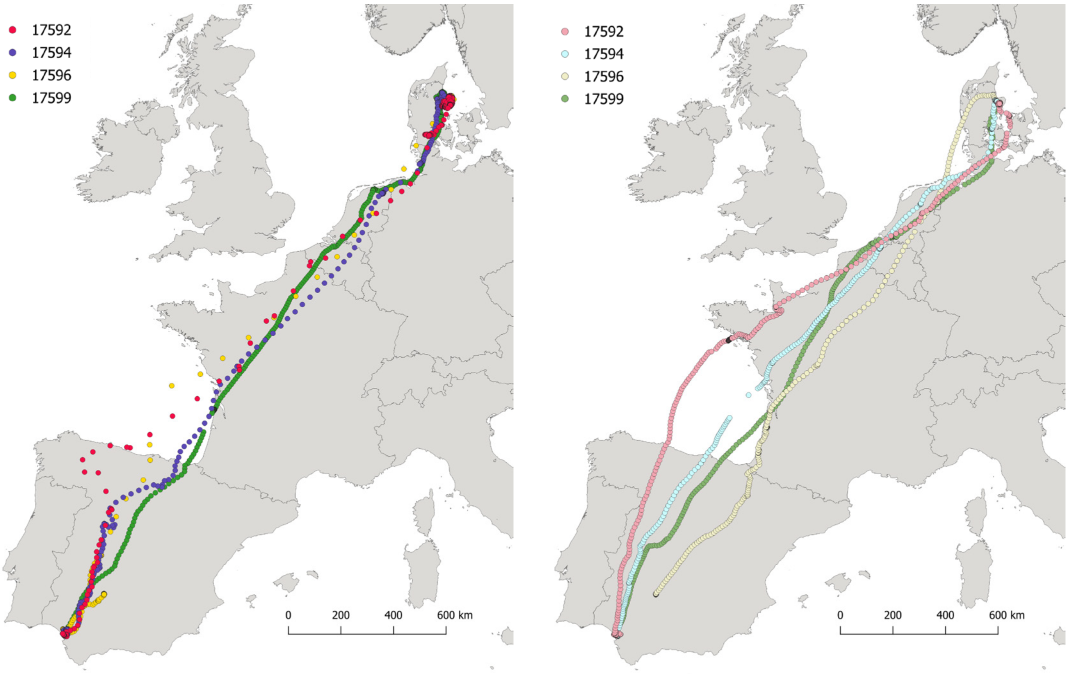

Fig. 2. Migratory routes of four Greylag Geese (*Anser anser*) tagged in Kastrup Mose, Denmark in 2021 and wintering in Coto Doñana, Spain during the winter 2021/2022. Left: Autumn migration. Right: Spring migration up to 31 March. The same colours (but paler in spring) in the two seasons represent the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

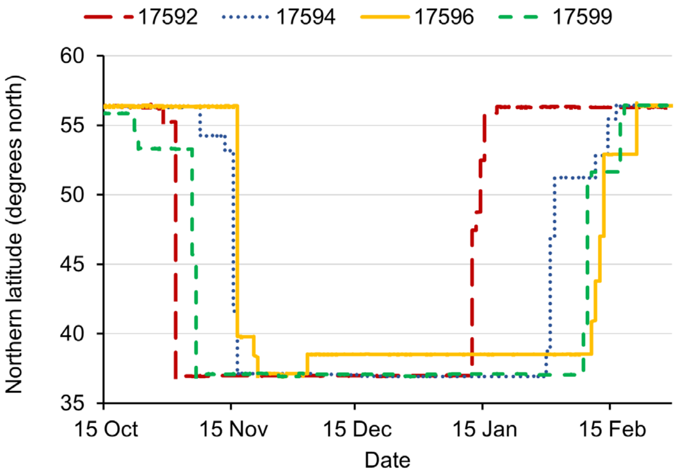

Fig. 3 Seasonal changes in latitude of four GPS-tagged migratory Greylag Geese (*Anser anser*) during 15 October 2021 to 1 March 2022 illustrating their migratory speed and staging sites from the tagging site in Kastrup Mose, Djursland to their wintering quarters in Coto Doñana, Spain.

