

Family size dynamics in wintering geese

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INTRODUCTION

Living in groups entails both costs and benefits for animals. Group members benefit from more social interactions, and from the increased sensory and physical capabilities of the group (Krause and Ruxton 2002). For instance, birds 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. Individuals 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* (???). 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 in long-distance migrants, especially on 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). However, 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 (???). 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

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to maintain them longer (???, 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 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 the number of juveniles in a family influences where it winters is not well understood.

Though the maintenance of family bonds in geese is beneficial, separation of juveniles from parents is the norm. 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 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 (Philippona 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 being 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 (???, 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, farther 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.

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Observation data

We censused flocks of wintering white-fronted geese 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, and the number of families of each size were recorded in a subset of censused 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 class, online (geese.org, dataset *C*). These data included records of single geese and pairs without accompanying juveniles (unsuccessful families).

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 ^a ; 32,630 ^b	32,630	3.9 - 7.9 E, 51.3 - 54.3 N	2013 ^c , 2014 ^d , 2016 ^e

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

Table 1: Summary of filtered datasets.

To estimate the effect of migration mortality, we censused geese on the breeding grounds on Kolguyev Island (ca. 69°N, 49°E) in August 2016, approximately 1 month prior to the autumn 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 neck-banded geese without juveniles were also removed. We obtained 7,149 flock counts from 75 observers at 123 geocoded sites (automated 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 goose families from Kolguyev Island.

Whole family tracking

We also collected half-hourly 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 displacements of greater than 1km, 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 (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

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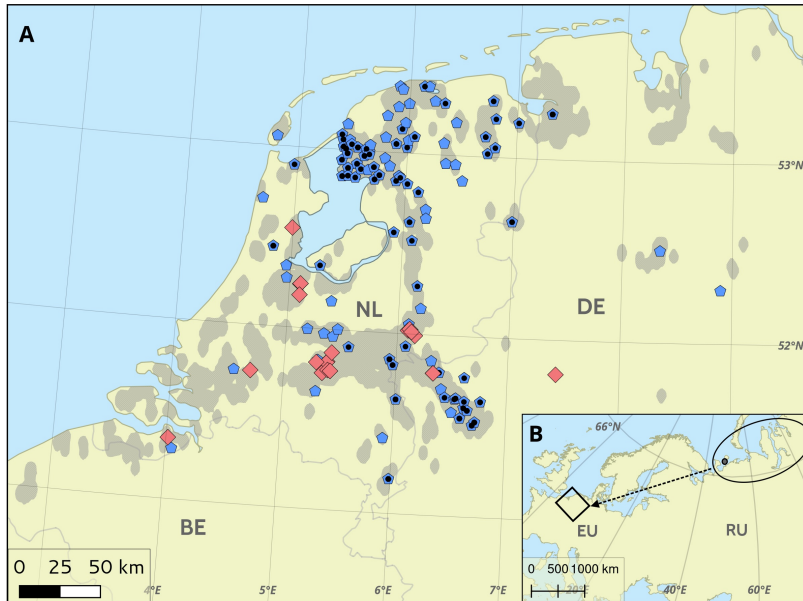


Figure 1: *a.* Wintering grounds of greater white-fronted geese *Anser a. albifrons* in the Netherlands and northern Germany, with 65 sites (dots) where 51,037 successful families in 1,884 flocks were recorded. 21 splits (diamonds) were observed in 13 GPS tracked families. Shaded area bounds 10,635 observations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

Island. The index takes into account the cyclical 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. Here, 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 was explained by a combination of flock size, the number of days since the arrival of geese in autumn, and the level of summer predation. We also tested 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*. To place these results in 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 Poisson *lme4* (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 (2.b) and binomial (4) 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 independent random effects, and effects included in models were dependent on their availability in the datasets used (see Tab. A1). We assessed the importance of each predictor using Type II Wald χ^2 tests, and effect sizes using Cohen's f^2 (see Appendix 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, spring (Aprils, $n = 24$) and early autumn (Septembers, $n = 76$) had the fewest records, with most observations from winter (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, marked geese were observed 626 times overall (range: 62 - 1143) were observed each year, accompanied by 0.59 juveniles (range: 0 - 11) (see Appendix 1, Figs. A1, A2). 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 each day (range: 0 - 306). At the

