

# Spatial ecology and movements of wintering White-fronted geese (*Anser albifrons*)

Family size dynamics in wintering geese

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## Abstract

The ecology of migratory Arctic-breeding birds on their wintering grounds is affected both by many factors. Hypotheses of interactions between family size, flock size, foraging site, and age-ratio of geese over the course of winter have emerged from field observations in western Europe, but are not well tested. We collected long-term observation data for flocks of wintering greater white-fronted geese *Anser albifrons albifrons* from the Netherlands and northern Germany, and tracked a total of 13 whole families of the species over three winters (2013, 2014, 2016) with GPS transmitters. Taking into account effects carried over from the summer, we explored how distance of the wintering site from breeding grounds on Kolguyev Island (69°N, 49°E), number of juveniles in a family, number of individuals in a flock, age-ratio of flocks, and time spent by geese on the wintering grounds are related. We related the probability of a family splitting to the number of times, and the distance that it flew. Families with more juveniles winter farther west after the first 60 days following autumn arrival, where flocks are smaller. The number of juveniles in a family, flock size, age-ratio and the number of families were well correlated with the number of days since arrival. Families that undertook more flights in winter were more likely to split. Our data suggest that 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.

## Introduction

Living in groups entails both costs and benefits for individuals. Group members benefit from more social interactions, and from the increased sensory and physical capabilities of the group (Krause and Ruxton 2002). It has been shown that geese in larger flocks spend less time on the lookout for predators and have more time to feed (Roberts 1996). Among the costs of group living is the increased competition for limited resources in larger groups (Krause and Ruxton 2002). Living in families offers all the benefits of groups, while costs are shared with relatives. Animals may lose some direct fitness in family groups, but this is offset by the inclusive fitness gained from related group members (Hamilton 1964, Rodman 1981). Thus animal societies composed of one or more families are common across taxa, from eusocial insects (Crozier

and Pamilo 1996) to large herbivores (Archie et al. 2006) and cooperative carnivores (Van Horn et al. 2004).

Many waterbirds, such as geese *Anserini*, live in groups composed of families. This is most apparent in winter, when families gather to form foraging and migratory flocks (Elder and Elder 1949). Maintaining family bonds within flocks confers benefits since families are dominant over pairs and individuals. Family dominance rank increases with the number of members, for example in Canada geese *Branta canadensis* (Hanson 1953), snow geese *Anser caerulescens* (Gregoire and Ankney 1990), and barnacle geese *B. leucopsis* (Loonen et al. 1999). This allows larger families to occupy optimal foraging positions in flocks at lesser cost, and win access to better resources (Black et al. 1992). Both parents and offspring benefit from family bonds maintained across seasons, as juveniles gain access to more uninterrupted feeding in winter, and parents gain dominance rank (Black and Owen 1989). Parents of some species benefit in summer from the presence of nest-attending sub-adults (Fox and Stroud 1988); barnacle geese that are associated with their young through a winter, for example, are more likely to return with a brood the next year (Black and Owen 1989).

From the summer breeding season, through autumn migration, on the wintering grounds, and often up to and beyond the return spring migration, goose family bonds are affected by a number of factors. A combination of weather conditions and levels of summer predation on the breeding grounds plays an important role in the success of a pair hatching and fledging young (Summers 1986, Dhondt 1987, Summers and Underhill 1987, Bêty et al. 2004). The effect of summer predation linked to the abundance, or lack thereof, of lemmings and voles *Arvicolinae* has historically been significant enough in some species to be detectable at the population level in winter (Summers and Underhill 1987, Jongejans et al. 2015). Autumn migration takes a further toll on long-distance migrants, especially yearling birds (Owen and Black 1989, Francis et al. 1992). In spring, juvenile geese become independent of parents (Prevett and MacInnes 1980, Johnson and Raveling 1988, Black and Owen 1989), being chased off in some species (Black and Owen 1989, Poisbleau et al. 2008). Some juveniles may remain associated with parents through the spring migration and on the breeding grounds, where they help fend off predators and competitors (Ely 1979).

