

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

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Study species

Whitefronts (*Anser albifrons*) are Arctic breeding grey geese with a circumpolar summer distribution, with the western continental Europe wintering nominate subspecies breeding between the 10°C and 4°C isotherms in the Russian Nenets and Yamal regions, from the Kanin Peninsula (45°E) to the River Yenisei (85°E) (1). These birds use the Baltic-North Sea flyway (2) and are presently concentrated in the Lower Rhine Dutch-German border region during winter, a change from their historical wintering grounds between East Frisia and the Elbe (3). Whitefronts show high site fidelity during winter (4), but the flyway populations do mix, and western European wintering geese have increased markedly since the 1960s (5), possibly at the cost of more south-easterly ones (6). The species is variable in its foraging habits, with Eurasian birds found largely on natural or cultivated grass fields (7). Adults form life-long pair bonds, and family bonds are long-lasting. Families regroup successfully after individual release in both wintering (8) and breeding areas (*pers.obs*) Juveniles frequently accompany parents on more than one migration (7). The fitness benefits of large families in dominance contests in winter (9)(10), and in anti-predator defence through nest-attendance (11) (12)(13) in the breeding season might promote their extended maintenance.

Study site

We used a combination of 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 lon-

gitudes 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 (14). 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 (15)(16). Geese have become habituated to wind turbines which might once have made parts of the landscape unavailable (17). Whitefronts have stabilised at around 1.4 million individuals from historic lows in the 1960s, following several years of conservation-enabled and crop-feeding boosted exponential growth (18)(5). They are the most abundant species of migratory geese, and make up a larger proportion in mixed flocks than before (18)(19)(20).

Goose observations

Geese have long been observed on their wintering grounds within the study area. Individual 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 (21). This mark-resight method is well developed and has been used to study other goose species (22). The neckbands are reported and displayed on the purpose-built website geese.org. The number of associated first-winter juveniles if any, the identity of the partner if present, the nearest settlement, habitat type, and the flock size are among the reported attributes. Geographic coordinates of the observation are geocoded and displayed on a map from the name of the nearest settlement, and can be manually edited. Observers are volunteers, and most observations are made *ad hoc*, often as part of flock counts (*see below*). Geese regularly allow observers to approach within a hundred metres, a marked difference from their breeding grounds (*pers. obs.*).

Counts of goose flocks in order to monitor populations have taken place regularly across the study area, more consistently so (15). Observers count flocks at both fixed and *ad-hoc* sites. Flocks too large to be counted completely in the field are subsampled, care being taken to sample a representative, since flocks are expected have heterogeneous composition (23). Counts also determine the flock's percentage of first winter juveniles, a valuable indicator of breeding success, with 30% considered the long term mean (24). Some observers ($n = 19$) also record the frequencies of families of different sizes, with families considered to be one or more first winter birds associated with one or more adults.