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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. Flock flight intensity reached the 90th percentile for autumns between September 26 and October 30, and was at the 90th percentile for the last time between March 03 and April 01. Representing the arrival and departure of geese, respectively, this resulted in a mean goose winter of 165 days. 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 a family wintered in the first sixty days after arrival (dataset *B*: successful families in flocks, and *C*: families of marked geese, model 1, χ^2 *B* = 1.135, *p* *B* = 0.286, χ^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 (χ^2 = 4.194, *p* = 0.041), while dataset *C* (families of marked geese) did not reveal any influence of juvenile number on wintering site (χ^2 = 0.27, *p* = 0.6033).

Family size in winter

The number of juveniles in a family (dataset *B*: successful families 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 Fig. A3). Family sizes of marked geese (dataset *C*: families of marked geese, model 2.a adapted) decreased over time (χ^2 = 19.936, *p* = < 0.001, see Fig. 3), but showed an increase with the level of summer predation (χ^2 = 12.935, *p* < 0.001, see Fig. A3). 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* (χ^2 = 0.1321, *p* = 0.716, see Fig. A3). The number of successful families in flocks increased with flock size (χ^2 = 7162, *p* < 0.001), and the number of days since goose arrival in autumn (χ^2 = 171.3, *p* < 0.001, see Fig. 4), 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 = 12.73, *p* = 0.0004, see Fig. 5).

Family size and autumn migration

Families of geese observed approximately 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 (χ^2 = 66599, *p* = < 0.001, see Fig. A5), and grew slightly over the winter (χ^2 = 4975, *p* < 0.001). Within flocks, juvenile proportions increased through the winter (χ^2 = 19.43, *p* = 0.001, see Fig. A4), and decreased with increasing flock size (χ^2 = 5.921, *p* = 0.015, see Fig. A6), but did not show any effect of distance from the breeding grounds (χ^2 = 1.015, *p* = 0.314), or of summer predation (χ^2 = 0.021, *p* = 0.883).