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

3.5. Moult movements

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

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

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

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

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

3.6. Subsequent winter movements

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

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

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

4. Discussion

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

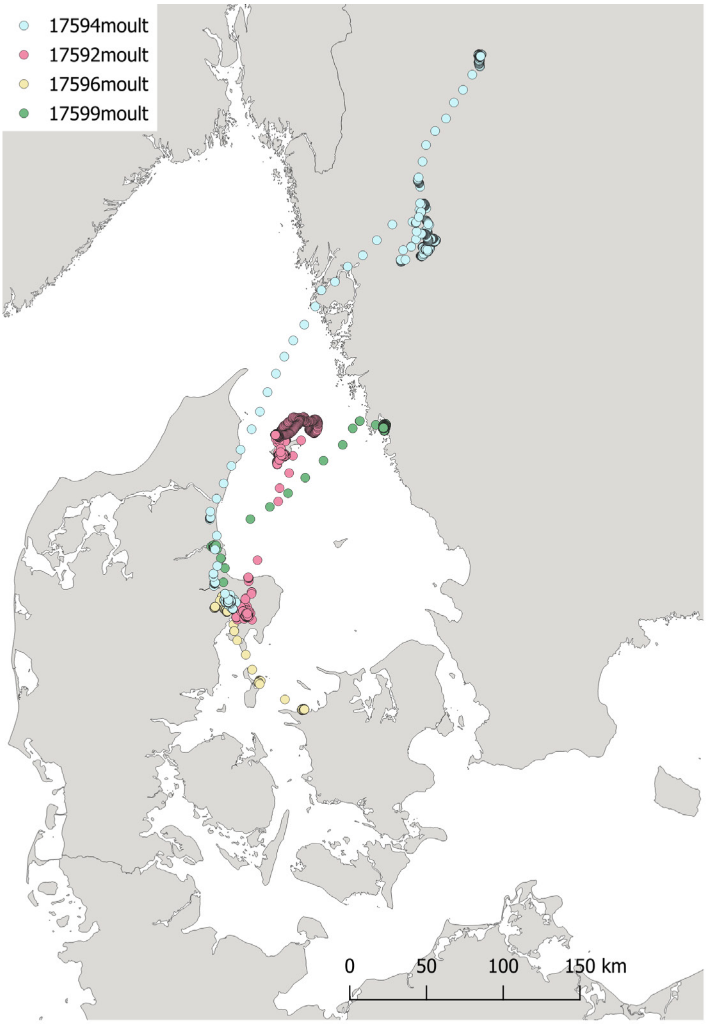

Fig. 4. Post-breeding movements of four Greylag Geese (*Anser anser*) away from the breeding area in Kastrup Mose to moulting sites in Sweden and Denmark during 1 April to 31 May 2022. Prior to these movements, all four geese returned to the site where they were tagged, after wintering in Coto Doñana,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

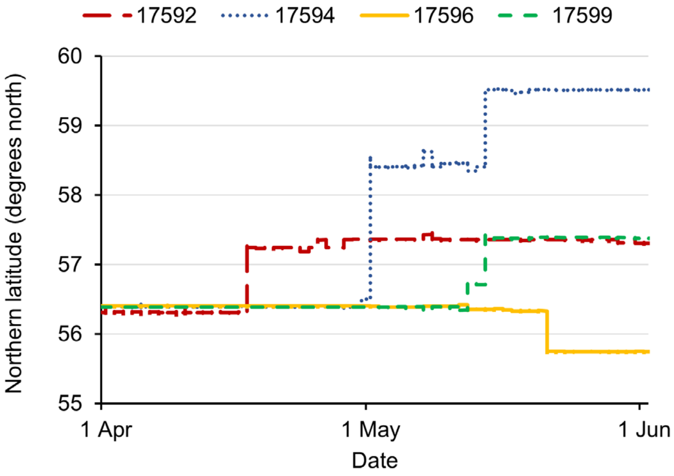

Fig. 5. Seasonal changes in latitude of four GPS-tagged Greylag Geese (*Anser anser*) between 1 April and 31 May 2022, the year after being tagged at Djursland (56°23'N, 10°22'E). Staging sites at 31 May: #17592: Nordre Rønner, Læsø, Denmark (57°21'N, 10°55'E); #17594: Karlstad, Vänern, Sweden (59°31'N,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

