JOURNAL OF AVIAN BIOLOGY

Family size dynamics in wintering geese

Journal:	*Journal of Avian Biology*
Manuscript ID	Draft
Wiley - Manuscript type:	Article
Keywords:	White-fronted goose (Anser a. albifrons), Differential migration, Family sizes

Abstract:	Many species live in family groups where juveniles receive parental care. The families of some large migrating species often stay together through one or more migration events. How the social status of families, pairs and single animals influences their migration timing and space-use is not yet well understood. Here we focus on the family size dynamics of greater white-fronted geese (Anser a. albifrons) on their wintering grounds. We gathered 17 years of observation data on foraging flocks of wintering geese in the Netherlands and northern Germany, and tracked 13 complete families with GPS transmitters. Taking into account effects carried over from the summer, we explored how the distance of the wintering site from the breeding grounds, number of juveniles in a family, number of individuals in a flock and the age-ratio of flocks develop over time. We related the probability of a family splitting to the number of flight events. Sixty days after the first autumn arrivals, families with more juveniles winter farther west, where flocks are smaller. The number of juveniles in a family, flock size, age-ratio, and the number of families in flocks is correlated with the number of days since first arrival. Families that undertake more flights in winter are more likely to split. Our data suggest that many juvenile white-fronted geese separate from their parents during the winter, and that this species is differentially migratory by age and social class in both autumn and spring. These findings are important for further investigation of the influence of climate and habitat change on large migrants that subsist in families long after hatching, and their conservation and management.

Abstract

Many species live in family groups where juveniles receive parental care. The families of some large migrating species often stay together through one or more migration events. How the social status of families, pairs and single animals influences their migration timing and space-use is not yet well understood. Here we focus on the family size dynamics of greater white-fronted geese *Anser a. albifrons* on their wintering grounds. We gathered 17 years of observation data on foraging flocks of wintering geese in the Netherlands and northern Germany, and tracked 13 complete families with GPS transmitters. Taking into account effects carried over from the summer, we explored how the distance of the wintering site from the breeding grounds, number of juveniles in a family, number of individuals in a flock and the age-ratio of flocks develop over time. We related the probability of a family splitting to the number of flight events. Sixty days after the first autumn arrivals, families with more juveniles winter farther west, where flocks are smaller. The number of juveniles in a family, flock size, age-ratio, and the number of families in flocks is correlated with the number of days since first arrival. Families that undertake more flights in winter are more likely to split. Our data suggest that many juvenile white-fronted geese separate from their parents during the winter, and that this species is differentially migratory by age and social class in both autumn and spring. These findings are important for further investigation of the influence of

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Keywords *Anser albifrons*, family size, differential migration, foraging flocks, family separation

Introduction

Most species' young receive direct or indirect parental care, which improves their own survival and provides inclusive fitness gains to their relatives (Hamilton 1964). Such care is usually in the form of food, shelter and protection (Clutton-Brock 1991). The duration of care varies strongly between and within species (Clutton-Brock 1991). Large migratory species often stay in family groups throughout the first or later migration events (see Warren et al. 1993, Kruckenberg 2005). This has direct survival and fitness benefits for both young and parents in terms of shared vigilance and higher social status within larger aggregations (Black and Owen 1989, Roberts (1996)).

Many large waterbirds, such as the geese *Anserini*, live in groups composed of families throughout much of the year. Flocking behaviour is most apparent in winter, when goose families gather to form often enormous feeding flocks (Elder and Elder 1949). Maintaining family bonds within flocks confers benefits as larger social units are dominant over smaller ones, and dominance rank increases with the number of members in the unit (e.g. in Canada geese *Branta canadensis*; Hanson 1953 and barnacle geese *B. leucopsis*, Loonen et al. 1999). The size advantage allows larger families to occupy optimal foraging positions in flocks at lesser cost and win access to better resources (Black and Owen 1989, Black et al. 1992). In addition, parents of some species benefit in summer from the presence of nest-attending sub-adults (Fox and Stroud 1988).

Over the course of a year, goose family bonds are affected by a number of factors. The success of a pair hatching and fledging young is often determined by a combination of weather conditions and levels of summer predation on the breeding grounds (Summers 1986, Dhondt 1987, Bêty et al. 2002). The impact of summer predation linked to the abundance of lemmings and voles *Arvicolinae* has historically been significant in some species, as to be detectable at the population level in winter (Summers 1986, Nolet et al. 2013). Autumn migration takes a further toll in long-distance migrants, especially on juvenile birds (Owen and Black 1989, Francis et al. 1992). In spring, juvenile geese often become independent of parents (Prevett and MacInnes 1980, Johnson and Raveling 1988, Black and Owen 1989), but some juveniles may remain associated with parents through the spring migration and on the breeding grounds, where they help to fend off predators and competitors (Ely 1979). Some even remain associated with their parents the following winter (Kruckenberg 2005). The mechanistic causes underlying family separation might be of either accidental nature (Prevett and MacInnes 1980), or the result of adults chasing off juveniles prior to spring migration (Black and Owen 1989, Poisbleau et al. 2008).

The development of family bonds in winter appears to be variable between species and populations. In general, smaller species that are observed in mixed flocks tend to dissolve families in winter (Johnson and Raveling 1988, Jónsson and Afton 2008), whereas larger species tend to maintain families for longer (Warren et al. 1993, Kruckenberg 2005). Moreover, migration speed and spatial distribution may differ between population classes, such as pairs with and without offspring (Cooke et al. 1975, Cristol et al. 1999, Green and Alerstam 2000, Schamber et al. 2007). Previous studies have noted a change in goose distribution in winter in response to severe cold (Philippona 1966, Lok et al. 1992). Such distributional changes serve as a convenient starting point for an examination of climatic factors affecting spatial patterns in goose flocks and families, especially in light of drastic changes observed in the spatial and migration ecology of similar species sharing the wintering site.

Greater white-fronted geese *Anser a. albifrons*, hereafter white-fronted geese, are among the most abundant geese wintering in continental Western Europe and occupy a wide wintering range (Madsen et al. 1999), thus offering an interesting opportunity to investigate the wintertime dynamics of goose families. We draw on long-term field observations and high frequency GPS tracks of whole families of white-fronted geese from their wintering grounds in the Netherlands and northern Germany to test the following observational hypotheses: 1. Families with more juveniles winter closer to the breeding grounds, 2. Larger families winter in smaller flocks, 3. Families decrease in size over the winter and 4. Family separation is triggered by flight related disturbances.