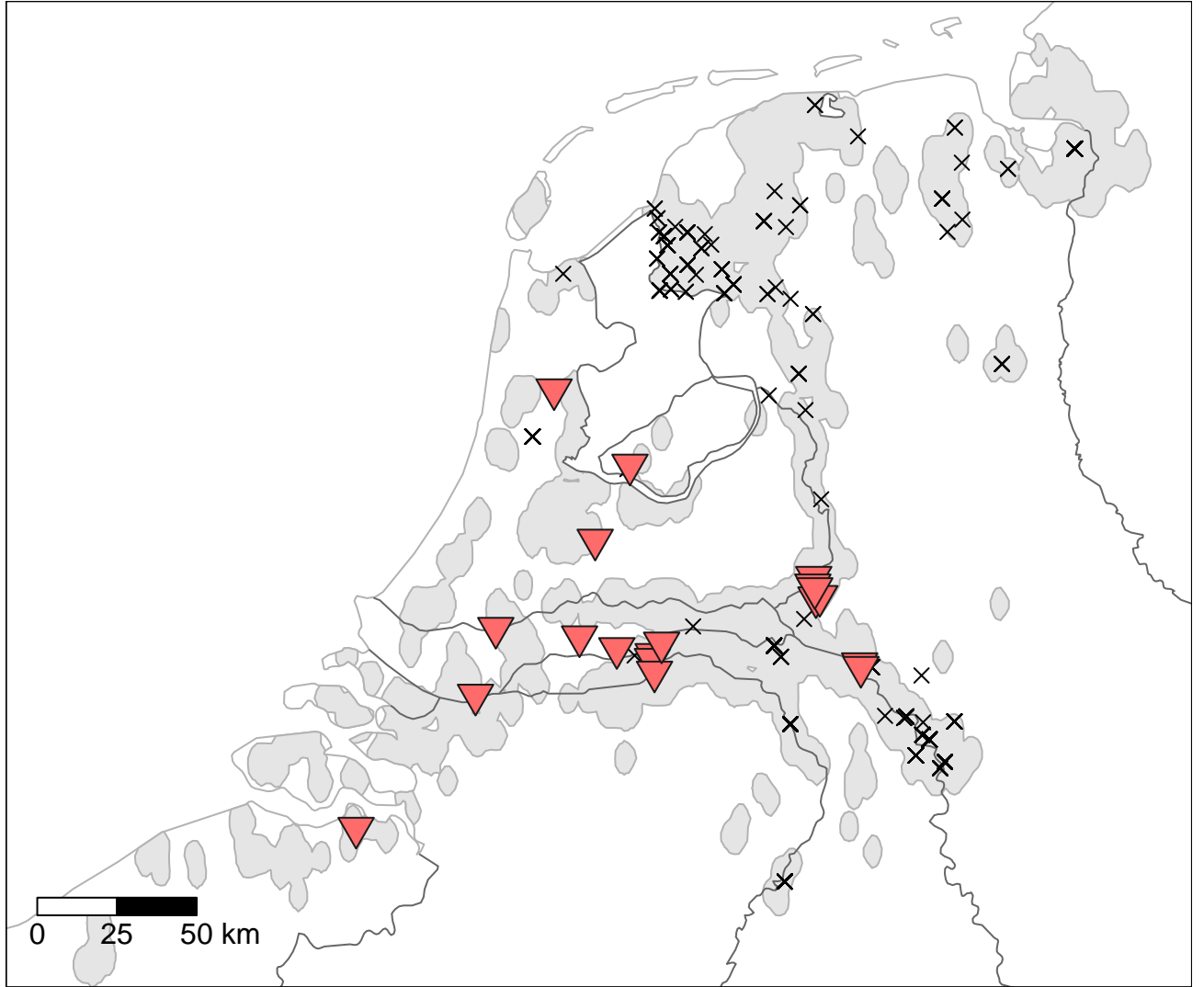


Figure 1: Three datasets used in the study are represented on a map of the main wintering grounds of the North Sea population of Whitefronts. Lines represent coasts (light) and major rivers (dark). Crosses mark sites ($n = 64$) where family frequencies within flocks ($n_{flocks} = 1,884$, $n_{families} = 50,941$) 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 ($n_{obs} = 10,635$, $n_{sites} = 8,416$).

The timing of goose arrival in autumn, and of departure in spring is representative of the goose winter. Goose flight activity is recorded by ground based observers at Trektellen (trektellen.org) sites across the Netherlands. 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 help quantify when geese arrive and leave on migration, however they do not always differentiate between long distance migratory flights and daily flights between night roosts and foraging areas.

Thirteen families were 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 (Theo Gerrits, madebytheo, The Netherlands). Loggers were set to record with a baseline sampling interval of 30 minutes, but the actual fix frequency depended on the mode in which the device were operating. Data from these loggers were uploaded remotely to the animal tracking database Movebank, and were retrieved using either the functions in the *move* package in R (25) or manually.

Data filtering

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.