The development of family bonds in winter, however, is

not fully understood, and appears to be variable. Small species, such as Ross' geese *A. rossii* show weak family bonds in winter, perhaps because these confer no dominance benefit against much larger snow geese with which they form mixed flocks (Jónsson and Afton 2008). Similarly, cackling geese *B. hutchinsii* grazing in large, dense flocks show weak pair and family associations in winter which strengthen as they move to areas with fewer geese (Johnson and Raveling 1988). In contrast, larger taxa such as giant Canada geese *B. canadensis maxima* and Greenland white-fronted geese *A. albifrons flavirostris* show strong, extended family bonds (Warren et al. 1993). In general, small, grazing species tend to dissolve families in winter (Johnson and Raveling 1988), while large species that need to teach juveniles to locate and handle high quality foods tend to maintain them longer (Warren et al. 1993, Kruckenberg 2005).

The question of what space-use and movement decisions families make on the wintering grounds has also not been well explored, especially in the context of the number of accompanying juveniles. Some effect is expected, since the flight of dark-bellied brent geese *Branta b. bernicla* on autumn migration is affected by the presence of juveniles (Green and Alerstam 2000). Like other birds, geese can be differentially migratory with different population classes occupying different wintering areas (Cristol et al. 1999). For example, the white and blue morphs of snow geese show longitudinal separation during migration (Cooke et al. 1975). Further, more juveniles of Pacific black brent geese *B. b. nigricans* winter closer to the breeding grounds (Schamber et al. 2007). However, how accompanying juveniles influence where families winter is not well understood.

Though the maintenance of family bonds in geese is beneficial, separation of juveniles from parents is the norm, as among most animals. The mechanistic causes underlying family separation are not well studied. In wintering snow geese, family separation is held to be caused by a lack of coordination between members during chaotic take-offs in large flocks, and is thus seen as accidental (Prevett and MacInnes 1980). Separated birds attempt to locate their families, and similar behaviour is observed in Canada geese (Elder and Elder 1949). Investigating the role of flight events in such family size dynamics requires accurate, fine-scale knowledge of individual positions, and obtaining such data for whole families of highly mobile species has historically presented challenges.

Greater white-fronted geese *Anser albifrons albifrons*, hereafter white-fronted geese, are among the most abundant geese wintering in continental western Europe (Madsen et al. 1999), and offer an interesting opportunity to investigate the wintertime dynamics of goose families. Accounts suggest that in the Baltic-North Sea flyway population of white-fronted geese (Philippson 1972), larger families winter farther west than smaller ones. Further, these families are observed in smaller flocks, but this may be an artefact of smaller flocks observed farther west. Family bonds reportedly weaken within winters, contrary to the trend for

families of large taxa to stay together through the winter, and sometimes beyond (Warren et al. 1993, Kruckenberg 2005). 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 (Mooij 1991, Madsen et al. 1999, Fox et al. 2010) to test the hypotheses that: 1. Larger families winter to the west, further from the breeding grounds 2. Larger families winter in smaller flocks, 3. Families decrease in size over the winter, 4. Family size in winter shows effects carried over from summer predation and autumn migration, and 5. Family separation is predicted by the number and frequency of flights, and the time since take-off.

## Methods

### Observation data

Flocks of wintering white-fronted geese were censused on their wintering grounds in western Europe by direct counts using field scopes. Observers counted the total number of birds (flock size), and identified first winter juveniles (juveniles) among them from plumage characteristics (dataset A). Families were identified by characteristic behaviours, and were defined as pairs with at least one associated juvenile (successful families). The number of juveniles associated with a pair (family size), and the number of families of each size were recorded in a subset of flocks (dataset B). Censuses occurred at both fixed points and *ad hoc* sites. Observers further reported sightings of individual geese marked with numbered plastic neckbands, including their position and social status, online ([geese.org](http://geese.org), dataset C). These data included records of geese with no juveniles (unsuccessful families). To add context, we censused geese on the breeding grounds on Kolguyev Island (ca. 69°N, 49°E) in August 2016, approx. 1 month pre-migration, noting the size and social composition of all groups of geese seen (dataset D). Both successful and unsuccessful families were recorded.

Winter data were filtered to exclude records outside the spatial (2 - 10°E, 50 - 54°N) and temporal (autumn 2000 - spring 2017, breeding years 2000 - 2016) limits of our study. Records of unpaired neckbanded geese without juveniles were also removed. We obtained 7,149 flock counts from 75 observers at 123 geocoded sites (implemented using Kahle and Wickham 2013). Of these, 1,884 flocks counted by 17 observers at 65 sites held 51,037 successful families. A further 10,635 marked geese were observed at 8,416 sites. Observations of marked geese did not include details on habitat type, flock size and observer. We obtained 116 records of families from Kolguyev Island.