Methods

Age ratios and family size

We and others observed flocks of feeding geese in winter, and determined age-ratios by counting the number of adult and juvenile birds in each flock. Both age classes of white-fronted geese are told apart by their plumage throughout winter and into early spring Koffijberg (2006). In a sub-sample of flocks, the number of juveniles per pair was assessed (and defined as one family), making use of characteristic behaviour and social interactions. Most counts were carried out at a large number of sites within the core wintering range (Fig. 1A) from October to January (81%), gradually declining in February (11%) and March (7%). April and September had many fewer counts, as most geese had not then arrived, or had already departed the wintering grounds. We obtained 7,149 flock counts from 75 observers at 123 geocoded sites. Of these, 1,884 flocks counted by 17 observers at 65 sites held 51,037 successful families (Tab. 1).

Additionally, we gathered pair status and the number of young from sightings of neck-banded geese submitted by observers to the *www.geese.org* portal. In contrast with age-ratio counts, these included records of pairs without accompanying juveniles (defined as unsuccessful families). Observations of marked geese did not include details on habitat type, flock size and observer. Data from 10,635 marked individuals, observed at 8,416 sites, were obtained after filtering for data from single geese with unknown pair status or without data on offspring (Tab. 1).

To estimate the effect of autumn migration mortality, we determined family sizes on the breeding grounds on Kolguyev Island, Russia (approx. 69°N, 49°E, Fig. 1B) in August 2016, approximately one month prior to the autumn migration. On Kolguyev Island, 116 records of successful and unsuccessful families were collected (Tab. 1).

Family tracking

We collected half-hourly positions of a total of 13 complete goose families (13 adult pairs, 38 juveniles) fitted with GPS transmitters in the core wintering range within the Netherlands, between November and January (2013, n = 3, 2014, n = 4: e-obs GmbH, backpacks with Teflon harness, weight 45 g; 2016, n = 6: madebytheo, integrated into neckband, weight 35 g). These selectively large families were tracked within the study site (2 - 10°E, 50 - 54°N) during winter (before 1 April) for 34 – 135 days. A reference bird was identified in each family as the parent with the greater number of GPS fixes within the study period, which was the male in all cases except one. For all families, we identified the day and position where splits were first detected as a decrease in the number of family members within a 1000m radius of the reference bird (see Fig. 1A). We then determined the daily split probability by a binomial fit on the classification of each day as a success or failure (1 or 0) depending on whether a split occurred or not. We defined ‘flights’ as displacements >1 km over the 30 minute sampling interval, and counted their number and daily frequency.

Context data

To relate our observations to the timing of migration we extracted peaks of daily counts (n = 6,266) of visible migration in the Netherlands (*www.trektellen.nl*; Van Turnhout et al. 2009) to determine yearly arrival dates in autumn and departure dates in spring. Data were pooled for 84 spring and 180 autumn counting sites. We excluded counts from sites close to night roosts, and records which did not match the direction of migration appropriate to the season; both in order to avoid bias by local movements.

Following previous work (Jongejans et al. 2015) we estimated an index of summer predation for the breeding grounds of this population from rodent abundance data (*www.arcticbirds.net*). We calculated a pooled mean of 0 - 2 (low - high) lemming indices for all available sites in the region, taking care to always include a value of 0 to reflect the absence of lemming cycles in the core breeding area on Kolguyev Island. The predation index takes into account the cyclical change in lemming abundance, with higher values when lemming abundance has decreased from the previous year, reflecting the increased predation pressure on Arctic birds due to abundant predators switching to alternative prey (see Dhondt 1987).

To test whether spatial patterns in this population could be explained by environmental effects, we gathered daily data from 51 sites (Koninklijk

Nederlands Meteorologisch Instituut, Netherlands; Deutscher Wetterdienst, Germany) for minimum temperature, total precipitation, and mean wind-speed. Sites were on average 20km (range: 4 - 83km) from the positions at which flocks were observed.

Analyses

We first tested whether (1.) the number of juveniles, which determines family size, was correlated with the distance from the breeding grounds at which families were observed (family size counts and ring-sighting data; Tab. 1, Supplementary Material Tab. A1). Further, we tested whether (2.a.) the number of juveniles in a family and (2.b.) the total number of successful families was explained by flock size, the number of days since the arrival of geese in autumn or the level of summer predation (using family size counts; Tab. 1). To test for an effect of climate on the number of successful families in flocks, we added daily minimum temperature, daily total precipitation, and daily mean wind-speed as variables in model 2.b. Further, we tested whether (2.c) the number of juveniles in families was different on the breeding grounds one month prior, and up to two months after autumn migration in 2016 (using family size counts in the wintering region, and from Kolguyev Island, and ring-sighting data).

To place our results in the wider context of migration and the social and physical environment of geese, we examined (3.) how flock size (from age-ratio counts) was related to distance from the breeding grounds, the number of days since arrival, summer predation, climatic variables, and examined whether (4.) the proportion of juveniles in flocks was explained by the flock size, distance from the breeding grounds, number of days since arrival, and summer predation (using age-ratio counts; see Supplementary material Tab. A1). Finally, we examined whether (5.) daily split probability was predicted by the family size, the number of flights on each day, the distance travelled each day, and the time since winter arrivals (using GPS tracking data; Supplementary Material Tab. A1).

All analyses were performed in the R environment (R Core Team 2017, see Supplementary Material Tab. A1). We used Poisson lme4 (Bates et al. 2015) linear and generalised linear mixed models (LMMs & GLMMs) to test 1 and 2.a, a simple Poisson-error generalised linear model to test 2.c and a binomial-error GLMM for 5. In 2.b, 3, and 4, we used mgcv (Wood 2013) Poisson (2.b) and binomial (4) generalised additive mixed models (GAMMs) to include smooth functions of the flock size (in 2.b) and the number of days since winter (in 4) as predictors. We included the breeding year, the observer identity, the goose identity if known, and the habitat type as independent random effects. Effects included in models were dependent on their availability in the datasets used (see Supplementary Material Tab. A1).