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 records before autumn 2000 ($\sim 7\%$). In cases where the day was missing ($n = 32$), we assigned it to the 15th.

Flocks were recorded at 1567 unique sites. These were geocoded using the Google Maps Geocoding API accessed by the function `geocode` from the package `ggmap` (26) 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, and was thinned to a randomly selected half of its records. We used this thinned data ($n = 38,567$) for further analyses.

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. We 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. Whitefronts usually began to arrive between September 26 and October 30, and the last geese left between March 03 and April 01.

Logger data were filtered to remove: fixes outside the spatio-temporal extents of the study area, fixes with a sampling interval under 10 minutes, and fixes where the logger position error was estimated to be above the 90th percentile. To better account for irregularities, the remaining data were averaged over every half hour. Using the adult in each family with the greater number of logged positions as a ‘reference’, we matched the records of the other birds to the reference by the timestamp. Reference – individual distance was calculated using the Vincenty ellipsoid method for geographic coordinates (27) implemented by the `geosphere` package (28). To account for logger error, the family size per day was obtained as the maximum number of members within 250m over all subsequent days. We did not differentiate cases in which the adult pair of the family split from other types of family size decrease.

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
Flight activity	6,266	118	3.4 – 7.2, 50.8 – 53.5	2000 – 2016

Summer predation

Arctic rodent abundance – primarily of lemmings (*Lemmus spp.*, *Dicrostonyx spp.*) – has a cascade effect on goose numbers, as predators shift to goose eggs and young when lemmings are scarce (29), making estimation of lemming abundance and the level of summer predation an important step in modelling the populations of Arctic breeding birds (30). We could not assess rodent abundance for the breeding grounds from the literature, which focuses largely on lemming abundance from the Taimyr Peninsula (98°E) (31). While lemming cycles may be synchronised over limited spatial scales (32)(33) 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 (21). We decided not to 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 (34), 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 (35), 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 (37), 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).

$$P_t = \frac{L_{t-1} - L_t + 3}{2} \quad (1)$$

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 (34). 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 (38). 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” (38).

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 (39), 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 (40).

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 ($p < 2 \times 10^{-16}$). 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 ($p = 1.17 \times 10^{-5}$).

As hypothesised, flocks were smaller in the west, and also tended to be larger the more days since the first autumn arrivals had passed ($p < 2 \times 10^{-16}$). Consistent with the earliest ideas on how geese form flocks (41), the number of families in flocks increased very rapidly with their size ($p < 2 \times 10^{-16}$), 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 ($p = 6.45 \times 10^{-6}$). 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 ($p = 7.13 \times 10^{-16}$). This did not translate into a lower juvenile proportion ($p = 0.931$), or decreased flock sizes ($p = 0.308$).

The goodness of fit of mixed models has not been easy to score. We examined a number of methods of calculating a traditional R^2 , and settled on the Ω_0^2 metric, which compares the residual variance of the full model against the residual variance of a (fixed) intercept-only null model (42). GAMs as implemented in R return an R^2 value. These are reported below.

Table 3: Goodness of fit scores.

Response	Model	Ω_0^2 or R^2
Family size, flocks	GLMM	0.563
Family size, marked geese	GLMM	0.786
Family size, successful marked geese	GLMM	0.661
n families, flocks	GAM	0.99
Juv. proportion, flocks	GAM	0.104