### Whole family tracking

We also collected positions of a total of 13 goose families (13 adult pairs, 38 juveniles) fitted with GPS transmitters (2013,  $n = 3$ , 2014,  $n = 4$ : e-obs GmbH, & 2016,  $n = 6$ : madebytheo) (dataset E). In addition, 2016 transmitters collected short 0.5

Hz bursts of position data from take-off events. Families fitted with GPS transmitters were tracked within the study site (2 - 10°E, 50 - 54°N) in winter (pre-April 01) for 78 days on average (range: 34 - 135). For all families, we identified the day and position where splits were first detected as a decrease in the number of birds within a 250m radius of a designated reference bird (see Fig.1). Before analysing the daily probability of splitting, we defined 'flights' as displacement events over 1km every day, and counted their number and daily frequency. For 2016 families, we identified the half-hour when they split, and identified take-offs as 0.5 Hz records with a ground speed above 2 m/s. We then calculated the time since the last take-off at each half-hour.

### Supplementary data

To relate observation data to migration timing, we collected daily records ( $n = 6,266$ ) of flock flight intensity pooled over 84 spring and 180 autumn (overlap = 72) Trektellen sites (*trektellen.org*, Van Turnhout et al. (2009)) in the Netherlands. We excluded flight activity records from sites close to night roosts, and records which did not match the direction of migration appropriate to the season. We used these data to find the beginning and end of each goose winter across the study period. We took the goose winter to begin with the first mass arrival of geese in autumn, and to end with the last mass departure in spring.

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

### 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. For this, we used datasets *B* and *C*. Using dataset *B*, we tested whether (2.a.) the number of juveniles in a family, and (2.b.) the total number of successful families were explained by flock size, number of days since the arrival of geese in autumn, and level of summer predation. We also tested using whether (2.c) the number of juveniles in families was different 1 month prior, and up to 2 months after autumn migration in 2016 using datasets *B*, *C* and *D* and . To add context, we searched for (3.) an effect on flock size (from dataset *A*) of distance from the breeding grounds, the number of days since arrival, and summer predation, and examined whether (4.) the proportion of juveniles in flocks (from dataset *A*)

was explained by the flock size, distance from the breeding grounds, number of days since arrival, and summer predation (see Tab. A1).

Further, using dataset *E* we examined whether (5.a.) the split probability (no-split or split, binomial distribution) each day was predicted by the days since arrival, the number of flights that day, the cumulative number of flights until that day, the distance travelled that day, the cumulative distance travelled until that day, and the family size on that day. For the 2016 families we tested (5.b.) the half-hourly split probability in relation to the time since the last take-off and the distance travelled in the previous half hour (see Tab. A2).

All analyses were performed in the *R* environment (R Core Team 2017) (see Tab.A1). We used a simple Poisson-error generalised linear model to test 2.c. We used *Poissonlme4* (Bates et al. 2015) generalised linear mixed models (GLMMs) to test 1, 2.a, and 3, and binomial-error GLMMs for 5.a and 5.b. In 2.b and 4, we used *mgcv* (Wood 2013) Poisson generalised additive mixed models (GAMMs) to include smooth functions of the flocksize (in 2.b) and the number of days since winter (in 4) as predictors. We included some covariates as random effects, and models were dependent on the datasets used for the effects tested in each (see Table 1). We assessed the importance of each predictor using Type II Wald  $\chi^2$  tests, and effect sizes using Cohen's  $f^2$ .

## Results

### Data filtering

Flock count data from 16 breeding years and subsequent winters yielded a mean 420 flock counts per year (range: 67 (2001) - 672 (2005)). Except one record in August 2016, Aprils ( $n = 24$ ) and Septembers ( $n = 76$ ) had the fewest records, with most observations from October - January (81%,  $n = 5,785$ ). Observations declined over February (11%) and March (6.8%). The mean flock size was 712 (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 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, 626 marked geese (range: 62 - 1143) were observed each year, accompanied by 0.59 juveniles (range: 0 - 11). Families on Kolguyev Island in 2016 had a mean of 2.26 juveniles (range: 0 - 6).