Results

Age ratios and family sizes

The mean flock size was 712 birds (range: 2 - 20,000), with a mean proportion of first-winter birds of 0.18 (range: 0 - 0.87). Flocks in which families were counted (family size counts) held on average 540 birds (range: 3 - 11,000), with an average of 27 families (range: 1 - 333) accompanied by a mean of 1.78 juveniles (range: 1 - 10). On average, the family status of marked geese (ring-sighting data) was recorded 626 times each year (range: 62 - 1143), and these were accompanied by 0.59 juveniles (range: 0 - 11) (see Appendix 1, Supplementary material Figs. A1.1, A1.2). The 116 observed families on Kolguyev Island in 2016 had a mean of 2.26 juveniles (range: 0 – 6).

Context data

Autumn migrants arrived between 26 September and 30 October, and departed between 3 March to 1 April, resulting in a wintering period for geese of on average 165 days (range: 124 – 183). Lemming abundance from the breeding grounds transformed into a predation index ranged between 1.17 and 1.9, with very low variance between years ($\sigma 2$ = 0.048).

Juveniles and wintering site choice

We found no influence of the number of juveniles in a family on how far from the breeding grounds that family wintered in the first sixty days after arrival, in either age-ratio data (χ^2 = 3.27, p = 0.071), or in ring-sighting data (χ^2 = 2.18, p = 0.134, Fig. 2). Later in winter, age-ratio data indicated that larger families winter somewhat farther west (χ^2 = 6.026, p = 0.014), while ring-sighting data did not reveal any difference (χ^2 = 0.023, p = 0.879). Even among only the successful families in the ring-sighting data, no effect could be found (χ^2 = 0.892, p = 0.345). This difference is likely due to lower sample size and fewer observed random effects in the ring-sighting data. The proportion of successful pairs, assessed by ring-sighting data, was not related to the distance of their wintering site from the breeding grounds (χ^2 = 1.071, p = 0.301).

Family size in winter

The number of juveniles in a family (successful families counted in flocks, model 2.a) decreased through the winter (χ^2 = 74.166, p < 0.001, see Fig. 3), but was insensitive to flock size (χ^2 = 0.270, p = 0.6033) and summer predation (χ^2 = 0.337, p = 0.562, see Supplementary material Fig. A2). Family sizes of ringed geese (model 2.a adapted) decreased over time as well (χ^2 = 19.936, p = < 0.001, see Fig. 3); flock sizes of this dataset were not available.

Surprisingly, family sizes of ringed geese increased with the level of summer predation (χ^2 = 12.935, $p < 0.001$, see Supplementary material Fig. A2). However, this increase was very low with on average 0.78 additional juveniles per family per unit increase in the predation index. When excluding unsuccessful pairs from the ring-resighting data, the relation with summer predation became insignificant (χ^2 = 0.1321, p = 0.716, see Supplementary material Fig. A2), indicating a qualitative rather than quantitative effect of predation on nest success.

The number of successful families in flocks (model 2.b) increased with flock size (χ^2 = 7250, $p < 0.001$) and the number of days since goose arrival in autumn (χ^2 = 158.3, $p < 0.001$, see Fig. 4A), but was unaffected by summer predation (χ^2 = 0, p = 0.98). Further, there were more successful families in flocks farther from the breeding grounds (χ^2 = 11.253, p = 0.0008, see Fig. 5A). Also, the number of successful families in a flock was higher when daily minimum temperatures were higher (χ^2 = 7.318, p = 0.007), and decreased weakly with rising daily precipitation (χ^2 = 3.931, p = 0.047). Wind speed was not an important predictor (χ^2 = 2.644, p = 0.104).

Flock size in winter

Flocks (model 3) were significantly smaller farther from the breeding grounds (χ^2 = 93,629, p = < 0.001, see Fig. 5A), and grew slightly over the winter (χ^2 = 4,824, $p < 0.001$). Flock size was affected by each of the climatic predictors, decreasing with worsening weather: increasing precipitation (χ^2 = 3193, $p < 0.001$) and increasing daily wind speed (χ^2 = 25,906, $p < 0.001$).

However, flock sizes increased with decreasing daily minimum temperatures ($\chi^2 = 365$, $p < 0.001$).

Within flocks, juvenile proportions increased through the winter ($\chi^2 = 18.82$, $p = 0.001$, see Fig. A4b), and decreased with increasing flock size ($\chi^2 = 5.921$, $p = 0.015$, see Fig. A4c), but did not show any effect of distance from the breeding grounds ($\chi^2 = 0.979$, $p = 0.323$), or of summer predation ($\chi^2 = 0.013$, $p = 0.908$).

Family size prior to autumn migration

Families of geese observed approximately one month prior to the onset of migration in the breeding area on Kolguyev Island had significantly more juveniles than successful families (family size count) in flocks (GLM, $z = -4.285$, $p < 0.001$) and families of marked geese (ring-sighting data) (GLM, $z = -14.511$, $p < 0.001$) recorded in the first two months following the population's arrival on the wintering grounds (model 2.c).

Probability of family splits

Families fitted with GPS transmitters travelled on average 11 km each day (range: 0 - 306). On average, they travelled a distance > 1km twice per day (range: 0 - 10) and in total 98 times (range: 63 - 367) over the tracking period. 21 family split events were recorded in our 13 families; they were not restricted to juveniles.

The correlation of time in winter and family size as fixed effects was high (0.728). To avoid this multi-collinearity, we chose to omit time in winter in the final model, reasoning thus: first, that we had adequately characterised the development of family sizes over the course of winter. Further, including a predictor whose value increased monotonically in the data would imply non-independence of the response (split probability) across days, i.e., that the probability of a family separating on any given day was a function of the probability of splitting on prior days.

The daily split probability of families (model 5) was significantly lower in larger families (χ^2 = 5.522, p = 0.019, see Fig. 6). While the number of flights per day was not important (X^2 = 1.057, p = 0.304), the distance covered influenced the likelihood of splitting (X^2 = 3.939, p = 0.047).

Discussion

We quantified the spatial-temporal distribution and size dynamics of white-fronted goose families in wintering flocks in the context of winter climate, predation risk in summer, and mortality during autumn migration. In support of our hypothesis, we found that large families wintered farther from the breeding grounds, but only during the second half of winter. Larger families did not select for smaller flocks, but flocks were generally smaller in the west. As expected, family size decreased over the winter, but our results indicate that larger families were less likely to split accidentally.

