Spatial ecology of wintering Greater White-fronted geese (*Anser albifrons*)

Contents

List of Figures

Study species

Greater White-fronted geese (*Anser albifrons*), or whitefronts, are grey geese similar in size but somewhat smaller than the Greylag goose (*A. anser*). They are named for the distinctive patch of white feathers at the base of the bill and beginning of the forehead. Adults are also identified by the black tiger-stripe markings on the chest. First winter birds lack the white front, the black chest stripes, and the neck grooves common to the to adults of many *Anser* species. The species is variable in its foraging habits, with the Greenlandic subspecies (*A. albifrons flavirostris*) historically preferring tubers, and the western Russian (*A. a. albifrons*) found largely on natural or cultivated grass fields (*1*).

Some of the most comprehensive information on the spatial ecology of this species is compiled in *Goose Populations of the Western Palearctic* (*2*). Whitefronts have a circumpolar distribution, and breed in the tundra between the 10°C and 4°C July isotherns. The Palearctic populations winter across Europe and Asia, with one of the largest combined ranges among the geese. The Eurasian breeding range is now exclusively within Russia (*3*), and stretches from the Kanin Peninsula (45°E) to the Kolyma river (155°E) in the Russian far-east. The Western Palearctic population which winters in Europe breeds between the Kanin Peninsula the Khatanga river (104°E). This population is further divided into five main wintering groups based on the flyways they use (*4*). Geese reaching western Europe and Britain from Russia take the Baltic - North Sea

flyway. The species has been ringed and neckbanded for some decades of, and while the species shows high site fidelity during winter (*5*), populations from the different flyways have been found to mix (*6*). Overall, the western European wintering population has increased dramatically since the 1970s, while there have been corresponding decreases in populations wintering in Croatia (*Pannonic*) and Turkey (*Pontic*) (*6*).

Adults form life-long pair bonds, and migrate, feed and roost together. Family bonds between parents and juveniles, and between siblings, are strong and long-lasting. Families regroup successfully after capture and subsequent individual release in both wintering (*7*) and breeding areas (*pers.obs*) Juveniles follow parents on their first autumn migration, and are almost always seen with them or with siblings during their first winter. In a study of the Greenland subspecies (*A. albifrons flavirostris*), it was found that around 40% of juveniles are still with their parents in the second winter, 30% in the third, and 20% in the fourth (*1*). In a number of goose species - Snow geese (*A. caerulescens*), Dark-bellied Brent geese (*Branta b. bernicla*), and Barnacle geese (*B. leucopsis*) - larger families are also more dominant in contests with con- and heterospecifics within wintering flocks than smaller ones or pairs (*8*). This may be assumed to hold for whitefronts as well, promoting the maintenance of family bonds. Additionally, when in dispersed family groups, families may accrue the benefits of flocking while sharing the costs only with related individuals (*1*). Nest attendance and anti-predator defence on the breeding grounds the following spring are a likely benefit of maintaining these bonds through the spring migration, and have been sporadically reported in the Greenland (*12*) and Pacific subspecies (*13*), while being better studied and confirmed in the Canadian Arctic breeding population (*14*).

Study site

The main wintering grounds of the North Sea whitefronts have undergone a shift since the 1970s, when they were concentrated in northwestern Germany along the River Elbe (~ 9.2°E) and in the Dollart at the mouth of the River Ems in East Frisia, to the Lower Rhine area between the German Ruhr Valley and the River IJssel in the Netherlands (*15*). We used a combination of this historical and contemporary winter distribution, and the locations of observations of whitefronts reported from north-western continental Europe to define a spatial extent for our study area. This is bounded by the 0°E and 10°E longitudes and the 50°N and 54°N latitudes.

The climate is continental, and snow is common away from the coasts during winter. The topography is largely flat and part of the North European Plain. The major rivers are the Rhine, Meuse, IJssel, Ems and Elbe (*16*). The landscape is human dominated,

with urban centres surrounded by agricultural land. Freshly planted winter crops and harvest remains serve as dense, high energy food sources for up to 2.5 million individuals of five main species of migratory geese (*17*). The presence of wind turbines may once have made parts of the landscape unavailable for migrating geese, but this avoidance has largely disappeared as geese in general appear to have become habituated to them (*19*).

The population of whitefronts has stabilised at around 1.4 million from historic lows in the 1960s, following several years of conservation-enabled and crop-feeding boosted exponential growth (*20*). Whitefronts also make up a larger proportion of wintering *Anser* geese than they used to in most parts of the study area, and this trend has largely been at the cost of the once dominant and now decreasing Bean geese (*A. fabalis*) (*20*). While forming largely homogeneous flocks sometimes thousands strong, whitefronts are also to be seen in mixed flocks in which another species – Barnacle geese near coasts, Pink-footed geese (*A. brachyrhynchus*) in Frisia, and Greylag geese (*A. anser*) in the Rhinelands – form a significant proportion.


Goose observations

Sightings of marked geese

Geese have long been observed on their wintering grounds within the study area, and these observations have focused on different levels of goose organisation. At the level of the individual, this takes the form of records of individually marked geese. Whitefronts have been fitted with coloured plastic neckbands bearing alphanumeric codes during the course of a number of expeditions to various summer moulting/breeding sites (*24*). This mark-resight method has been used in other species of geese as well, for example, to estimate populations of Svalbard breeding Pink-footed geese (*25*), and the technique is well developed.