Families fitted with GPS transmitters travelled on average 11 km per day (range: 0 - 306). At the daily scale, families travelled a distance > 1km a mean of twice per day (range: 0 - 10), and on average 98 times (range: 63 - 367) over the tracking period. In 2016 families, take-offs occurred on average 5 times (range: 1 - 15) a day, and 470 times (range: 328 - 659) over the tracking period. 21 family splits occurred in the 13 families tracked and were not restricted to juveniles. Geese began to arrive between September 26 and October 30, and the last geese left between March 03 and April 01, resulting in a mean goose winter of 165 days. Lemming abundance from the breeding grounds transformed into a predation in-

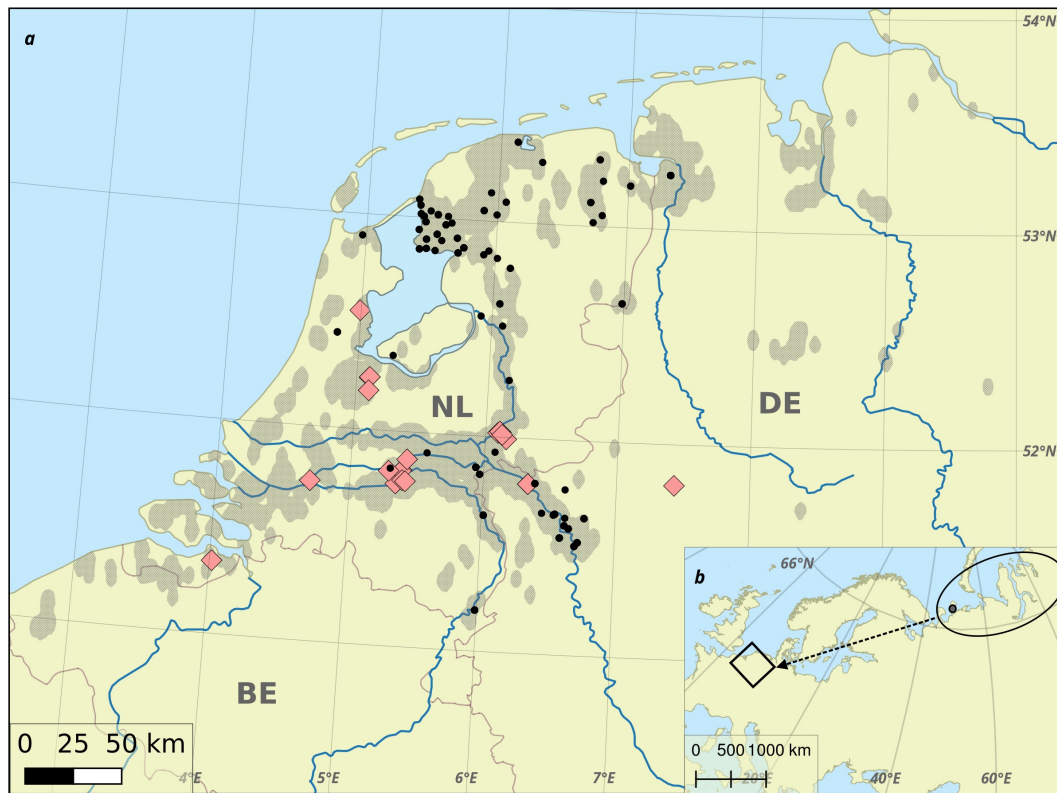


Fig. 1: *a*. Wintering grounds of greater white-fronted geese *Anser a. albifrons* in the Netherlands and northern Germany, with 65 sites (dots) where 51,037 successful families in 1,884 flocks were recorded. 21 splits (diamonds) were observed in 13 GPS tracked families. Shaded area bounds 10,635 observations of marked geese. Data were collected from 2000 - 2017. *b*. Breeding grounds (ellipse) with Kolguyev Island (dot) and general direction of migration (arrow) to wintering area (rectangle).