Spatial dynamics of family size

Our baseline result that flock sizes are smaller in the west of the wintering region — further from the breeding sites — can be explained by metabolic constraints that determine maximum flight distances and durations, even during migration (Klaassen 1996). This is supported by the fact that family sizes do not vary spatially during the early winter months. However, once all geese have arrived and wintering sites begin filling up, food becomes more limited, and it seems that large, socially dominant families (Vangilder and Smith 1985, Schamber et al. 2007) make further movements to occupy climatically milder sites. This supports the earlier suggestion of differential use of wintering sites (Jongejans et al. 2015) according to social status.

Contrary to expectations, larger families were generally not associated with smaller flocks. Rather, larger families as well as small flocks are coincidentally found further from the breeding sites. Furthermore, spatial differences in family wintering areas might have led to the finding that larger flocks appeared to have a lower proportion of juveniles (Jongejans et al. 2015). Large goose families selecting for optimal sites seem to be one driver of the variation in juvenile proportion between wintering sites (Schamber et al. 2007), but independent juveniles observed in wintering flocks (Hanson 1953, Loonen et al. 1999) may dampen this variation.

Temporal dynamics of family size

The finding that family size decreased through the winter points towards a steady reduction in the number of juveniles associated with families, and to high variation in the age at which young geese leave their parents. Some young geese may be found associated with parents even in their second or third winter (Ely 1979, Warren et al. 1993, Kruckenberg 2005). While juvenile independence from parents should result in concurrently steady reduction in the number of apparently successful families in flocks over the winter, our findings went against this expectation. We suggest two possible explanations, first, that most pairs do not become dissociated from all their young over a single winter, i.e., that split events are accidental rather than triggered by the parents (Prevett and MacInnes 1980). Furthermore, families with juveniles likely begin spring migration later than pairs without young, mirroring their differential autumn migration arrival, which is later than that of other adult geese (Jongejans et al. 2015).

This proposed differential migration timing is further supported by the strong, non-linear temporal increases in proportions of juveniles in foraging flocks. We hypothesise that in spring, it is adults without young that leave the wintering grounds for Arctic breeding and moulting sites, followed by families with young, with indpendent juveniles bringing up the rear. While this is contrary to previous studies on the spring migration of pink-footed *A. brachyrhynchus* and snow geese (Bêty et al. 2001), it is interestingly similar to the migration of juvenile snow geese, which appear to arrive somewhat later that adults on the spring breeding grounds (Prevett and MacInnes 1980).

Data from our 13 GPS tracked goose families support the suggestion that winter dissociations of first-year juveniles from their families are accidental (Prevett and MacInnes 1980), taking place when geese make long-distance movements, but not necessarily when the number of flights is high. This may indicate that only disturbances sufficient to compel geese to relocate to distant sites prompt family splitting. In most cases, juveniles split off one at a time, and not all at once. In the chaotic take-off conditions hypothesised to promote accidental separation of individuals from their families (Prevett and MacInnes 1980), larger families might be easier to adhere to, possibly explaining why they are less likely to split.

Effects of winter climate conditions

The negative responses of the number of successful families in flocks, and of flock size to cold and wet weather are in line with current knowledge of goose foraging preferences (Fox and Madsen 2017). Geese will tolerate snow depths of about 15 cm before relocating to areas with better access to forage (Philippona 1966). Such conditions have become rare over the past decade, and usually do not occur in the Netherlands before midwinter. This ties in with spatial differences in family size only being observed in late winter. Large, dominant families thus seek to occupy the rather limited westerly, coastal sites with moderate temperatures. Limited habitat availability in the west of the Netherlands and Belgium — combined with high hunting pressure in France, and the high energetic costs of long flights — seems to lead to geese aggregating in large flocks on the remaining accessible grassland sites on cold, snowy days.

Relation to summer conditions

Our result that families were significantly larger prior to migration than in the first two months on the wintering grounds is in line with previous findings of high juvenile mortality on autumn migration (Owen and Black 1989, Francis et al. 1992). We suspect that mortality in our population is also mainly due to strong density-driven competition for resources prior to and during autumn migration. Previously, juvenile survival of Arctic-breeding birds — geese included — was understood to be indirectly driven by the cyclical abundance of Arctic rodents, and concomitant levels of predation (Summers and Underhill 1987).

However, our study supports the idea that the breeding success of white-fronted geese on the Baltic-North Sea flyway has been unrelated to summer predation in recent years (Jongejans et al. 2015). This may possibly be due to faltering lemming cycles (Nolet et al. 2013), or because an increasing proportion of the population breeds in areas like Kolguyev Island, that altogether lack Arctic rodents and associated phenomena (Kruckenberg et al. 2008). On the other hand, our finding that the number of juveniles seen with marked geese is higher during years of increased predation suggests a qualitative rather than quantitative response, to wit that in years of high predation, some geese succeed in raising large families, but many more suffer total brood failure.

General conclusion

Based on the spatial and temporal patterns of wintering goose families, we argue that management actions (Stroud et al. 2017) must consider that the proportion of juvenile geese in foraging flocks is higher in some areas, and at some times of the year. It is crucial to distinguish between adult survival and recruitment for population control (Madsen 2010), as well as conservation. Climate, habitat change, and change in feeding habits are suggested to have led to increased goose densities, range expansion, and range shifts (Fox et al. 2005). As high densities lead to low recruitment in the Arctic breeding grounds (Owen and Black 1989, Francis et al. 1992), goose populations might become less flexible and highly vulnerable to rapidly changing conditions. Our results show that increased disturbances on the wintering sites and migration stopovers, *e.g.* as a result of increased management actions, would induce more goose family splits, possibly altering population structure and survival rates. Such disruption of the mechanisms of cultural transmission of space use could cause levels of adaptability to changing environmental conditions to change in unpredictable ways.

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Supplementary material provided as Appendix 1.

Tables

Type	Records	Sites	Spatial extent
Age-ratio counts	7,149	123	4.0° - 8.8°E, 51.1° - 53.4°N
Family sizes	51,037	65	4.8° - 7.3°E, 51.1° - 53.4°N
Ring-sighting data	10,635	8,416	2.7° - 9.7°E, 50.9° - 53.9°N
Familie sizes on Kolguyev	116	26	49°E, 69°N
GPS tracking of families	32,630[a], 13[b]	32,630	3.9° - 7.9°E, 51.3° - 54.3°N
a: Half-hourly family positions, b: Number of families tracked			

Table 1: Datasets of goose observations and tracking.