The neckbands provide a point of focus for birdwatchers observing goose flocks, and are easily reported and displayed on the purpose-built website `geese.org`. Observers report the neckband code of the bird, the number of associated first-winter juveniles if any, the identity of the partner if present, the nearest settlement, habitat type, and the numbers of individuals of each anserine species in the flock. The geographic coordinates of the observation are geocoded and displayed on a map from the name of the reported nearest settlement, and prior to final entry, they can be changed via a drag-and-drop map marker if found to be incorrectly located. Observers are volunteers,
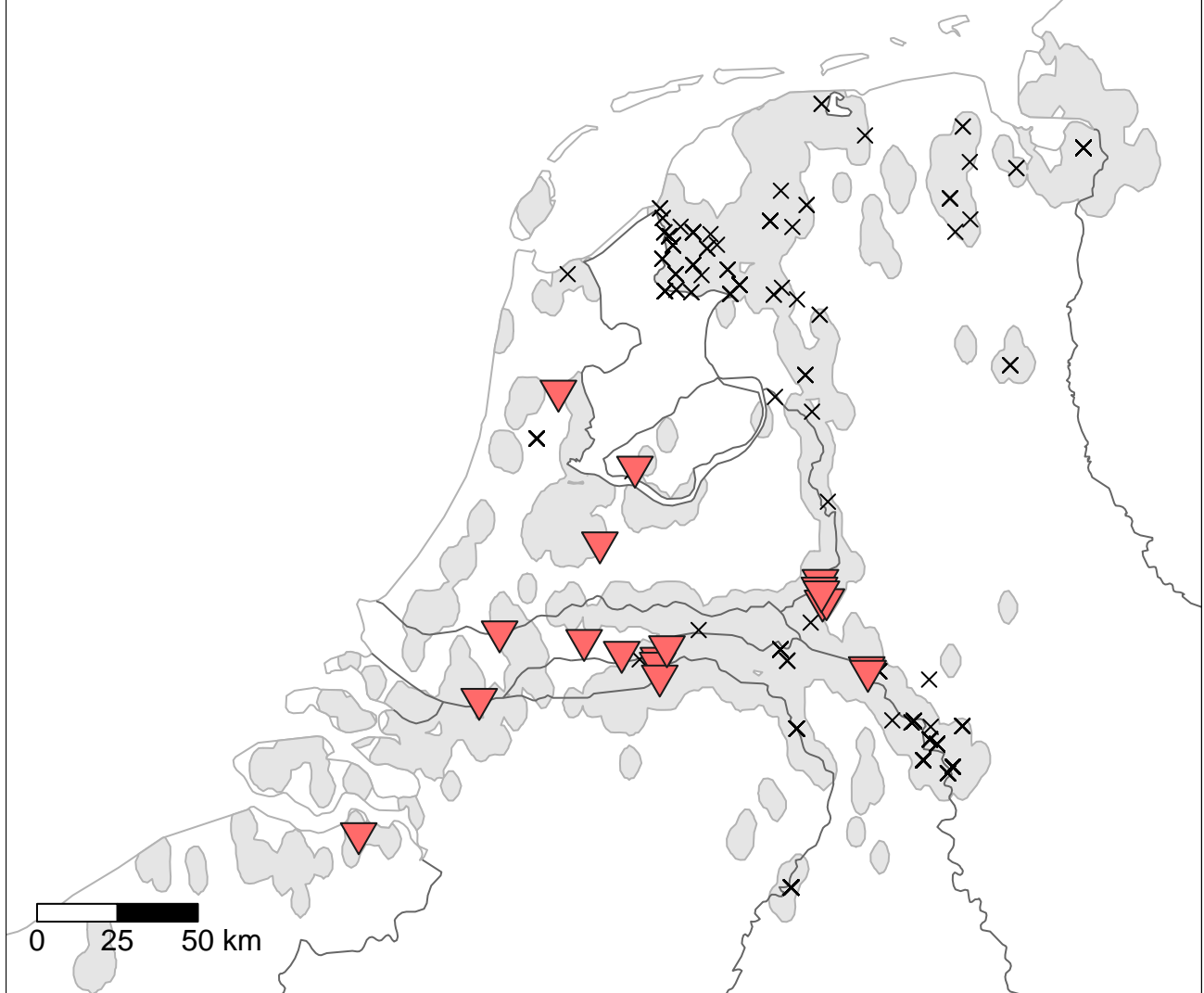
Figure 1: Three datasets used in the study are represented on a map of the main wintering grounds of the North Sea population of Whitefronts. Lines represent coasts (light) and major rivers (dark). Crosses mark sites ($n = 64$) where family frequencies within flocks ($n_{flocks} = 1,884$, $n_{families} = 50,941$) were recorded between autumn 2000 and spring 2017. Triangles mark positions ($n = 19$) from 13 GPS tracked families of geese (3 in 2013, 4 in 2014, 6 in 2016) where individuals left the family (see details in text). Sites where geese with numbered neckbands were observed, and their family sizes counted, between 2000 and 2017, are bounded by a kernel shaded grey ($n_{obs} = 10,635$, $n_{sites} = 8,416$).

and most observations are made *ad hoc*, often as part of flock counts (*see below*). Geese in their wintering grounds appear to be accustomed to human presence, and regularly allow observers to approach within a hundred metres, a marked difference from their breeding grounds (*pers. obs.*). Geese with numbered neckbands have been observed since the first records in 1998, with greater numbers of neckbands being deployed since 2000.

Flock counts

Counts of goose flocks in order to monitor populations have taken place regularly in the countries and sub-national administrative regions of the study area since the 1960s (*17*), but the effort has been consistent only since the 2000s. Observers count goose flocks at a number of sites, which may be either fixed census sites used as part of the annual waterbird census, or *ad hoc* sites where geese are observed. When flocks are too large to be counted completely in the field, observers are encouraged to divide the flock into simple fractions and to sample one or more of these subsets of the flock. Care is taken to sample the flock representatively. In the case of elliptical flocks, this involves sampling a 'slice' of the flock, which should ideally include the various regions (edge, periphery, centre), which are expected to have different compositions (*26*). Flock size and age-ratio are then extrapolated from the number of geese sampled.

The information noted in the flock counts is similar to that reported on *geese.org* for marked individuals, but with the addition of the flock's percentage of first winter juveniles. This age-ratio is valuable as an indicator of breeding success, and 0.3 has been considered to be the long-term mean proportion of first winter birds in flocks (*27*). Alongside the flock's age ratio, a number of observers ($n = 19$) also recorded the frequencies of families of different sizes, with families considered to be one or more first winter birds associated with one or more adults. This system of classification excludes unsuccessful pairs, ie, those with no juveniles, from the ambit of family-size frequency counts.

Flight activity

The start of goose arrivals *en masse* in autumn, and the end of goose departures during spring bookend the stay of geese in the wintering grounds. The timing of each is representative of geese's perception of winter. Goose flight activity is recorded by ground based observers at Trektellen (*trektellen.org*) sites across the Netherlands. Whitefronts are more readily identified in flight than other grey geese due to the black chest stripes, as well as their distinctive call. Observers at these sites (n spring $= 84$, n autumn $= 180$,

n both = 72) count the number of whitefronts seen flying in the different cardinal directions. These data are helpful in quantifying when geese arrive and leave on the autumn and spring migrations. One drawback to these data is that they do not always differentiate between long distance migratory flights and daily flights between night roosts and foraging areas.