Dataset	Type	Records	Sites	Spatial extent (°)	Temporal extent (yr)
A	Flock counts	7,149	123	4.0 - 8.8 E, 51.1 - 53.4 N	2000 - 2017
B	Family counts	51,037	65	4.8 - 7.3 E, 51.1 - 53.4 N	2000 - 2017
C	Marked geese	10,635	8,416	2.7 - 9.7 E, 50.9 - 53.9 N	2000 - 2017
D	Family counts	116	26	49 E, 69 N	2016
E	Family GPS tracks	13 <sup>a</sup> ; 32,630 <sup>b</sup>	32,630	3.9 - 7.9 E, 51.3 - 54.3 N	2013 <sup>c</sup> , 2014 <sup>d</sup> , 2016 <sup>e</sup>

*a*: Number of families, *b*: Number of half hourly positions, *c*: 3 families, *d*: 4 families, *e*: 5 families

Tab. 1: Summary of filtered datasets.

dex 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 a family wintered in the first sixty days after arrival (dataset B: successful families in flocks, and C: families of marked geese, model 1,  $\chi^2 B = 1.135$ ,  $p B = 0.286$ ,  $\chi^2 C = 2.007$ ,  $p C = 0.157$ , see Fig.2). Later in the winter, larger families from dataset B (successful families in flocks) wintered farther west ( $\chi^2 = 4.194$ ,  $p = 0.041$ ), while dataset C (families of marked geese) did not reveal any

influence of juvenile number on wintering site ( $\chi^2 = 0.27$ ,  $p = 0.6033$ ). In all cases, geese were found farther west with increasing number of days since arrival ( $\chi^2 = 116.5641$ ,  $p < 0.001$ , see Fig.2).

### Family size in winter

The number of juveniles in a family (dataset B: successful families in flocks, model 2.a) decreased through the winter ( $\chi^2 = 74.166$ ,  $p < 0.001$ , see Fig.3), but was insensitive to flock size ( $\chi^2 = 0.270$ ,  $p = 0.6033$ ) and summer predation ( $\chi^2 = 0.337$ ,  $p = 0.562$ , see Fig.4). Family sizes of marked geese (dataset C: families of marked geese, model 2.a adapted) decreased

over time ( $\chi^2 = 19.936$ ,  $p < 0.001$ , see Fig.3), but showed an increase with the level of summer predation ( $\chi^2 = 12.935$ ,  $p < 0.001$ , see Fig.4). We tested whether the exclusion of unsuccessful pairs from family counts in flocks biased the data by similarly excluding such records from observations of marked geese. We confirmed this bias in sampling method by failing to find any effect of summer predation after excluding unsuccessful pairs from data C ( $\chi^2 = 0.1321$ ,  $p = 0.716$ , see Fig.4). The number of successful families in flocks increased with flock size ( $\chi^2 = 7162$ ,  $p < 0.001$ , see Fig.5), and the number of days since goose arrival in autumn ( $\chi^2 = 171.3$ ,  $p < 0.001$ , see Fig.6), but was unaffected by summer predation ( $\chi^2 = 0$ ,  $p = 0.98$ ). Further, there were more successful families in flocks farther from the breeding grounds ( $\chi^2 = 12.73$ ,  $p = 0.0004$ , see Fig.7).

### Family size and autumn migration

Families of geese observed approx. one month pre-migration on Kolguyev Island (dataset D) had significantly more juveniles than successful families (dataset B) in flocks (GLM,  $z = -4.285$ ,  $p < 0.001$ ) and families of marked geese (dataset C) (GLM,  $z = -14.511$ ,  $p < 0.001$ ) recorded in the first two months following the population's arrival on the wintering grounds.

### Flock size in winter

Flocks were significantly smaller farther from the breeding grounds ( $\chi^2 = 66599$ ,  $p < 0.001$ , see Fig.8), and grew slightly over the winter ( $\chi^2 = 4975$ ,  $p < 0.001$ ). Within flocks, juvenile proportions increased through the winter ( $\chi^2 = 19.43$ ,  $p = 0.001$ , see Fig.9), and decreased with increasing flock size ( $\chi^2 = 5.921$ ,  $p = 0.015$ ), but did not show any effect of distance from the breeding grounds ( $\chi^2 = 1.015$ ,  $p = 0.314$ ), or of summer predation ( $\chi^2 = 0.021$ ,  $p = 0.883$ ).