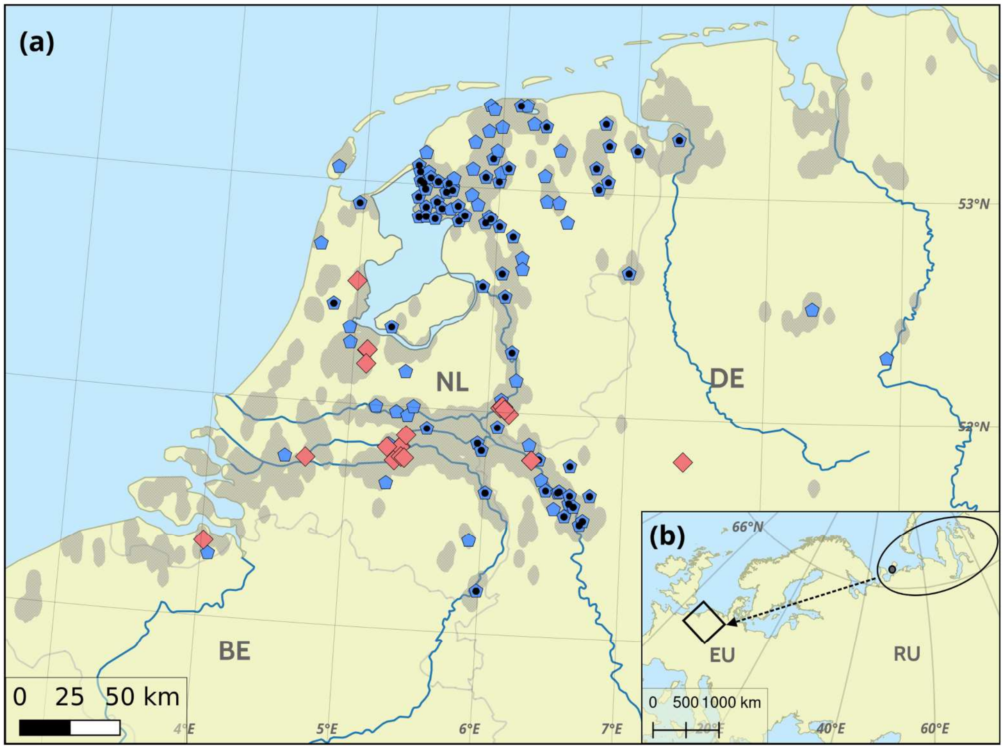

Fig. 1. (a). Wintering grounds of greater white-fronted geese Anser a. albifrons in the Netherlands and northern Germany, showing 123 sites (blue pentagons) where the age-ratio of 7,149 focks was determined, a subset of 65 sites (black dots) where 51,037 successful families were recorded in 1,884 flocks. Shaded area bounds 10,635 ring-resightings. 21 split events (red diamonds) were observed in 13 GPS tracked families. Observations correspond well with major rivers and waterbodies, marked in blue. Data were collected from 2000 - 2017. (b) Breeding grounds (ellipse) in Russia with Kolguyev island (dot) and general flyway (arrow) to wintering area (rectangle) (adapted from Madsen et al. 1999).

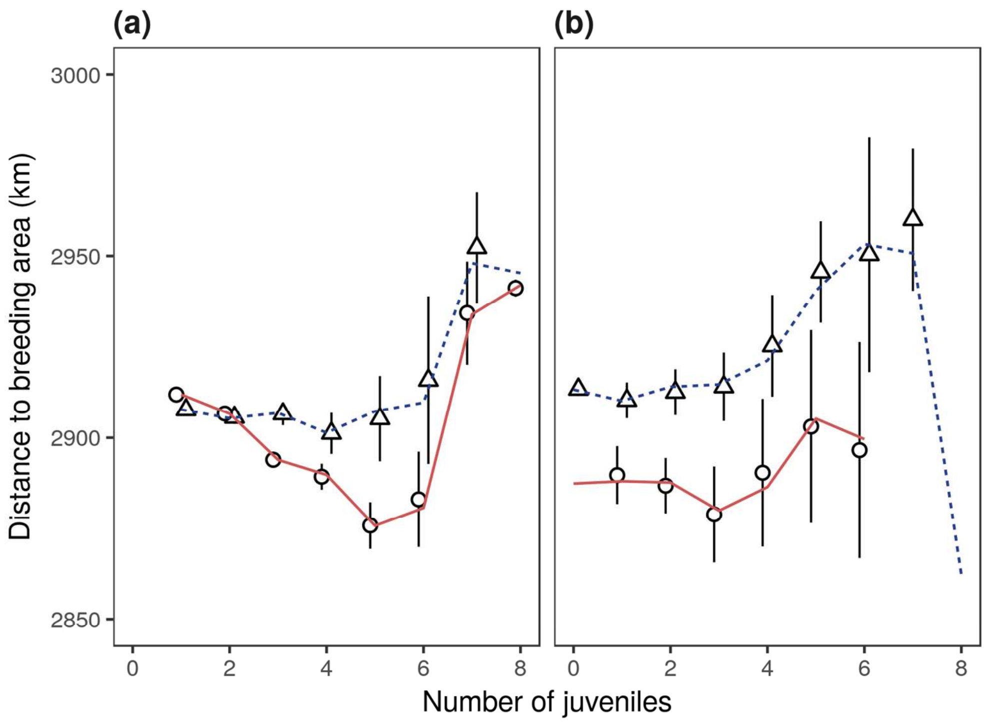

Fig. 2. LMM fts (lines), and mean distance of wintering sites from Kolguyev island (symbols) per number of juveniles in a family for (a) family size counts and (b) ring-resightings. Data and fit for records from < 60 days after arrival to the wintering grounds (circles and solid red lines), and data and fit for records 60 days after arrival (triangles and dashed blue lines), and 95% confidence intervals for the data are shown.