Satellite telemetry

The only families for which trends in size and position could be studied with certainty were those which had been fitted with GPS position logger/transmitters during the winters of 2013 (*n* = 3), 2014 (*n* = 4), and 2016 (*n* = 6). Position loggers in 2013 and 2014 were backpacks (e-obs GmbH. Grünwald, Germany), and in 2016 were numbered neckband loggers supplied by Theo Gerrits (madebytheo, Netherlands). These loggers were set to record a baseline sampling interval 30 minutes, but the actual fix frequency depended on the mode in which the remotely programmable device was then operating. Data from these loggers were uploaded remotely to the animal tracking database Movebank. Movebank data were retrieved using either the functions in the *move* package in *R* (*28*) or manually.

Data filtering

Observations of marked geese

We obtained the data described above from the volunteers involved (*n* = 75) across western and central Europe (*n* = 8764). From the observations of marked geese, we removed the following types of records: those in which a goose was seen with neither juveniles nor a social partner, one of the two records in which two birds of a pair had been reported separately when seen together, and those in which the bird was less than two years old at the time of observation, since whitefronts are not expected to breed before their second winter. We also excluded records which lay outside the spatial extent of the study area. We chose to match the temporal extents of the data we acquired so as to make comparisons possible, and filtered these data to exclude records made before 2000. 10,635 records remained, reported from 8,416 unique coordinate pairs.

Flock counts

Prior to filtering the flock count data, we substituted the 6% of flock sizes which were missing with the related (and in 31% of cases, identical) number of geese sampled, or, if that value was also missing ($n = 28$), as the sum of the number of adults and juveniles. In cases where the percentage of first winter birds was missing ($n = 50$), it was calculated from the number of juveniles and the flock size. We then filtered the data temporally, removing the records made before autumn 2000 (~ 7%). In order to facilitate downstream analyses, we checked whether each record had a complete date (year, month, day), and in cases where the day was missing ($n = 32$), we assigned it to the 15th. We use 'year' to refer to the goose breeding year, which begins in June.

Nearly all (> 99%) flock counts had associated site names, with flocks recorded at 1567 sites. These were geocoded using the Google Maps Geocoding API accessed by the function geocode from the package ggmap (*29*) using one of 123 unique look-up names associated with the site names. Exclusion of sites without geocoded coordinates, and from outside the study area left 7149 records of flocks, in 1884 of which family sizes and frequencies were also known. We expanded the flock level family frequency data to family level data (*n* families = 51,037), with all families from the same flock inheriting its attributes. Each record was assigned one of the zones, "East Frisia", "IJsselmeer", "Rhinelands", and "Southwest", based on the province in the Netherlands, or the district in Germany, in which it was made. Zones cover areas in or around the names given. The Rhinelands zone had almost as many records as the other zones combined. We thinned the data such that the 'Rhinelands' zone contributed only a randomly selected half of its records. We used this thinned data ($n = 38,567$) for further analyses.

Flight activity

We filtered *Trektellen* flight activity data to exclude sites that lay close to goose night roosts so as to avoid noise in the data from daily, rather than migratory, movements. Data were further filtered to exclude flights that did not match the direction appropriate to migration in that season: south and west in spring, north and east in autumn. We then calculated the first date in each autumn (ending December) and the last date in each spring (ending July) on which the number of geese flying per hour of observation time was at or above the 90th percentile of within-breeding year season-specific activity. This excluded unusually early arrivals and stragglers. We took these dates to represent the beginning of goose arrival from the autumn migration, and the end of goose departure on the spring migration, respectively, for each breeding year. By our method, whitefronts usually began to arrive between September 26 and October 30,

and the last geese likely left between March 03 and April 01. We added these dates to the individual, flock, and family level data, matching them by breeding year, and then calculated the number of days between each observation and the two extremes of goose migration.

Satellite telemetry

Logger data were Logger data were filtered to fit within the spatial extents of the study area. Data collected after March 31, the upper limit of the end of goose departures on spring migration, were excluded. A major component of the remaining data were 'flight bursts', high fix frequency (0.5 or 1 Hz) records triggered by takeoff as measured by on-board accelerometers. These bursts were removed, and only data with the baseline sampling interval retained. Fixes where the logger position error was estimated to be above the 90th percentile of errors were also removed. To better account for irregularities in sampling interval introduced by the logger not functioning as ideal, the remaining data were averaged over every half hour so as to obtain a regular timeseries of data.

The adult in each family with the greater number of logged positions was set to be the 'reference'. In doing so, we hoped to obtain a longer sequence of reference-to-individual distances, which might also result in capturing more family dynamics. We then matched the records of all individuals to the reference by the timestamp. The distance between the reference and all other individuals in the family was calculated using the Vincenty ellipsoid method for geographic coordinates (*30*) implemented by the geosphere package in (*31*). These distances were used to determine the number of family members within a 250m radius of the reference, and the family size per day was obtained as the maximum number of members within that radius during a day. Due to an accretion of errors at the level of the logger and in rounding and averaging the data, the sizes of some families as calculated above fluctuated drastically over time. We then considered the family size on each day to be maximum of the family sizes on all days between that one and the final day. We did not differentiate cases in which the adult pair of the family split from other types of family size decrease, which in our data included juvenile independence, juvenile death, and logger malfunction.

Table 1: Overview of filtered goose observation data.

Data type	Records	Unique sites	Spatial extent	Temporal extent
Flock count	7,149	123	4.1 – 8.9, 51.2 – 53.4	2000 – 2016
Family frequency	1,884	64	4.8 – 7.3, 51.2 – 53.4	"
Family size	51,037	64	4.8 – 7.3, 51.2 – 53.4	"
GPS telemetry	1013/13	1013	3.9 – 7.4, 51.3 – 53.2	2013, 2014, 2016

Data type	Records	Unique sites	Spatial extent	Temporal extent
Flight activity	6,266	118	3.4 – 7.2, 50.8 – 53.5	2000 – 2016

Summer predation

The number of geese observed on the wintering grounds is a function of the breeding success of the species in the Arctic. This in turn is thought to be linked to the abundance of Arctic rodents, primarily lemmings (*Lemmus spp.* and *Dicrostonyx spp.*). This shows a cyclical pattern with a 3 – 4 year period, with a 'lemming peak' year followed immediately by a 'crash' year, with abundance rising until the next peak. The factors underlying that are thought to be largely intrinsic, but may also be related to the form of precipitation and its effect on the availability of vegetation to lemmings (*32*).