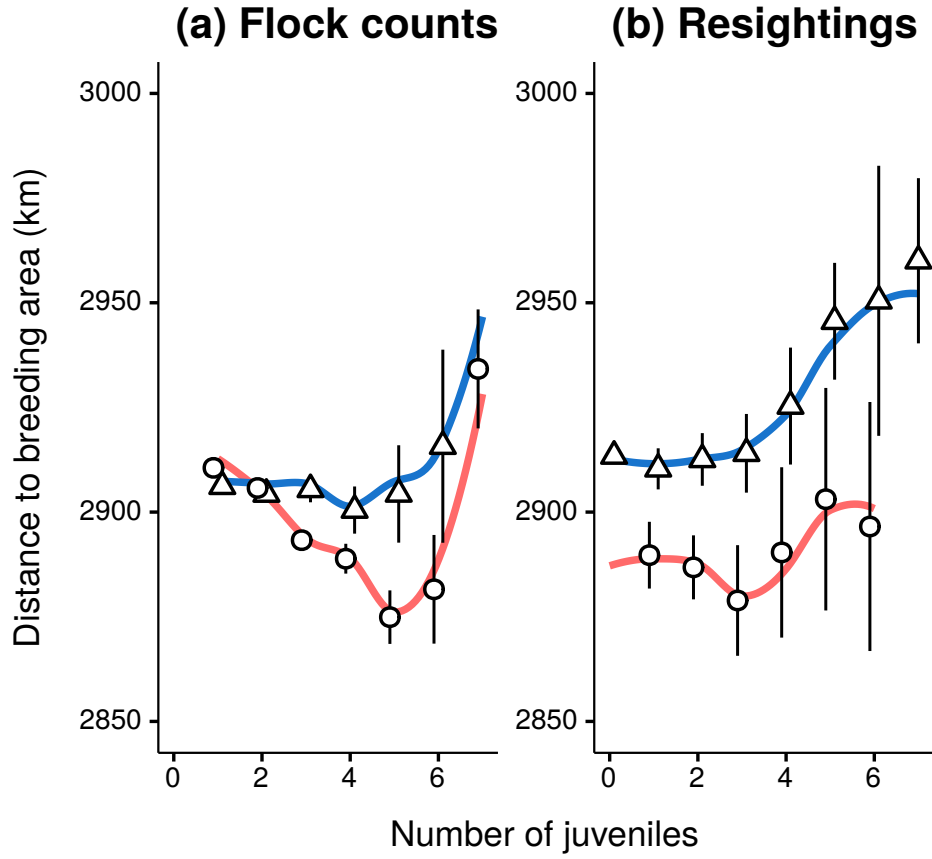


Figure 2: GLMM fits (lines), and mean distance of wintering sites from Kolguyev Island (symbols) per number of juveniles in a family. Data and fit for records from < 60 days after arrival are shown in red; data and fit for records > 60 days after arrival are in blue. Triangles & dotted lines represent data from marked geese (dataset *C*), circles and solid lines family counts (dataset *B*).

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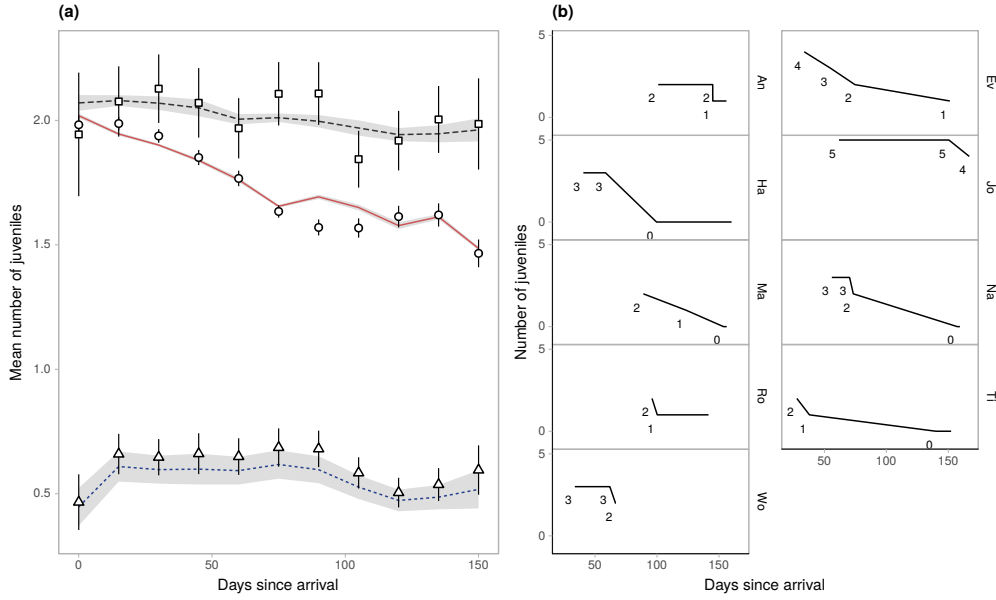


Figure 3: GLMM fits (lines) and mean number of juveniles per family on each day since goose autumn arrival pooled across years (dots). Successful families in flocks (dataset *B*) are shown in red, and families of marked geese (dataset *C*) are shown in blue. Arrows show development of size of 9 GPS tracked families that underwent splits.

Probability of family splits

The daily probability of families separating (see Fig. 6) 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 ($\chi^2 = 0.389$, $p = 0.533$).