### Probability of family splits

The daily probability of families separating (see Fig.10) was significantly lower later in the winter ( $\chi^2 = 8.314$ ,  $p = 0.004$ ), and lower in larger families ( $\chi^2 = 11.41$ ,  $p < 0.001$ ). There was no effect of the daily number of flights ( $\chi^2 = 0.018$ ,  $p = 0.893$ ), nor the daily distance moved ( $\chi^2 = 2.99$ ,  $p = 0.083$ ). Split probability was higher in families that made cumulatively more flights over the period leading up to the split ( $\chi^2 = 143.23$ ,  $p < 0.001$ ), but decreased in families that moved a shorter cumulative distance over the days leading up to splits ( $\chi^2 = 182.63$ ,  $p < 0.001$ ). At the half-hour scale, split probability increased with time since the previous take-off ( $\chi^2 = 6.07$ ,  $p = 0.014$ ), but was not related to the distance travelled in the previous half hour ( $\chi^2 = 0.389$ ,  $p = 0.533$ ).

## Discussion

We studied how the size of white-fronted goose families is related to where, when and with how many flockmates they are

seen in the wintering grounds. We found support for the effect of the size of successful families on how far they migrate from the breeding grounds, but only later in winter. Further, the number of successful families in flocks was higher in the west. We also confirmed that family size decreases over the winter, but found that it is insensitive to flock size, and shows mixed responses to summer predation. Families are less likely to split later in winter, and with increasing family size. We found only indirect evidence that flights are responsible for family splits in winter. We showed that flocks are smaller farther from the breeding grounds, and found that they increase in size over the winter. Additionally, larger flocks have more successful families. The proportion of first year birds in flocks is lower in larger flocks, but increases as winter progresses.

Social status has been found in previous studies to influence geese's selection of wintering sites, with dominant social units displacing subordinate ones from optimal wintering locations (Vangilder and Smith 1985, Schamber et al. 2007). Our finding that larger families winter to the west of the study area is similar to one found by Jongejans et al. (2015). It fits the idea that dominant social units occupy optimal wintering sites if the spatial distribution of white-fronted goose families reflects habitat suitability. Geese can exploit most of the highly productive landscape, and have become tolerant of human disturbance and previously deterrent structures such as wind turbines (Madsen and Boertmann 2008, Fox and Madsen 2017). Any habitat selection is thus likely to be against conditions that impede foraging, such as snow and ice cover coupled with strong winds (Philippona 1966). Geese tolerate snow depths of ca. 15cm, conditions in excess of which are not noted in the Netherlands before midwinter (Philippona 1966), and have become rare within the study period. Western areas near the North Sea coast may be expected to benefit from its moderating effect on temperature, with fewer instances of conditions that geese would prefer to avoid. This could explain why adults with juveniles would choose to winter there after midwinter. The movement of geese to the south later in winter has been reported before, with peak counts of white-fronted geese in the Netherlands in November (Hornman et al. 2015), but only in January in Belgium (Devos and Kuijken 2010).

Juvenile independence has been reported across goose taxa (eg. Prevet and MacInnes 1980, Johnson and Raveling 1988, Black and Owen 1989) as being concurrent with the arrival of spring. Previous studies have shown that spring copulation in the breeding pair triggers juvenile departure (Fischer 1965, Prevet and MacInnes 1980). We find support for the hypothesis that the number of juveniles with adults decreases through the winter. The dissociation of juveniles from parents should result in some families losing their only offspring, thus reducing the number of successful families counted in flocks over time. Our finding that the number of families seen in flocks increases with time contradicts this expectation. An explanation would be that social status predicts variation in spring migration timing, as

it does the autumn arrival (Jongejans et al. 2015), but previous studies have not found such an effect (Madsen 2001, Bêty et al. 2004). Migration related juvenile mortality has previously been shown to be significant in long distance migrants that make few stop-overs. It has been shown that the probability of barnacle geese from Svalbard successfully reaching the wintering grounds in Scotland (3,500 km away) is dependent on a number of factors. Important among these is the higher competition for resources that results from an increased abundance of geese at summer sites. In deteriorating tundra habitats, juvenile geese are suggested to be unable to accumulate the reserves necessary for migration, and thus fail to complete the journey. Similar effects are suggested in lesser snow geese (Francis et al. 1992), and our result that the number of juveniles seen in families prior to migration is higher than in the first two months on the wintering grounds is in line with this prior work. As Arctic geese reach superabundance, reduced juvenile recruitment due to density dependent effects might help stabilise populations (Francis et al. 1992).