Goose breeding success was originally hypothesis to be high in 'lemming peak' years, since Arctic predators switch from their preferred lemming prey to goose eggs and young when lemmings are scarce (*33*). This alternate prey hypothesis (AHP) was amended to reflect that predator populations are linked to, but also lag behind, lemming abundance. Goose breeding success is thus predicted to be lowest in the years immediately following lemming peaks, when a dearth of lemmings and a surfeit of predators combine to produce predation pressure on goose young that's higher than the mean (*34*). This logic has been found to explain winter estimates of breeding success of both geese and waders wintering in Scandinavia (*35*), and of Dark-bellied Brent geese (*Branta b. bernicla*) wintering along the North Sea coast (*36*).

With this background, we sought to obtain an index for the summer predation pressure on our population. The breeding grounds of our population lie above the Arctic Circle (66.5°N), and between the Kanin Peninsula (45°E) and the River Yenisei (85°E) in the Nenets and Yamal regions of Russia (*2*). Within this region, around 30% of the North Sea whitefront population spends the summer on the Barents Sea island of Kolguyev (69°N, 49°E), which is thought to represent the core breeding area of the Palearctic population of the species (*24*). We could not asses rodent abundance for this area from the literature, which focuses largely on lemming abundance from the Taimyr Peninsula (98°E) (*37*). While it is suggested that lemming cycles in some regions of Scandinavia (*38*), and in the high Arctic of Svalbard (*32*) may be synchronised, we did not expect lemming cycles in the Nenets and Yamal regions to be synchronised with those of Taimyr. Further, while most breeding whitefronts remain on Kolguyev, birds seen on Taimyr are mostly failed breeders that arrive there from the Nenets area

(*24*). We decided not not use lemming data from Taimyr to calculate the predation index.

Hypotheses and predictor variables

Hypotheses

We sought to test the following three hypotheses related to family size: *1.* More successful families winter in the west, *2.* Larger families are seen in smaller flocks, and, *3.* Family sizes decrease over the winter. To disentangle the relationship between flock size, family size and space, we also tested whether *4.* Flock sizes are smaller in the west. Finally, we also tested whether *5.* The proportion of juveniles in flocks increases over the winter.

Predictor variables

We chose main predictors to match our hypotheses. The longitudinal position of each observation, the flock size, and the time in winter were selected as hypothesis testing predictors, and were always included in further analyses. We added the summer predation index as an auxiliary predictor. Longitude was available for all records in both the observations of marked geese and the flock counts. While the individual observations were expected to hold information on the number of flock members and the habitat type, we could not obtain these and the analyses could not include flock size as a predictor when modelling the individual observation data.

We then chose between time since arrival, and time to departure to represent the time in winter as experienced by geese. To do so, we specified two generalised linear mixed models (GLMMs) from the `lme4` package (*39*), with one model using the number of days since the first goose arrivals on the autumn migration, and the other using the number of days to the end of goose departures on the spring migration as predictors of family size. We ran these models on the family level data, and included breeding year, observer identity, and habitat type as *iid.* random effects. We ranked the two models by their AICc scores (here equivalent to AIC) using the `MuMIn` package (*40*), and days since arrival ($AICc = 25,396$) was selected over days to departure ($AICc = 25,729.7$) as a proxy for the time in winter.

To quantify summer predation, we first obtained rodent (lemming) abundance indices for the breeding grounds from the website *Arctic Birds* (`www.arcticbirds.net`), an

initiative of the International Breeding Conditions Survey on Arctic Birds. This approach has been previously used to fill in gaps in trapping datasets (*36*). Sites on *Arctic Birds* are marked on a map and binned into four classes: "Unclear", "Low or absent", "Average", and "High". The same sites are not present in each year. We graded these sites on a 0 – 3 scale, with 0 for "Unclear, and 3 for"High". The distinction between sites graded 0 and 1 was itself unclear. Both 0 and 1 were used in different years to mark the island of Kolguyev, which is well known to have no lemming cycle. We took 0 to indicate a near or full absence of lemmings rather than an unsurveyed site, and also included an entry of 0 for Kolguyev in each year. Breeding birds form the major prey base for the island's predators, the majority of geese on the island are breeders (*41*), lending inclusion of the index for Kolguyev quite some value. We averaged the lemming index across the sites in each year, and then for each year *t*, we calculated a predation index (P_t).

$$P_t = \frac{L_{t-1} - L_t + 3}{2} \tag{1}$$

We matched this predation index to observations by the breeding year.

Hypothesis testing

Modelling family sizes

We used the family data and the individual data to model family sizes and so test the first three hypotheses. We constructed generalised linear mixed models (GLMMs) using the `lme4` package (*39*). Mixed models allow for the inclusion of factors that may introduce grouping in the response, but which are not predictors. The main predictors were included as fixed effects. We further specified the breeding year, the habitat type, and the observer as *iid.* random effects in the model run on family data.

We could not retrieve the habitat type and observer identity for the individual observations, and these could not be included as random effects when modelling the individual data. However, we did have information on the individual identity, and this was included as both an independent random effect as well as nested within the breeding year. We expected this structure to account for multiple observations of the same individual across and within breeding years. Table 2 shows the models and their effects. We used data for which there were complete cases for each and every one of the fixed and random effects. Since family sizes are discrete counts that can only

take whole number values and are bounded at the lower limit by zero, we specified a Poisson error distribution for both models.

Modelling flock sizes, juvenile proportions and number of families

We used the flock count data to model flock sizes and juvenile proportions. For flock size, we constructed a GLMM as described above. We chose to model juvenile proportion using a generalised additive model (GAM). GAMs are essentially generalised linear models which allow the inclusion of smoothed terms, where the response has a linear relationship with a smooth function of the predictor variable (*42*). As implemented through the `mgcv` package, they also allow for the modelling of random effects as penalised smoothed terms, specified using the smoothing basis "re" (*43*).