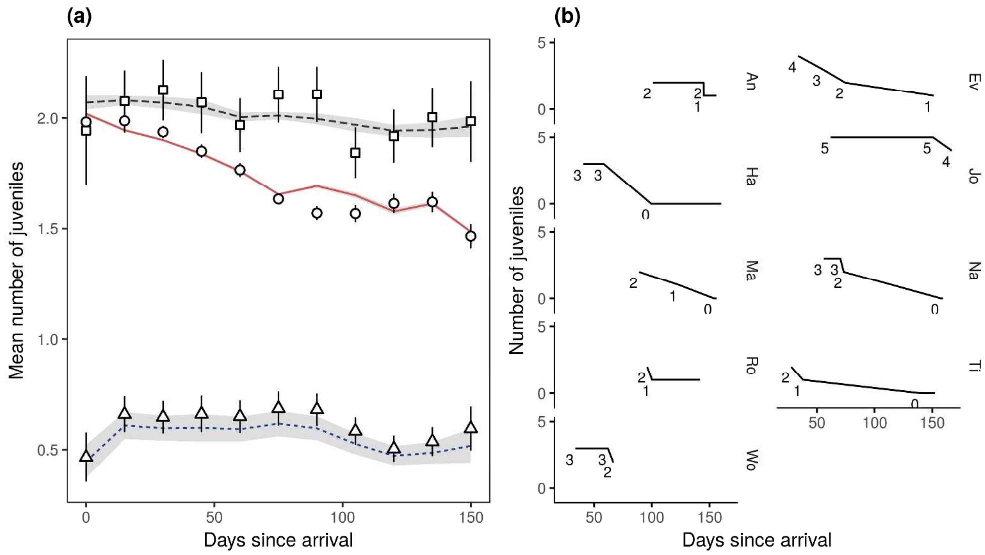

Fig. 3. (a). GLMM fits (lines) and mean number of juveniles per family every 15 days since goose autumn arrival (shapes) for each dataset. Successful families in flocks (circles and solid red line), ring-resightings including unsuccessful pairs (triangles and dotted blue line), and ring-resightings with only successful pairs (squares and dashed black line). (b). Number of juveniles in each family (name in box) which split, at the start of the tracking period, and following each subsequent juvenile split.

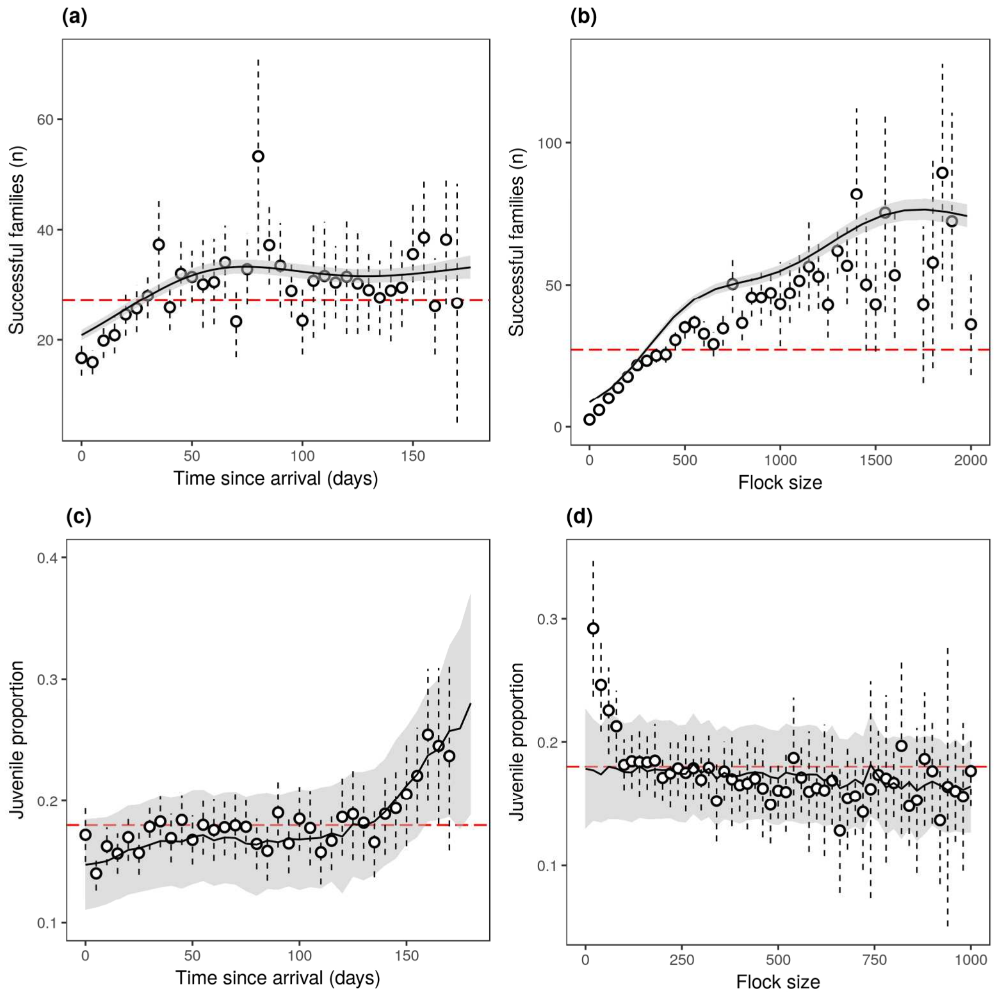

Fig. 4. GAMM fits (solid black lines), data (circles), 95% confidence intervals for data (vertical dashed lines) and fits (shaded grey areas), and overall observed mean response value (horizontal dashed red line) for (a) Mean number of successful families in flocks every 5 days after autumn arrival; (b) Mean number of families in flocks, in increments of 50 individuals; (c) Mean proportion of first-winter juveniles in flocks every 5 days; (d) Mean juvenile proportion of flocks, in increments of 20 individuals. Means and proportions were pooled across all years. Note that in C days since arrival was modelled as a smoothed covariate using thin plate splines, and 4 knots. Conditional fits shown in (c) and (d).