Summer predation, in turn driven by the cyclical abundance of Arctic rodents, is another mechanism by which the populations of Arctic-breeding birds, including those of geese, are suggested to be regulated prior to migration (Summers 1986, Summers and Underhill 1987, Blomqvist et al. 2002 etc.). Recent studies however indicate that since the 2000s, the breeding success of Baltic-North Sea flyway white-fronted geese no longer seems to be correlated with summer predation (Jongejans et al. 2015). This may explain our findings that the number of juveniles in successful families is not affected by summer predation intensity. Notably, the Pannonian population of white-fronted geese, which breeds on the Taimyr Peninsula, continues to show a correlation with predation, and by extension with rodent abundance. It has been suggested that more Baltic-North Sea white-fronted geese now breed on Kolguyev Island where they experience a constant level of predation, since the island lacks lemmings and associated phenomena (Kruckenberg et al. 2008). A large Arctic breeding range (45°E - 85°E, ca. 1,800km, Baltic-North Sea population) likely means that variation in predation pressure is lost due to year-wise averaging across sites. Future models could correct for this by accounting for predation at the summering site of each family observed in winter. Finally, lemming cycles in northern Russia appear to be faltering and this could also explain why cyclicity in goose breeding success has been reduced (Nolet et al. 2013). Angerbjörn et al. (2001) have shown that the cyclicity of lemming populations in Fennoscandia has been previously disrupted and re-established in the later-19th and 20th centuries. This lends support to the idea that northern Russian lemming cycles might be undergoing similar temporary disruption, following which they could be restored.

The increase in the number of juveniles seen with marked geese during years of increased predation could suggest that facing high predation pressure, geese either fledge large families or fail entirely. This could be the case if geese more effec-

tive at repelling predators also have higher fecundity. Body size may be an important driver. It has been observed that larger emperor geese *A. canagica* and white-fronted geese are better than smaller species at defending clutches from terrestrial predators (Thompson and Raveling 1987), and that larger black brent and lesser snow geese have higher fecundity than smaller ones (Davies et al. 1988, Sedinger et al. 1995), lending some support to the idea. Migration mortality might also be a significant factor in the decoupling of family size and summer predation.

Bird migration is strictly constrained by metabolic factors. Energy reserves and water balance especially determine how far and how fast a bird can fly, where it must stop-over, and thus by extension, where it terminates migration (Klaassen 1996). Our finding that flocks are smaller to the west of the wintering area (approx. 3 - 4°E) fit well in this context, and it is to be expected that fewer geese would choose to winter farther west when climatically suitable and similarly agricultural sites can be found to the east. Our results that larger flocks had a lower proportion of first-year birds must be considered in the context of the previous outcome that flocks are smaller in the west, where they have more successful families, and that larger families also winter to the west. This likely results in a higher juvenile proportion from small flocks, producing the trend we see. Consequently, one would expect a higher proportion of juveniles in westerly regions, as reported previously at the country scale (Jongejans et al. 2015), but we did not find that flock juvenile proportion varies over the study site. This is contrary to the expectation that goose families selecting for optimal sites drive variation in juvenile proportion over wintering areas (eg. Schamber et al. 2007). However, independent juveniles observed in wintering flocks (eg. Hanson 1953, Gregoire and Ankney 1990, Loonen et al. 1999) may dampen any variation.

The result that flock juvenile proportion rises non-linearly over the winter is in line with the previous finding that the number of successful families in flocks increases with time. However, this trend is probably due in larger part to white-fronted geese being age-differentially migratory, with pairs without young leaving the breeding grounds earlier than families and juveniles. An effect of age on spring departure timing has been unsuccessfully sought for in similar species (pink-footed geese Madsen 2001, snow geese, Bêty et al. 2004). In snow geese, the continued influx of juveniles to the breeding grounds for some weeks after the arrival of the breeding population does suggest that independent yearling geese follow a different migration schedule from adults (Prevett and MacInnes 1980). The question of age-differential migration would ideally be resolved with age-ratios of flocks in starting on spring migration. Since the population likely does not receive an influx of juveniles towards the end of winter, we must conclude that juveniles do indeed leave later than adults in spring.