We included each of the main predictors in both models, except flock size when it was the response. When modelling juvenile proportions, we made two changes to the model structure. First, we used a binomial error distribution as is appropriate for proportion data. Second, we specified the number of days since goose arrivals as a smoothed term using a thin plate spline penalty basis (*44*), while treating the remaining predictor as parametric fixed effects. We specified a maximum of three knots for the thin plate spline, allowing the GAM to choose up to that number using generalised cross validation (*45*).

We also modelled the sum of successful families in flocks using a GAM, with longitude, summer predation and time in winter as parametric fixed effects, and flock size as a smoothed term. Breeding year, habitat type, and observer identity were included as random effects using a "re" smoothing basis. We only used records in which the full flock had been sampled to build this model.

Table 2: Model structures; effect codes: *1* Longitude, *2* Flock size, *3* Days since arrivals, *4* Summer predation index, *5* Breeding year, *6* Habitat type, *7* Observer identity, *8* Goose identity.

| Response	Data source	Fixed effects	Random effects	Model
Family size	Family counts	1, 2, 3, 4	5, 6, 7	GLMM
Family size	Individual observations	1, 3, 4	5, 8	GLMM
Number of families	Family counts	1, 2, 3, 4	5, 6, 7	GAM
Flock size	Flock counts	1, 3, 4	5, 6, 7	GLMM
Juvenile proportion	Flock counts	1, 2, 3, 4	5, 6, 7	GAM

Results

The size of successful families recorded in flocks was found to be unexpectedly insensitive to most predictors. The number of juveniles accompanying pairs increased slightly with longitudinal position, ie, from west to east, but not significantly ($p = 0.874$), but did, however, decrease significantly as expected through the winter ($p < 2\text{x}10^{-16}$). Individual observations showed a different trend; while not significant, there was a slight decrease in size from west to east ($p = 0.244$), and the number of juveniles seen with individuals also decreased over the winter ($p = 1.17\text{x}10^{-5}$).

As hypothesised, flocks were smaller in the west, and also tended to be larger the more days since the first autumn arrivals had passed ($p < 2\text{x}10^{-16}$). Consistent with the earliest ideas on how geese form flocks (*46*), the number of families in flocks increased very rapidly with their size ($p < 2\text{x}10^{-16}$), but the size of successful families in flocks decreased slightly as flocks grew, but not significantly, ($p = 0.257$). Further, the proportion of first winter juveniles in flocks was not affected significantly by their longitudinal position ($p = 0.442$). However, it increased significantly through the winter as expected ($p = 0.00174$). Larger flocks also had a lower proportion of juveniles than expected ($p = 0.015$).

The effects of summer predation were not consistent across the levels of the population. The size of successful families in flocks increased, though not significantly, with the level of summer predation ($p = 0.377$), while the number of juveniles seen with marked geese was significantly decreased with high summer predation ($p = 6.45\text{x}10^{-6}$). The apparent difference in trends might be explained by the fact that only successful families were counted in flocks. The effect of summer predation on family size could be masked by such a sampling method, especially if higher levels of predation caused goose pairs to fail to fledge any young at all. On testing this idea by excluding observations of unsuccessful pairs from our analysis, we found a similar trend as that of the family data from flocks, though it was still not a significant one ($p = 0.896$). At a higher level, the number of successful families in flocks showed a marked decrease with the level of summer predation ($p = 7.13\text{x}10^{-16}$). This did not translate into a lower juvenile proportion ($p = 0.931$), or decreased flock sizes($p = 0.308$).
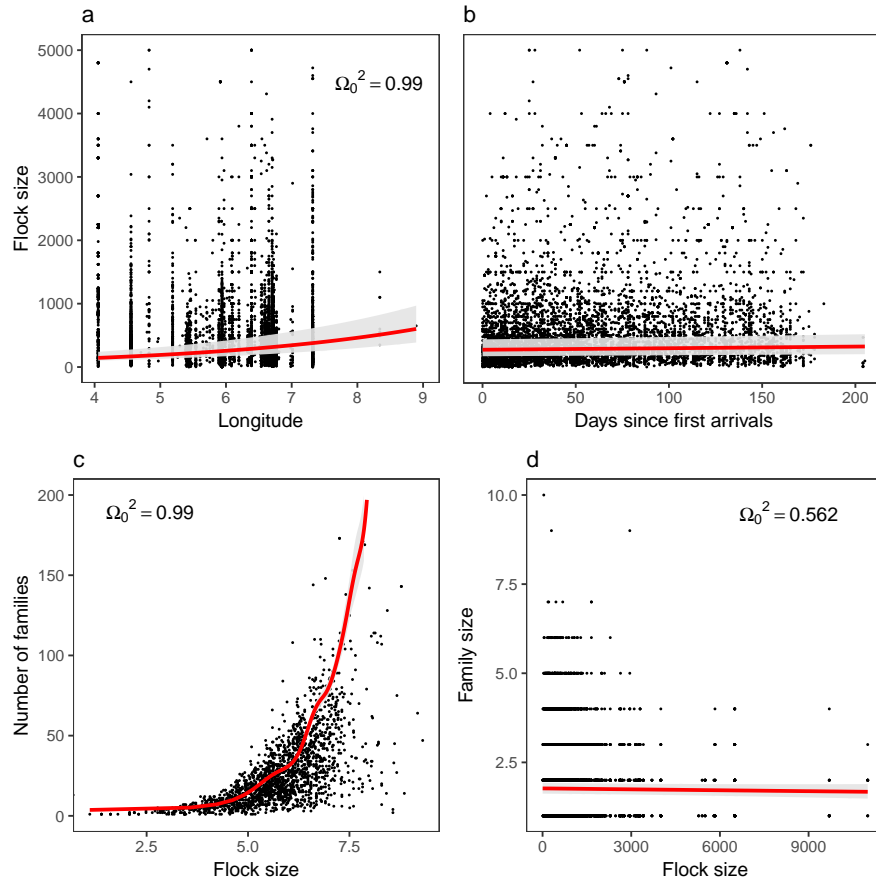