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

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

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

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

Although Greylag Geese are considered relatively winter site loyal and conservative in their use of habitat (*e.g.* Swann & Brockway 2007,Swann *et al.* 2015), subordinate geese (by virtue of their low dominance status) are often explorative and the first to find enhanced foraging opportunities, to which they subsequently attract other geese (Stahl *et al.* 2001). These mechanisms could explain the ability of the population as a whole to adapt to novel foraging opportunities outside areas they have traditionally occupied. Annual changes in the migration/wintering patterns of individuals are known among Pink-footed Geese, with an average of 54% changing wintering strategy from one year to the next, although with large individual variation. Individually, these changes were not related to hunting pressure or winter temperature but could be partly explained by a tracking of food resources (Clausen *et al.* 2018).

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

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

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

Classic migration theory hypothesizes that longer-distance migrants should minimize spring migration duration to enhance fitness by earliest occupation in best body condition of the best quality territories (Kokko 1999) and earliest first laying (Moore *et al*. 2005). Earlier nesting is associated with greater clutch size (Rowe *et al*. 1994) and better-quality offspring with higher survival rates during their first migration (Perrins 1970, McNamara *et al*. 1998). Most avian migration studies show that spring migration is faster than autumn migration (Nilsson *et al*. 2013), but this is not always the case among geese. For many Arctic breeding geese, spring migration takes significantly longer than that in autumn, for instance among Far East Greater White-fronted Geese (*Anser albifrons*, Deng *et al.* 2019) and Tundra Bean Geese (*Anser serrirostris*, Meng *et al.* 2022). In contrast, Swan Geese (*Anser cygnoides*), breeding in Mongolian-Manchurian steppe wetlands and wintering in China, undertake spring migration faster than autumn migration (Batbayar *et al.* 2013) as do Far East Asian Greylag Geese (Li *et al.* 2020b), which also breed in the steppe region. Our results from Danish nesting long-distance migrants to Spain suggest that the duration of autumn and spring migration differed little (3 vs. 4 days, 19 vs. 17, 7 vs. 14 and 16 vs. 10 respectively for the four birds) but varied in length due mainly to stopover duration in northern Europe that varied between birds. These results seem to confirm that while internally consistent, the difference in duration of autumn versus spring migration in different goose populations vary in relation to conditions encountered along their migration routes (as witnessed in studies of other goose populations), necessitating a more nuanced development of hypotheses to explain their relative length (*e.g.* Deng *et al*. 2019).

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

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

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

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

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References

Bacon, L., Madsen, J., Jensen, G. H., de Vries, L., Follestad, A., Koffijberg, K., Kruckenberg, H., Loonen, M. J. J. E., Månsson, J., Nilsson, L., Voslamber, B. & Guillemain, M. 2019: Spatio–temporal distribution of greylag goose *Anser anser* resightings on the north-west/south-west European flyway: guidance for the delineation of transboundary management units. — Wildlife Biology 2019(1): 1–10. https://doi.org/10.2981/wlb.00533

Batbayar, N., Takekawa, J. Y., Newman, S. H., Prosser, D. J., Natsagdorj, T. & Xiao, X. 2013: Migration strategies of Swan Geese *Anser cygnoides* from northeast Mongolia. — Wildfowl. 61: 90–109.

Bønløkke, J., Madsen, J. J., Thorup, K., Pedersen, K. T., Bjerrum, M. & Rahbek, C. 2006: Dansk Trækfugleatlas: the Danish bird migration atlas. — Rhodos.