Response	Model	Ω_0^2 or R^2
Flock size	GLMM	0.99

Model outputs

Trends in family size

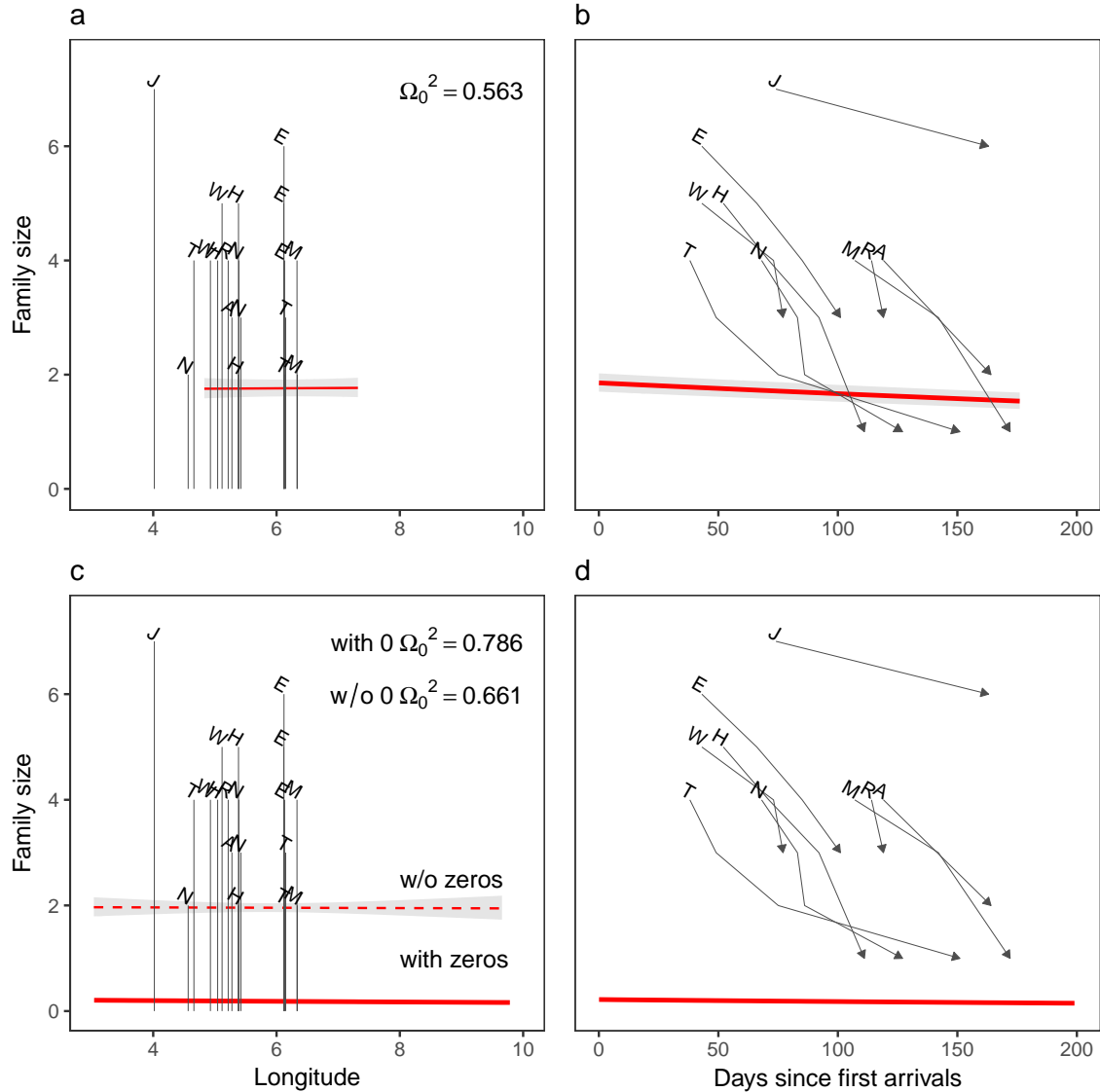


Figure 2: Top row: Model fit and data with longitudinal position, days since first autumn arrivals, predation index, and flock size as fixed effects. Habitat type, observer, and breeding year are *iid.* random effects. Data used were complete cases of counts ($n = 34,174$) of successful families in flocks. 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