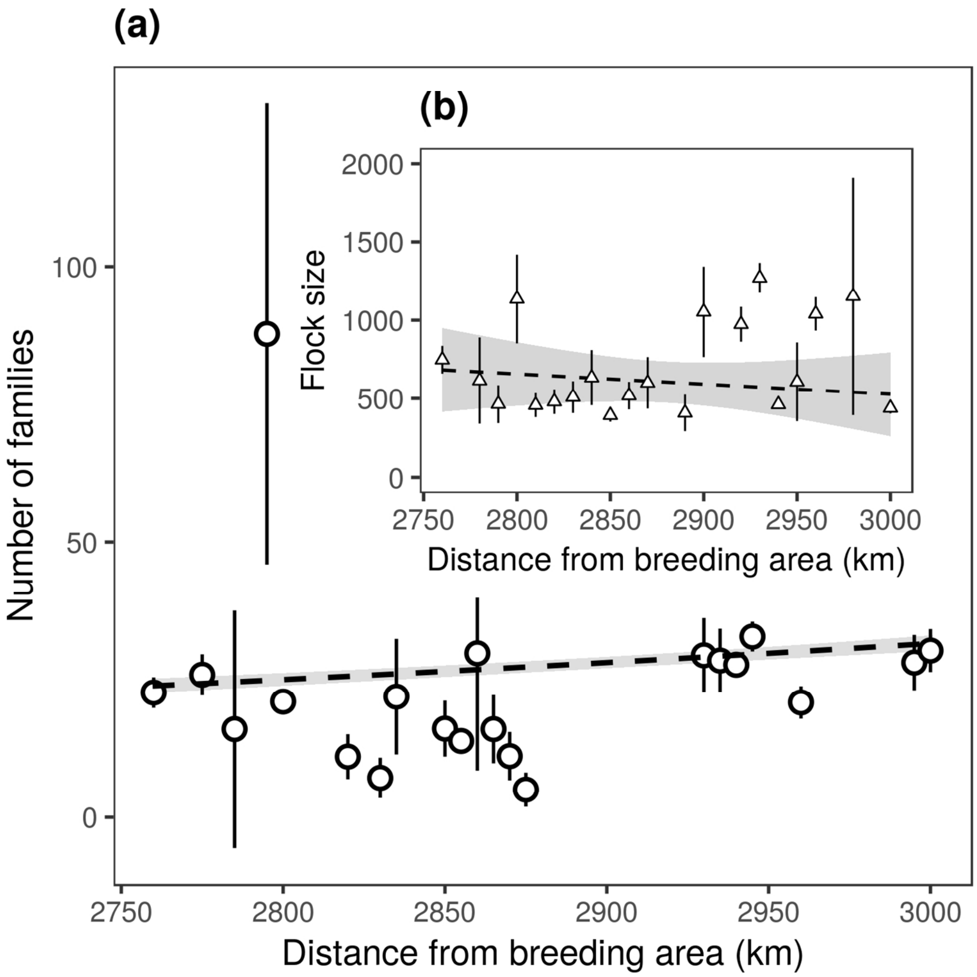

Fig. 5. GAMM fit (dashed line), data (circles), and 95% confidence intervals for data (vertical lines) and fits (shaded grey area) for (a) Mean number of families in flocks at distances from Kolguyev Island, in increments of 5km, and (b) Mean flock size at distances from Kolguyev Island, in increments of 25km. Sites to the north-east of the study site are approximately 500 km nearer to Kolguyev than sites in the south-west.

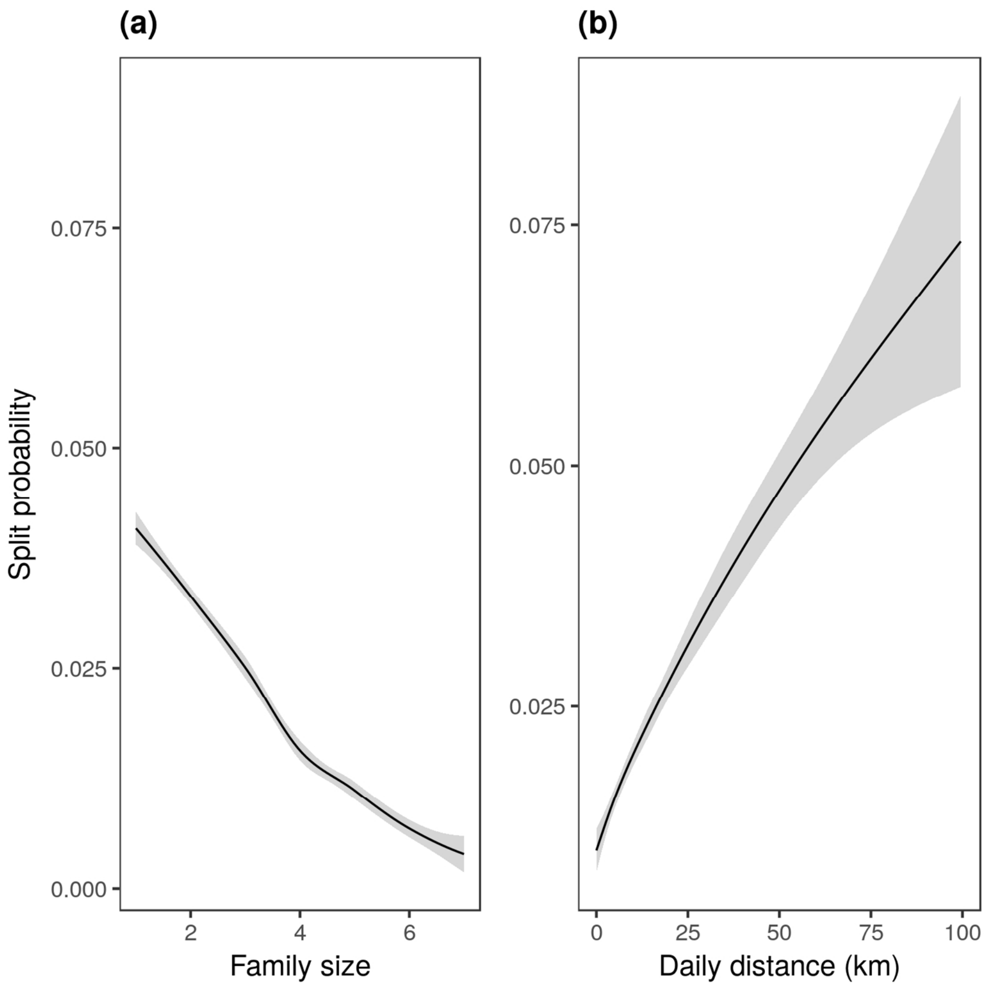

Fig. 6. GLMM fits (lines) for split probability in relation to (a) family size, and (b) daily distance travelled, with confidence intervals (shaded regions).

Supplementary Material: Appendix 1

Here we provide representations of the distribution of filtered observation data over yearly and monthly scales (Figs. A1.1 & A1.2). Arctic geese are expected to begin arriving at the eastern end of the study site by late September, and are present on Dutch and northern German sites by early - mid October. The heatmaps shown reflect this pattern.