Camacho, C., Negro, J. J., Elmberg, J., Fox, A. D., Nagy, S., Pain, D. J. & Green, A. J. 2022: Groundwater extraction poses extreme threat to Doñana World Heritage Site. — Nature Ecology and Evolution 6: 654–655. https://doi.org/10.1038/s41559-022-01763-6

Clausen, K. K., Madsen, J., Cottaar, F., Kuijken, E. & Verscheure, C. 2018: Highly dynamic wintering strategies in migratory geese: Coping with environmental change. — Global Change Biology 24: 3214–3225. https://doi.org/10.1111/gcb.14061

Clausen, K. K., Schreven, K. H. & Madsen, J. 2020: Effects of capture and marking on the behaviour of moulting Pink-footed Geese *Anser brachyrhynchus* on Svalbard. — Wildfowl 70: 13–29.

Clausen, K. K., Heldbjerg, H. & Fox, A. D. 2023: Status, origin and harvest of increasing numbers of Greylag Geese *Anser anser* occurring in Denmark throughout the annual cycle. — Wildfowl 73: 3–25.

Clausen, K. K., Dalby, L., Heldbjerg, H., Cao, L. & Fox, A. D. (in revision): Using tracking data to assess seasonal habitat use and conflict potential of Greylag Geese in Danish intensive agricultural landscapes. — European Journal of Wildlife Research.

Clements, S. J., Ballard, B. M., Eccles, G. R., Sinnott, E. A. & Weegman, M. D. 2021: Trade-offs in performance of six lightweight automated tracking devices for birds. — Journal of Field Ornithology 92: 506–517. https://doi.org/10.1111/jofo.12392

De Felipe, M., Aragonés, D. & Díaz-Paniagua, C. 2023: Thirty-four years of Landsat monitoring reveal long-term effects of groundwater abstractions on a World Heritage Site wetland. — Science of the Total Environment 880: 163329. https://doi.org/10.1016/j.scitotenv.2023.163329

Deng, X., Zhao, Q., Fang, L., Xu, Z., Wang, X., He, H., Cao, L. & Fox, A. D. 2019: Spring migration duration exceeds that of autumn migration in Far East Asian Greater White-fronted Geese (*Anser albifrons*). — Avian Research 10: 19. https://doi.org/10.1186/s40657-019-0157-6

DMI, Danish Meteorological Institute 2022: Sammendrag af forår 2022. Retrieved from https://www.dmi.dk/fileadmin/user_upload/Afrapportering/Seasonsammendrag/Sammendrag_2022_foraar.pdf (In Danish) (Accessed 23 January 2024)

Dybbro, T. 1976: De danske ynglefugles udbredelse: resultaterne af Atlas-projektet, kortlægningen af Danmarks ynglefugle 1971–74. — Dansk Ornithologisk Forening, Copenhagen. (In Danish)

Elmberg, J., Hessel, R., Fox, A. D. & Dalby, L. 2014: Interpreting seasonal range shifts in migratory birds: a critical assessment of 'short-stopping' and a suggested terminology. — Journal of Ornithology 155: 571–579. https://doi.org/10.1007/s10336-014-1068-2

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. & Abraham, K. F. 2017: Why geese benefit from the transition from natural vegetation to agriculture. — Ambio 46: 188–197. https://doi.org/10.1007/s13280-016-0879-1

Fox, A. D. & Madsen, J. 2017: Threatened species to super-abundance: The unexpected international implications of successful goose conservation. — Ambio 46: 179–187. https://doi.org/10.1007/s13280-016-0878-2

Fox, A. D., Heldbjerg, H., Clausen, K. K., Therkildsen, O. R., Zhao, Q., Negro, J. J. & Green, A. J. 2023: Danish Greylag Goose *Anser anser* use of the Coto Doñana sand dunes for gritting. — Wildfowl 73: 26–42.