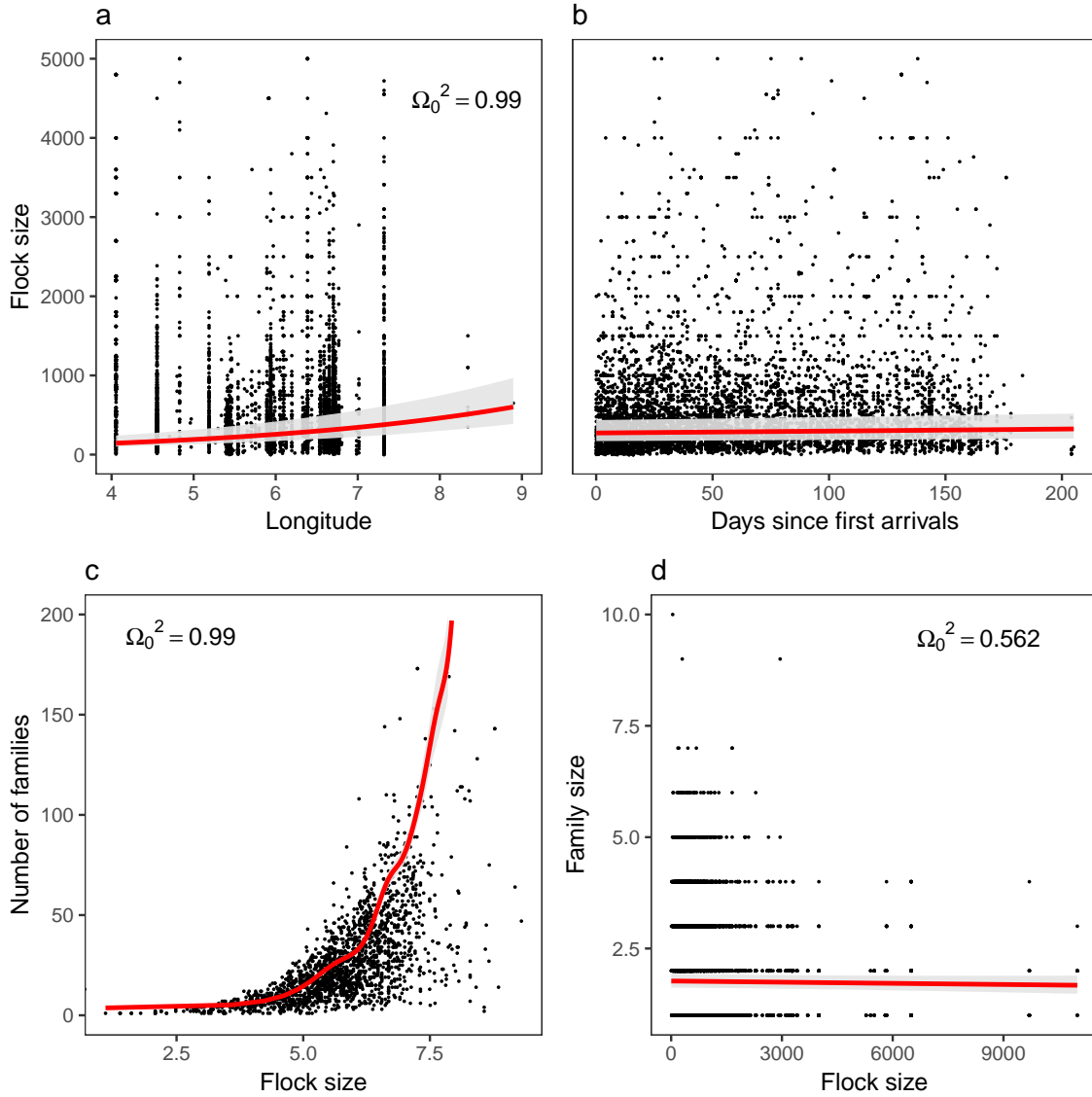


Figure 3: Top row: Model fit and data for flock size with longitudinal position, days since first autumn arrivals, and summer predation as fixed effects. Data used were complete cases of flock counts ($n = 5,700$). Lines show partial fits for (a) longitude, and (b) for days since goose arrivals in autumn. 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. 95% confidence intervals are shaded grey.