Model outputs

Trends in family size
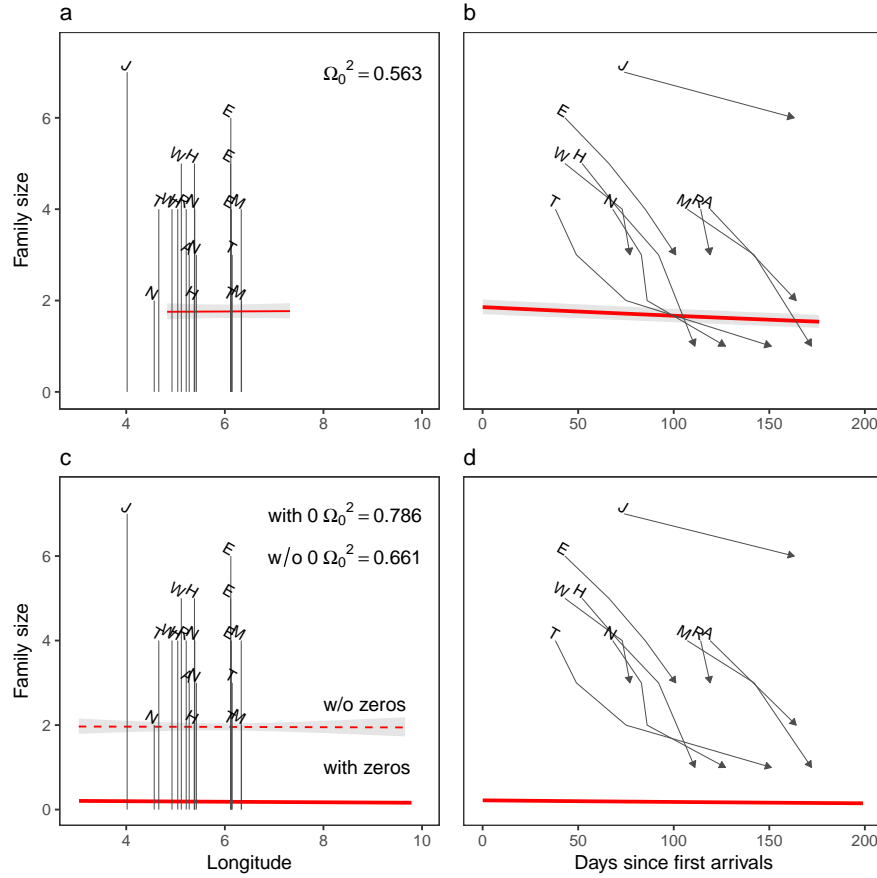
Figure 2: Top row: Model fit and data with longitudinal position, days since first autumn arrivals, predation index, and flock size as fixed effects. Habitat type, observer, and breeding year are *iid.* random effects. Data used were complete cases of counts ($n = 34,174$) of successful families in flocks. Lines show partial fits for **(a)** longitude, and **(b)** days since goose arrivals in autumn. Model $\Omega_0^2 = 0.563$. Bottom row: Model fit and data with longitudinal position, days since first autumn arrivals, and predation index as fixed effects. Individual identity and individual identity nested within breeding year are random effects. Data used were all families with marked geese ($n = 10,426$), and a subset of only successful families ($n = 3,102$). Lines show partial fits for **(c)** longitude, with all families (*solid line*), and only successful families (*dashed line*), and **(d)** days since arrivals. Model $\Omega_0^2 = 0.786$, all families; $\Omega_0^2 = 0.661$, successful families. 95% confidence intervals are shaded grey. Lines (a,c) and arrows (b,d) mark longitudes and times of decreases in GPS tracked families. Family initials included.
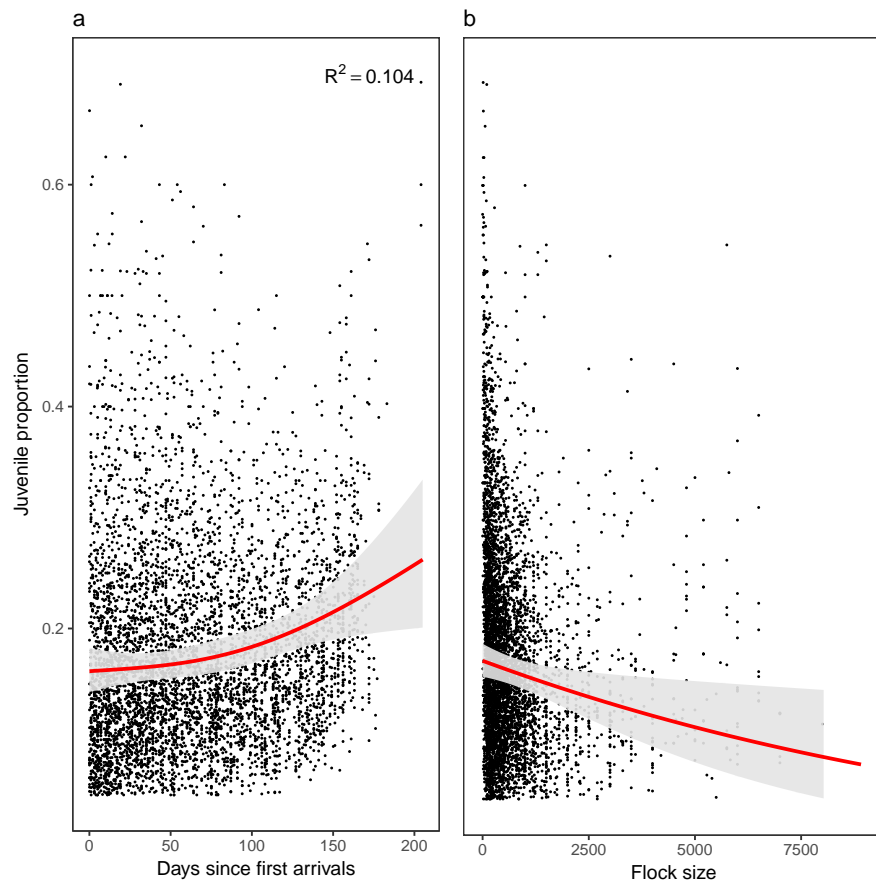
Trends in flocks