Green, A.J., Guardiola-Albert, C., Bravo-Utrera, M. Á., Bustamante, J., Camacho, A., Camacho, C., Contreras-Arribas, E., Espinar, J. L., Gil-Gil, T., Gomez-Mestre, I., Heredia-Díaz, J., Kohfahl, C., Negro, J. J., Olías, M., Revilla, E., Rodríguez-González, P. M., Rodríguez-Rodríguez, M., Ruíz-Bermudo, F., Santamaría, L., Schmidt, G., Serrano-Reina, J. A. & Díaz-Delgado, R. 2024: Groundwater Abstraction has Caused Extensive Ecological Damage to the Doñana World Heritage Site, Spain. — Wetlands 44: 20. https://doi.org/10.1007/s13157-023-01769-1

Jensen, R. A., Madsen, J., O'Connell, M., Wisz, M. S., Tømmervik, H. & Mehlum, F. 2008: Prediction of the distribution of Arctic-nesting pink-footed geese under a warmer climate scenario. — Global Change Biology 14: 1–10. https://doi.org/10.1111/j.1365-2486.2007.01461.x

Johnson, F. A., Heldbjerg, H., Nagy, S. & Madsen, J. 2022: Setting population-size targets for geese causing socio-economic conflicts. — Ambio 51: 209–225. https://doi.org/10.1007/s13280-021-01539-5

Kampp, K. & Preuss, N. O. 2005: The Greylag Geese of Utterslev Mose. A long-term population study of wild geese in an urban setting. — Dansk Ornitologisk Forening Tidsskrift 99: 1–78.

Kokko, H. 1999: Competition for early arrival in migratory birds. — Journal of Animal Ecology 68: 940–950.

https://doi.org/10.1046/j.1365-2656.1999.00343.x

Li, H., Fang, L., Wang, X., Yi, K., Cao, L. & Fox, A. D. 2020a: Does snowmelt constrain spring migration progression in sympatric wintering Arctic-nesting geese? Results from a Far East Asia telemetry study. — Ibis 162: 548–555. https://doi.org/10.1111/ibi.12767

Li, X., Wang, X., Fang, L., Batbayar, N., Natsagdorj, T., Davaasuren, B., Damba, I., Xu, Z., Cao, L. & Fox, A. D. 2020b: Annual migratory patterns of Mongolian-Manchurian Eastern Greylag Geese (*Anser anser rubrirostris*) revealed by GPS/GSM loggers. — Integrative Zoology 15: 213–223. https://doi.org/10.1111/1749-4877.12414

Månsson, J., Liljebäck, N., Nilsson, L., Olsson, C., Kruckenberg, H. & Elmberg, J. 2022: Migration patterns of Swedish Greylag geese *Anser anser*—implications for flyway management in a changing world. — European Journal of Wildlife Research 68: 15. https://doi.org/10.1007/s10344-022-01561-2

McNamara, J. M., Welham, R. K. & Houston, A. I. 1998: The timing of migration within the context of an annual routine. — Journal of Avian Biology 29: 416–423. https://doi.org/10.2307/3677160

Meng, F., Zhang J., Li, C., Zhao, Q., Solovyeva, D., Lee, H., Chen, L. & Fox, A. D. 2022: Differing migration patterns and year-round habitat-use of allopatric nesting Eastern Tundra Bean Geese (*Anser fabalis serrirostris*) in East Asia. — Avian Research 13: 100062. https://doi.org/ 10.1016/j.avrs.2022.100062

Moore, F. R., Smith, R. J. & Sandberg, R. 2005: Stopover ecology of intercontinental migrants: en route problems and consequences for reproductive performance. — In Birds of Two Worlds: The Ecology and Evolution of Migration (ed. Greenberg, R. & Marra, P. P.): 251–261. John Hopkins University Press Baltimore, Maryland.

Nagy S., Heldbjerg H., Jensen G. H., Johnson, Madsen J., Therkildsen O., Meyers E. & Dereliev S., (ed.). 2021: Adaptive Flyway Management Programme for the NW/SW European Population of the Greylag Goose (*Anser anser*). — AEWA EGMP Programme No. 1. Bonn, Germany.