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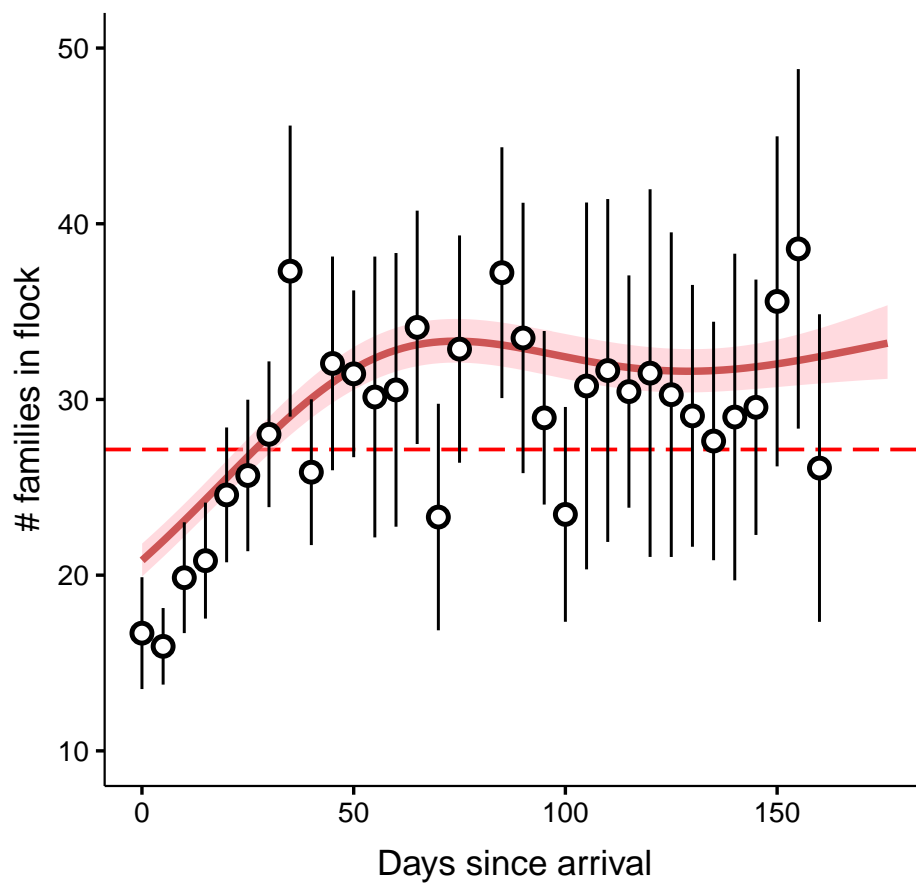


Figure 4: GAMM partial fit (line) and mean number of successful families in white-fronted goose flocks on each winter day, pooled across all winters (circles). 95% confidence interval is shaded grey.

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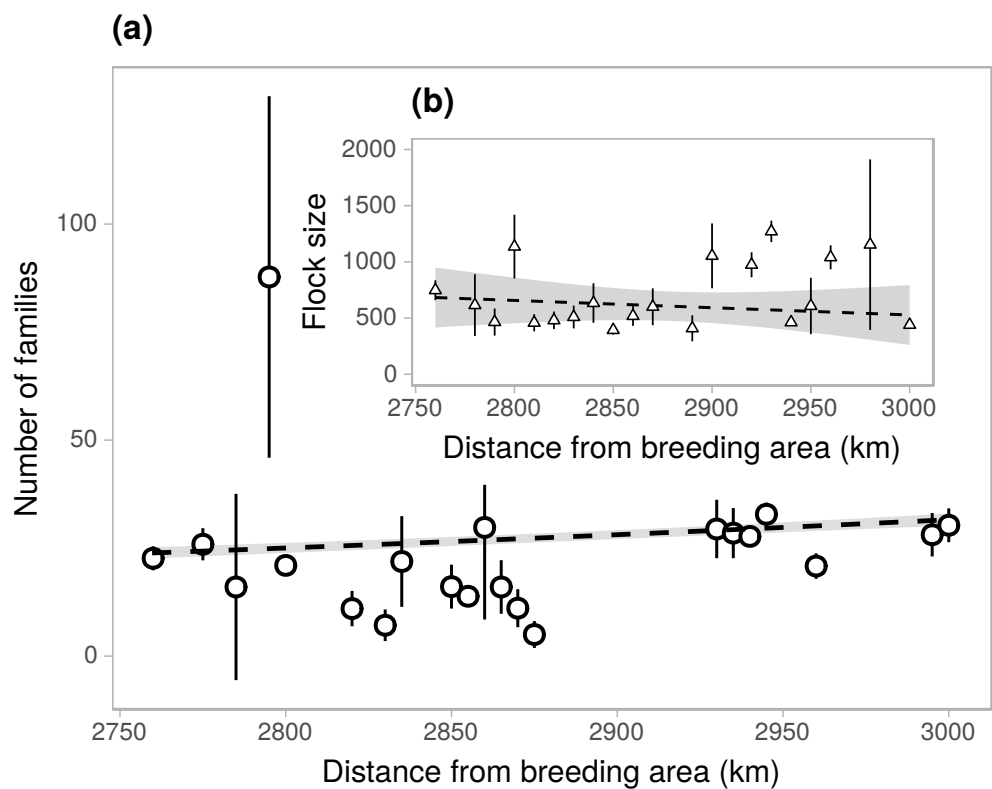