Figure 3: Top row: Model fit and data for flock size with longitudinal position, days since first autumn arrivals, and summer predation as fixed effects. Data used were complete cases of flock counts ($n = 5,700$). Lines show partial fits for **(a)** longitude, and **(b)** for days since goose arrivals in autumn . Model $\Omega_0^2 = 0.99$. Bottom row: Model fit line and data for (c) number of families in flocks, with summer predation and longitude as fixed parametric effects and flock size as a smooth term, and breeding year, observer and habitat type as random effects. Data used were family frequency data from flock counts ($n = 837$). Model $\Omega_0^2 = 0.99$. Model fit and data for (d) family size with longitude, flock size, days since first autumn arrivals, and summer predation as fixed effects. Data were family sizes from flock counts ($n = 34,174$). Line shows partial fit for flock size. Model $\Omega_0^2 = 0.562$. Habitat type, observer, and breeding year are *iid.* random effects in both cases.
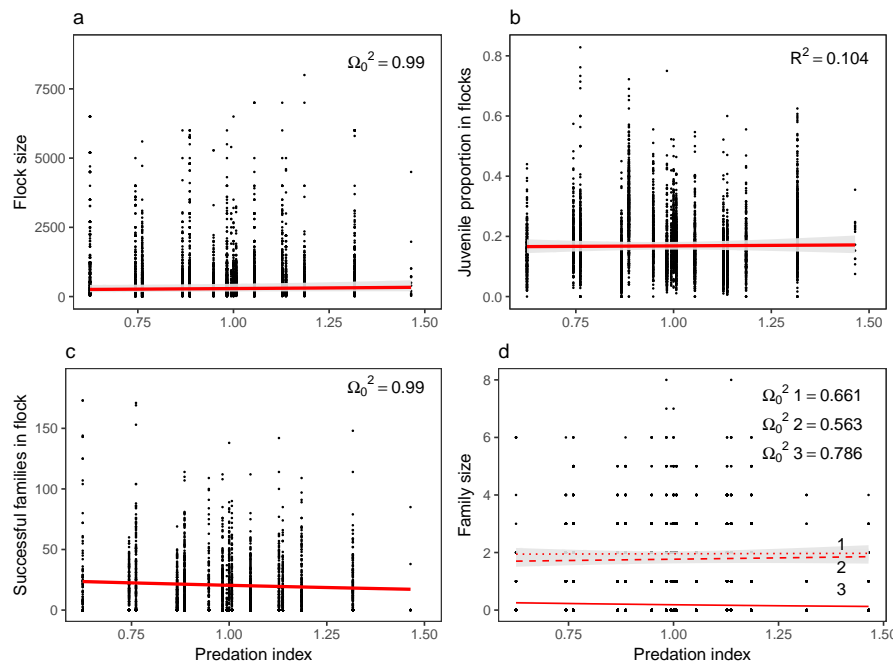
Trends in juvenile proportion

Figure 4: Model fit and data for juvenile proportion with longitudinal position and summer predation as fixed effects, and days since first autumn arrivals as a smooth term. Data used were complete cases of flock age ratios ($n = 5{,}659$). Lines show partial fits for **(a)** days since arrivals, and **(b)** flock size. Model $R^2 = 0.104$. 95% confidence intervals are shaded grey.

Trends due to summer predation

Figure 5: Model fits and data for **(a)** flock size with longitude, days since first autumn arrivals, and summer predation as fixed effects. Data used were complete cases of flock counts ($n = 5{,}700$). Model $\Omega_0^2 = 0.99$. **(b)** Juvenile proportion with flock size, longitude, and summer predation as fixed parametric effects, and days since arrivals as a smooth term. Data used were complete cases of flock age ratios ($n = 5{,}659$). Model $R^2 = 0.104$. **(c)** Number of successful families in flocks with longitude, days since autumn arrivals, flock size and summer predation as fixed effects. Data used were family frequencies from flock counts ($n = 5{,}659$). Model $\Omega_0^2 = 0.99$. **(d)** Family size with flock size, longitude, days since arrivals and summer predation as fixed effects. Data used were family sizes from flock counts ($n = 34{,}174$), and observations of individual geese ($n = 10{,}426$). Model $\Omega_0^2 = $ (*1*) 0.661, successful families in flocks, (*2*) 0.563, successful pairs observed individually, and (*3*) 0.786, all pairs including unsuccessful ones observed individually. Random effects in **(a)**, **(b)** and **(c)** & **(d)**(*2*) are *iid.* breeding year, observer, and habitat type, and in **(d)**(*1, 3*) are goose identity, and goose identity nested within breeding year. Lines in **(a)**, **(b)** and **(c)** show partial fit for summer predation index. Lines in **(d)** show partial fit of family sizes of (*1, 2, 3*) as described above for predation index. 95% confidence intervals are shaded grey.

References

1. S. M. Warren, A. D. Fox, A. Walsh, P. O'Sullivan, Extended parent-offspring relationships in greenland white-fronted geese (anser albifrons flavirostris). *The Auk.*

110, 145–148 (1993).

2. J. Madsen, G. Cracknell, Goose populations of the western palearctic (1999).

3. S. Alphéraky, The geese ofEuropeand asia. *Translated version, London* (1904).

4. J. Philippona, *Die blessgans: Zug und Überwinterung in europa und südwestasien* (Ziemsen, 1972).

5. H. Wilson, D. Norriss, A. Walsh, A. Fox, D. Stroud, Winter site fidelity in greenland white-fronted geese (*Anser albifrons flavirostris*), implications for conservation and management. *Ardea*. **79**, 287–294 (1991).

6. J. H. Mooij, B. S. Ebbinge, I. O. Kostin, J. Burgers, B. Spaans, Panmixia in white-fronted geese (anser a. albifrons) of the western palearctic. *Ecology of geese wintering at the Lower Rhine area (Germany).*, 109 (1996).

7. H. Miller, A. Dzubin, Regrouping of family members of the White-Fronted goose (*Anser albifrons*) after individual release. *Bird-Banding*. **36**, 184–191 (1965).

8. J. E. Jónsson, A. D. Afton, Lesser snow geese and ross's geese form mixed flocks during winter but differ in family maintenance and social status. *The Wilson Journal of Ornithology*. **120**, 725–731 (2008).

9. M. Poisbleau *et al.*, Social dominance correlates and family status in wintering dark-bellied brent geese, branta bernicla bernicla. *Animal Behaviour*. **71**, 1351–1358 (2006).

10. J. M. Black, M. Owen, Agonistic behaviour in barnacle goose flocks: Assessment, investment and reproductive success. *Animal Behaviour*. **37, Part 2**, 199–209 (1989).

11. M. J. J. E. Loonen, L. W. Bruinzeel, J. M. Black, R. H. Drent, The benefit of large broods in barnacle geese: A study using natural and experimental manipulations. *Journal of Animal Ecology*. **68**, 753–768 (1999).