Nielsen, R. D., Holm, T. E., Clausen, P., Bregnballe, T., Clausen, K. K., Petersen, I. K., Sterup, J., Balsby, T. J. S., Pedersen, C. L., Dalby, L., Mikkelsen, P., Mellerup, K. A. & Bladt, J. 2023: Fugle 2020–2021. NOVANA. Aarhus Universitet, DCE – Nationalt Center for Miljø og Energi. — Videnskabelig rapport fra DCE - Nationalt Center for Miljø og Energi nr. 531. (In Danish)

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. https://doi.org/10.1080/00063650109461211

Nilsson, C., Klaassen, R. H. G. & Alerstam, T. 2013: Differences in speed and duration of bird migration between spring and autumn. — American Naturalist 181: 837–845. https://doi.org/10.1086/670335

Nilsson, L. & Kampe-Persson, H. 2018: Changes in migration and wintering patterns of greylag geese *Anser anser* from southernmost Sweden during three decades. — Ornis Svecica 28: 19–38. https://doi.org/10.34080/os.v28.19521

Paludan, K. 1965: Grågåsens træk og fældningstræk. — Danske Vildtundersøgelser 12: 1–56. (In Danish)

Perrins, C. M. 1970: The timing of birds' breeding seasons. Ibis 112: 242–255. https://doi.org/10.1111/j.1474-919X.1970.tb00096.x

Powolny, T., Jensen, G. H., Nagy, S., Czajkowski, A., Fox, A. D., Lewis, M. & Madsen, J. (ed.) 2018: AEWA International Single Species Management Plan for the Greylag Goose (*Anser anser*) - Northwest/Southwest European population. — AEWA Technical Series No. 71. Bonn, Germany.

Ramo, C., Amat, J. A., Nilsson, L., Schricke, V., Rodríguez-Alonso, M., Gómez-Crespo, E., Jubete, F., Navedo, J. G., 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: e0140181. https://doi.org/10.1371/journal.pone.0140181

Rowe, L., Ludwig, D. & Schluter, D. 1994: Time, condition, and the seasonal decline of avian clutch size. — The American Naturalist 143: 698–722. https://doi.org/10.1086/285627

Schreven, K. H. T., Madsen, J. & Nolet, B. A. 2024: Effects of capture and GPS-tagging in spring on migration timing and reproduction in Pink-footed geese *Anser brachyrhynchus*. — Animal Biotelemetry 12: 10. https://doi.org/10.1186/s40317-024-00365-2

Stahl, J., Tolsma, P. H., Loonen, M. J. & Drent, R. H. 2001: Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks. — Animal Behaviour 61: 257–264. https://doi.org/10.1006/anbe.2000.1564

Swann, B. R. L., Brockway, I. K., Frederiksen, M., Hearn, R. D., Mitchell, C. & Sigfússon, A. 2005: Within-winter movements and site fidelity of Icelandic Greylag Geese *Anser anser*. — Bird Study 52: 25–36. https://doi.org/10.1080/00063650509461371

Swann, B. R. L. & Brockway, I. K. 2007: Site fidelity of Icelandic Greylag Geese between winters. — Ringing & Migration 23: 238–242. https://doi.org/10.1080/03078698.2007.9674371

Vikstrøm, T. & Moshøj, C. M. 2020: Fugleatlas - De danske ynglefugles udbredelse 2014–2017. — Dansk Ornitologisk Forening & Lindhardt og Ringhof. (In Danish)

Vikstrøm, T. Eskildsen, D. P. & Jørgensen, M. F. 2023: Overvågning af de almindelige fuglearter i Danmark 1975–2023. Årsrapport for Punkttællingsprogrammet. — Dansk Ornitologisk Forening. (In Danish)

Wisz, M., Dendoncker, N., Madsen, J., Rounsevell, M., Jespersen, M., Kuijken, E., Courtens, W., Verscheure, C. & Cottaar, F. 2008: Modelling pink-footed goose (*Anser* *brachyrhynchus*) wintering distributions for the year 2050: potential effects of land-use change in Europe. — Diversity and Distributions 14: 721–731. https://doi.org/10.1111/j.1472-4642.2008.00476.x

Online supplementary material

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