Trends in juvenile proportion

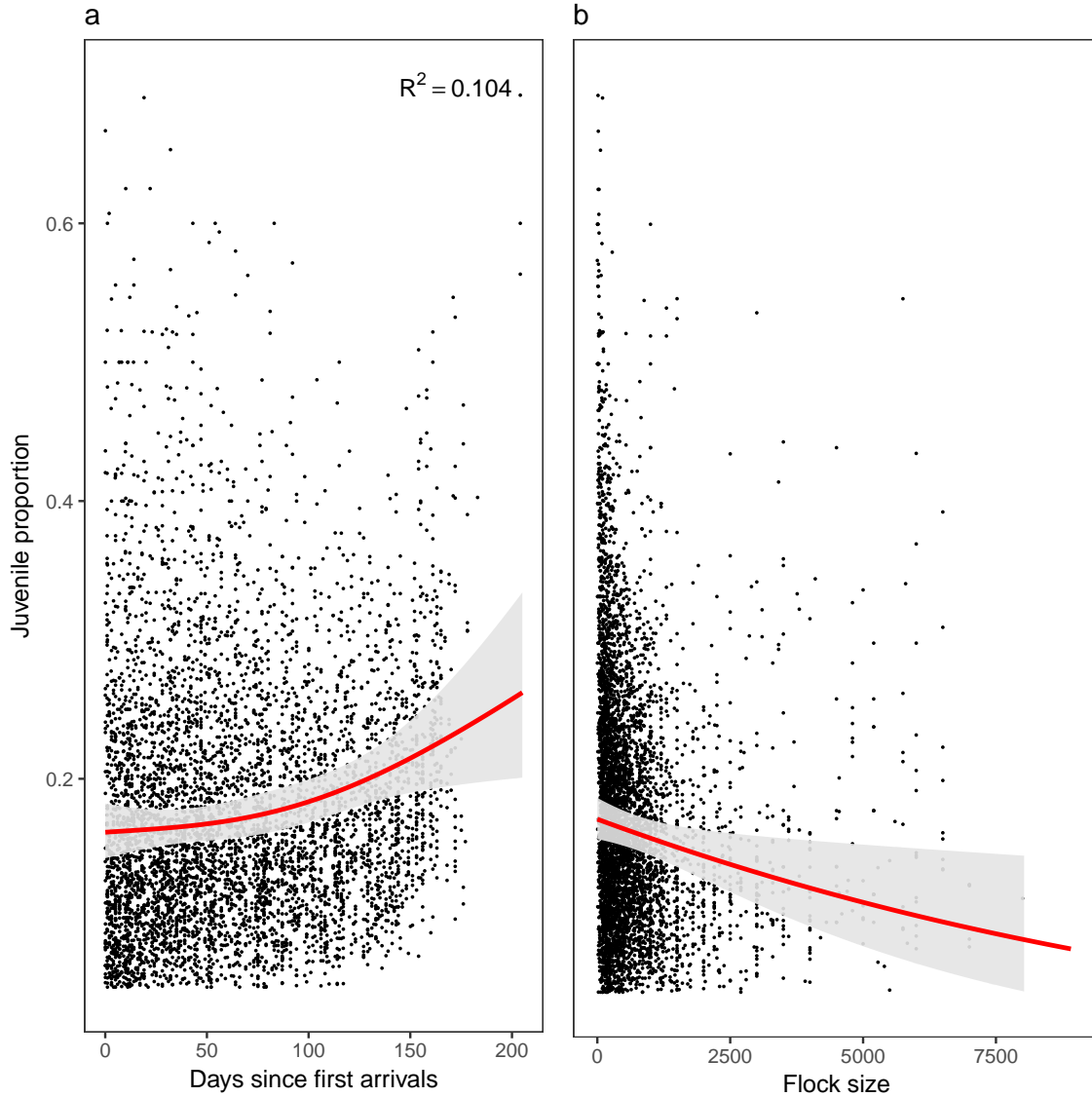


Figure 4: Model fit and data for juvenile proportion with longitudinal position and summer predation as fixed effects, and days since first autumn arrivals as a smooth term. Data used were complete cases of flock age ratios ($n = 5,659$). Lines show partial fits for (a) days since arrivals, and (b) flock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