12. D. A. Stroud, Observations on the incubation and post-hatching behaviour of the greenland white-fronted goose. *Wildfowl*. **33**, 63–72 (1982).

13. C. R. Ely, *Breeding biology of the white-fronted goose (anser albifrons frontalis) on the yukon-kuskokwim delta, alaska* (1979).

14. A. D. Fox, H. Boyd, R. G. Bromley, Mutual benefits of associations between breeding and non-breeding White-fronted Geese (*Anser albifrons*). *Ibis*. **137**, 151–156 (1995).

15. J. H. Mooij, Numbers and distribution of grey geese (genus anser) in the federal republic of germany, with special reference to the lower rhine region. *Ardea*. **79**, 125–

134 (1991).

16. T. M. Poulsen, W. G. East, Europe. *Europe: Relief* (2017), (available at https://www.britannica.com/place/Europe).

17. K. Koffijberg, H. Schekkerman, H. van der Jeugd, M. Hornman, E. van Winden, Responses of wintering geese to the designation of goose foraging areas in the netherlands. *Ambio*. **46**, 241–250 (2017).

18. A. D. Fox, K. F. Abraham, Why geese benefit from the transition from natural vegetation to agriculture. *Ambio*. **46**, 188–197 (2017).

19. J. Madsen, D. Boertmann, Animal behavioral adaptation to changing landscapes: Spring-staging geese habituate to wind farms. *Landscape ecology*. **23**, 1007–1011 (2008).

20. A. D. Fox *et al.*, Current estimates of goose population sizes in western europe, a gap analysis and assessment of trends. *Ornis svecica*. **20**, 115–127 (2010).

21. A. D. Fox, J. Madsen, Threatened species to super-abundance: The unexpected international implications of successful goose conservation. *Ambio*. **46**, 179–187 (2017).

22. J. Mooij, The" niederrhein"(Lower rhine) area (north rhine westphalia, federal republic of germany), a goose wintering area of increasing importance in the dutch-german border region. *Aquila*. **89**, 285–297 (1982).

23. H. Ballasus, Habitatwahl und -präferenz der bless- und saatgans anser albifrons, a. fabalis am unteren niederrhein : Historische veränderungen und mögliche ursachen. *Vogelwarte : Zeitschrift für Vogelkunde*. **43**, 123–131 (2008).

24. H. Kruckenberg, A. Kondratyev, J. MOOIJ, C. Zöckler, E. Zarigudinova, White-fronted goose flyway population status. *Angew. Feldbiol*. **2**, 77 (2008).

25. B. Ganter, J. Madsen, An examination of methods to estimate population size in wintering geese. *Bird Study*. **48**, 90–101 (2001).

26. J. M. Black, C. Carbone, R. Wells, M. Owen, Foraging dynamics in goose flocks: The cost of living on the edge. *Animal Behaviour*. **44**, 41–50 (1992).

27. J. Van Impe, Long-term reproductive performance in white-fronted geese anser a. albifrons and tundra bean geese a. fabalis rossicus wintering in zeeland (the netherlands). *Bird Study*. **43**, 280–289 (1996).

28. B. Kranstauber, M. Smolla, *Move: Visualizing and analyzing animal track data* (2016; https://CRAN.R-project.org/package=move).

29. D. Kahle, H. Wickham, Ggmap: Spatial visualization with ggplot2. *The R Journal*.

5, 144–161 (2013).

30. T. Vincenty, Direct and inverse solutions of geodesics on the ellipsoid with application of nested equations. *Survey review*. **23**, 88–93 (1975).

31. R. J. Hijmans, *Geosphere: Spherical trigonometry* (2016; https://CRAN.R-project.org/package=geosphere).

32. B. B. Hansen *et al.*, Climate events synchronize the dynamics of a resident vertebrate community in the high arctic. *Science*. **339**, 313–315 (2013).

33. R. Summers, L. Underhill, Factors related to breeding production of brent geese branta b. bernicla and waders (charadrii) on the taimyr peninsula. *Bird Study*. **34**, 161–171 (1987).

34. A. A. Dhondt, Cycles of lemmings and brent geese branta b. bernicla: A comment on the hypothesis of roselaar and summers. *Bird Study*. **34**, 151–154 (1987).

35. S. Blomqvist, N. Holmgren, S. Åkesson, A. Hedenström, J. Pettersson, Indirect effects of lemming cycles on sandpiper dynamics: 50 years of counts from southern sweden. *Oecologia*. **133**, 146–158 (2002).

36. B. A. Nolet *et al.*, Faltering lemming cycles reduce productivity and population size of a migratory arctic goose species. *Journal of animal ecology*. **82**, 804–813 (2013).

37. Y. Kokorev, V. Kuksov, Population dynamics of lemmings, lemmus sibirica and dicrostonyx torquatus, and arctic fox alopex lagopus on the taimyr peninsula, siberia, 1960–2001. *Ornis Svecica*. **12**, 139–143 (2002).

38. A. Angerbjörn, M. Tannerfeldt, H. Lundberg, Geographical and temporal patterns of lemming population dynamics in fennoscandia. *Ecography*. **24**, 298–308 (2001).

39. D. Bates, M. Mächler, B. Bolker, S. Walker, Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*. **67**, 1–48 (2015).

40. K. Barton, *MuMIn: Multi-model inference* (2016; https://CRAN.R-project.org/package=MuMIn).

41. A. Kondratyev, E. Zaynagutdinova, Greater white-fronted geese (*Anser albifrons*) and bean geese (a. fabalis) on kolguev island–abundance, habitat distribution, and breeding biology. *Vogelwelt*. **129**, 326–333 (2008).

42. S. N. Wood, *Generalized additive models: An introduction with r* (CRC press, 2006).

43. S. N. Wood, *Generalized additive models: An introduction with r* (Chapman; Hall/CRC, ed. 2, 2013).

44. S. N. Wood, Thin-plate regression splines. *Journal of the Royal Statistical Society (B)*.

65, 95–114 (2003).

45. S. N. Wood, Stable and efficient multiple smoothing parameter estimation for generalized additive models. *Journal of the American Statistical Association.* **99**, 673–686 (2004).

46. W. H. Elder, N. L. Elder, Role of the family in the formation of goose flocks. *Wilson Bull.* **61**, 133–140 (1949).