Finally, our findings that daily split probability decreases with the distance travelled, and is reduced later in winter are fairly novel. They contradict the consensus that geese

are likelier to become independent towards spring (Prevett and MacInnes 1980, Johnson and Raveling 1988, Black and Owen 1989, Scheiber et al. 2013). Given that we did not differentiate between juvenile separation, juvenile death, and separation of the breeding pair in our analysis, this coupled with our low sample size of 13 families could have biased the results. Nonetheless, our results that the number of flights undertaken by a family were a good predictor of whether it would split are in accordance with the idea that flights are disruptive events that contribute to family separation (Prevett and MacInnes 1980). As we have found, one would expect that in such scenarios larger families are easier to locate and cohere to. The positive relation between the probability of splitting at each half hour and the time since the last take-off is best ascribed to a very low sample size of 6 families in which only 8 splits were recorded.

Our results add significantly to the extant knowledge of greater white-fronted geese. White-fronted goose families likely leverage their dominance to occupy optimal sites as winter progresses. Simultaneously, they undergo a steady reduction in the number of associated juveniles. Our findings show that young split off from families earlier than previously thought in this species in which families are reported to remain together through the winter, and sometimes longer than a year (Ely 1979, Warren et al. 1993, Kruckenberg 2005). Remaining on the wintering grounds later than other social classes, families and independent juveniles make this population differentially migratory by both age and social class. Previous authors (Madsen 2001, Bêty et al. 2004) have sought such an effect, and we present it as a novel finding for European geese. At the policy level, this provides support for the continued yearly cessation of wild goose hunting in January, especially since families and juveniles tend to cluster and are already over-represented in autumn hunting bags (Madsen 2010).

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## Appendix 1

### Model summaries

We provide tables (Tabs. A1, A2) summarising model structures used in the analysis. This table includes Cohen's  $f^2$  effect sizes that are based on the variance explained. Cohen's  $f^2$  was calculated for each model thus:

$$f^2 = \frac{R^2}{1 - R^2} \quad (1)$$

where  $R^2$  is the coefficient of determination. We calculated pseudo- $R^2$  for our models as the  $R^2$  of a linear model taking the model response of a null generalised mixed model as the response, and the generalised mixed model fit as the predictor. These values corresponded closely with pseudo- $R^2$  provided by the *mgcv* package for generalised additive models and were considered reliable. Cohen's  $f^2$  values of 0.02, 0.15, and 0.35 are respectively considered small, medium, and large.

### Additional figures

Model	Type	Dataset	Response	Fixed effects	Random effects	Records used	Cohen's $f^2$
1	GLMM	B	5	1, 5	8, 9, 10	20,160 <sup>a</sup> ; 14,018 <sup>b</sup>	3.22 <sup>a</sup> ; 4.74 <sup>b</sup>
1	GLMM	C	5	1, 5	8, 11	3,289 <sup>a</sup> ; 7,320 <sup>b</sup>	4.87 <sup>a</sup> ; 4.43 <sup>b</sup>
2.a	GLMM	B	1	3, 5, 7	8, 9, 10	34,179	0.09
2.a	GLMM	C	1	5, 7	8, 11	10,426	7.72 <sup>c</sup> ; 0.62 <sup>d</sup>
2.b	GAMM	A	2	3, 5, 7	8, 9, 10	837	9.36
3	GLMM	A	3	5, 6, 7	8, 9, 10	5,700	0.199
4	GAMM	A	4	5, 6, 7	8, 9, 10	5,659	0.52

**Effects:** 1: Number of juveniles per family, 2: Number of families, 3: Flock size, 4: Proportion of juveniles, 5: Days since autumn arrival, 6: Distance to breeding grounds, 7: Predation index, 8: Breeding year, 9 Observer, 10: Habitat type, 11: Goose identity

a:  $\leq 60$  days after arrival, b:  $\geq 60$  days after arrival, c: All families, d: Only successful families

Tab. A1: Models and inputs based on observation data.

Model	Type	Response	Fixed effects	Random effects	Records used	Effect size
5.a	GLMM	1	2, 3, 4, 5, 6, 7	9	1,009 <sup>a</sup>	0.08
5.b	GLMM	1	3, 8	9	21,271 <sup>b</sup>	0.0004

**Effects:** 1: Split occurrence, 2: Family size, 3: Days since autumn arrival, 4: Daily number of flights, 5: Cumulative number of previous flights, 6: Daily distance travelled, 7: Cumulative distance previously travelled, 8: Time since last take-off, 9: Family identity

a: Daily positions, b: Half-hourly positions

Tab. A2: Models and inputs based on GPS tracking data.