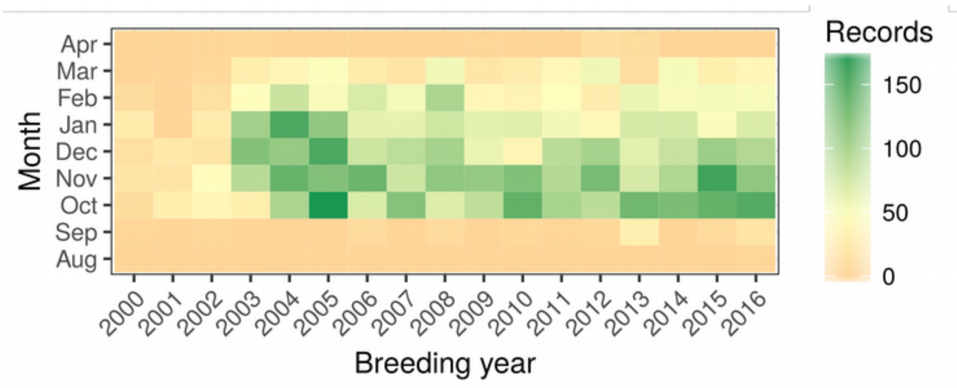

Fig. A1.1. Heatmap of number of flock counts per month in each calendar year. Data are sparse from the early 2000s. Data density is higher in the first three winter months (Oct, Nov,Dec) than the following ones (Jan, Feb, Mar). A mean of 47 flocks are censused per month (range: 0 - 177).

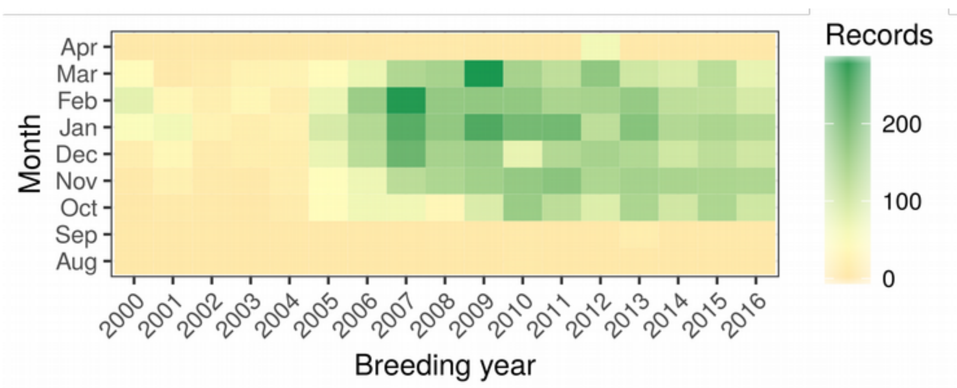

Fig.A

Fig. A1.2: Heatmap of number of observations of geese marked with numbered neckbands per month in each calendar year. Data are sparse until the mid 2000s. Marked geese are sighted in the study area earlier and later than censused flocks. On average, 49 marked geese are seen each month (range: 0 - 294).

Model	Type	Dataset	Response	Fixed effects	Random effects	Records used
1	LMM	Family size counts	Distance to breeding area	1, 5	8, 9, 10	20,191[a]; 14,020[b]
1	LMM	Ring-sighting data	Distance to breeding area	1, 5	8, 11	3,289[a]; 7,320[b]
2.a	GLMM	Family size counts	Number of juveniles	3, 4, 5	8, 9, 10	34,179
2.a	GLMM	Ring-sighting data	Number of juveniles	5, 4	8, 11	10,426
2.b	GAMM	Age-ratio counts	Number of families	3 – 7	8, 9, 10	1,723
2.c	GLM	Family sizes on Kolguyev	Number of juveniles	Dataset		2,615
3	GAMM	Age-ratio counts	Flock size	3 – 7	8, 9, 10	5,700
4	GAMM	Age-ratio counts	Juvenile proportion	3 - 7	8, 9, 10	5,658
5	GLMM	GPS tracking of families	Split occurrence	13 – 15	12	1,009

Effects: 1: Number of juveniles per family, 2: Flock size, 3: Days since autumn arrival, 4: Predation index, 5: Minimum temperature, 6: Daily precipitation, 7: Mean daily windspeed, 8: Breeding year, 9: Observer, 10: Habitat type, 11: Goose identity, 12: Family identity, 13: Daily distance travelled, 14: Daily number of flights, 15: Total family size

a: ≤ 60 days after arrival, b: ≥ 60 days after arrival, c: All families, d: Only successful families

Table A1: Statistical model responses, predictors, and data used.

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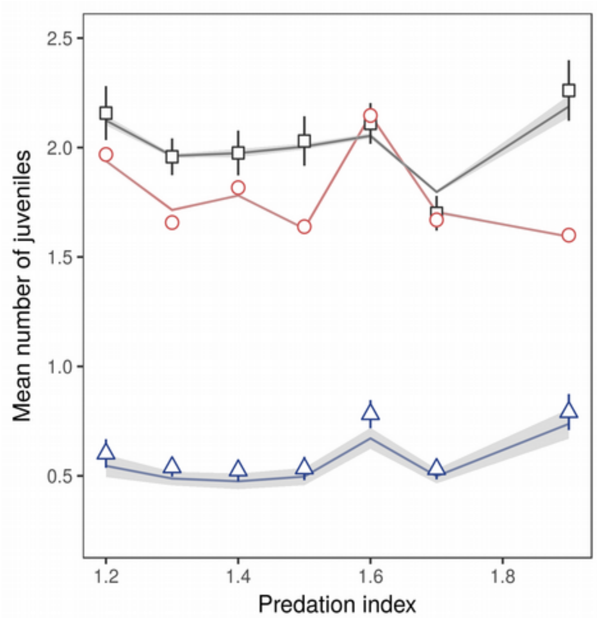

Fig. A2. GLMM fits (lines), mean number of juveniles per family at levels of pooled summer predation index, in increments of 0.1 (symbols), and 95% confidence intervals for data (vertical solid lines), and fits (shaded grey area), using family size counts (red circles and line), ring-resighting data including unsuccessful families (blue triangles and line), and ring-reisighting data without unsuccessful families (black squares and line).