Trends due to summer predation

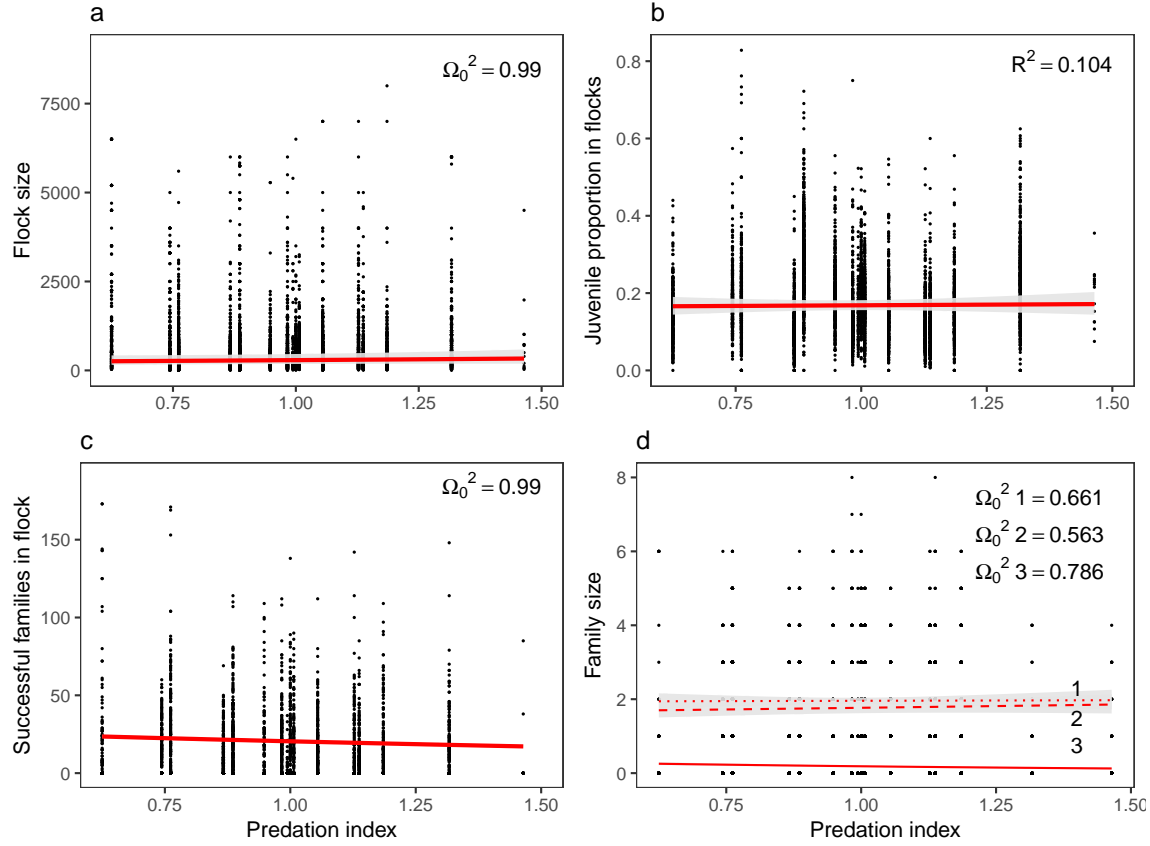


Figure 5: Model fits and data for (a) flock size with longitude, days since first autumn arrivals, and summer predation as fixed effects. Data used were complete cases of flock counts ($n = 5,700$). Model $\Omega_0^2 = 0.99$. (b) Juvenile proportion with flock size, longitude, and summer predation as 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.

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