Figure 5: GAMM fit (line) and mean number of successful families in white-fronted goose flocks at each site (circles, $n = 49$) as a function of its distance from Kolguyev Island. 95% confidence interval is shaded grey.

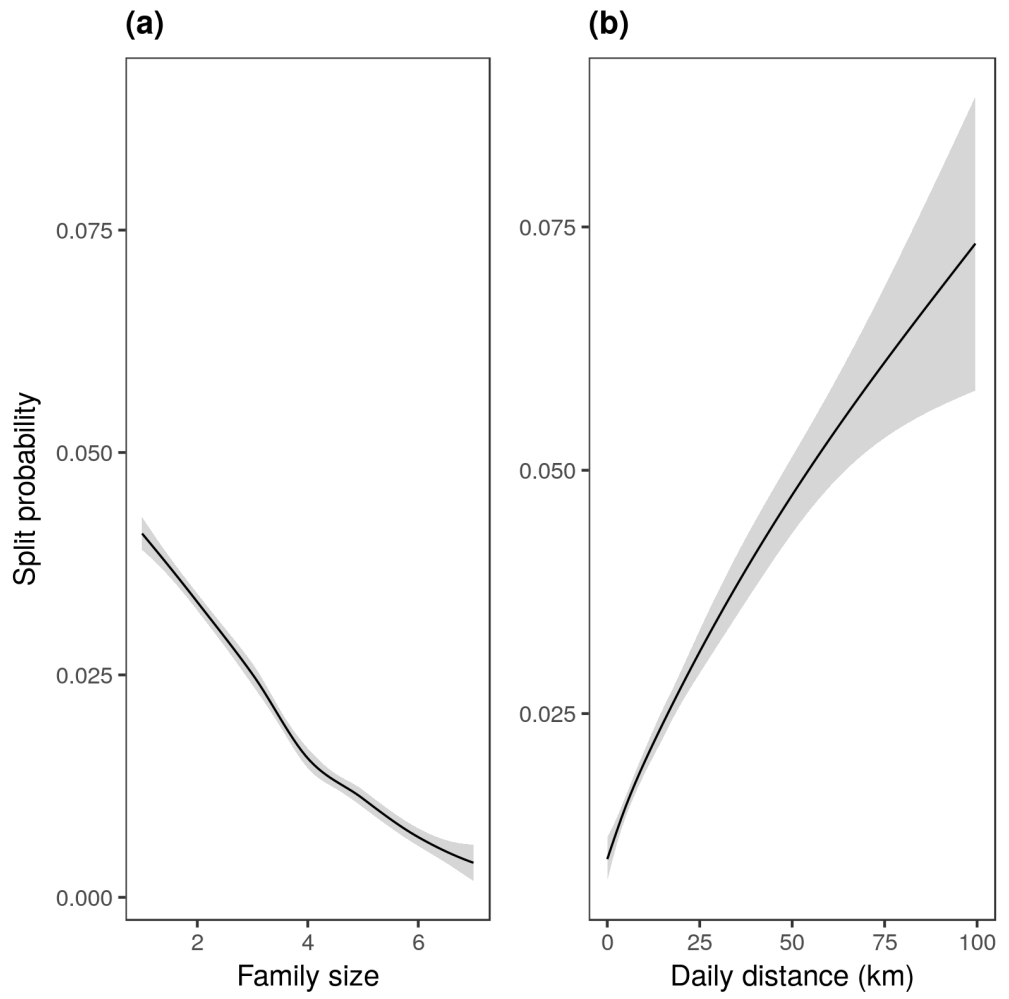


Figure 6: GAMM partial fits (lines) for (a) days since arrival, (b) cumulative number of flights over winter, (c) number of juveniles, and (d) cumulative number of displacements of more than 1000 km.

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