

# Family size dynamics in wintering geese

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## Abstract

Many populations are made up of social units with differences in size and dominance status; of these, the family and flock structure of geese *Anserini* is among the better known. How the association of juvenile geese with their parents in families influences the migration timing and space-use of families, as well as the events leading to juvenile independence are not well understood. We focus on family size dynamics of the Greater White-fronted Goose *Anser a. albifrons* on its wintering grounds in the Netherlands and Northern Germany, where we gathered 17 years of observation data on foraging flocks, and tracked 13 complete families with GPS transmitters. We explored how juveniles affect wintering site choice when in a family, and whether families use the wintering grounds differently from other social classes. We related the probability of a family splitting to the number and magnitude of flight events. We found that in winter, families with more juveniles winter farther west, where flocks are smaller. Family size, the population age-ratio, and the number of families in flocks is correlated with the number of days since first arrivals. Families that undertake longer daily flights in winter are more likely to split. We suggest that most juvenile White-fronted Geese separate from their parents over the winter, and that this species is differentially migratory by both age and social class in spring. These findings are important for the conservation and management of populations of large migratory species with complex age and social structure.

**Keywords** Greater White-fronted Goose *Anser albifrons*, family size, differential migration, foraging flocks, family separation, age-ratio

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## Introduction

Many animals live in groups, and animal groups often show age and social structure. Two common examples are adult individuals bonded to form a breeding pair, and pairs along with their offspring, which form a family (Krause and Ruxton 2002). Animals living in families gain the benefits of group-living, while the costs are shared with related individuals, increasing inclusive fitness (Hamilton 1964). Many species also spend part of the year in larger aggregations when smaller groups gather at resource sites. For example, many large waterfowl such as geese *Anserini* are associated in families over much of the year, and these families congregate with pairs and individuals to form large foraging and migratory flocks outside summer (Elder and Elder 1949). Larger flocks allow individuals to access enhanced group-living benefits such as increased anti-predator vigilance and information transfer (Roberts 1996; Krause and Ruxton 2002), while maintaining family bonds in larger aggregations is also beneficial as larger social units are dominant over small ones (Lamprecht 1986; Gregoire and Ankney 1990; Poisbleau et al. 2006). This allows large families of species such as Canada Geese *Branta canadensis* and Barnacle Geese *B. leucopsis* to occupy optimal foraging positions in wintertime feeding flocks, to distribute this cost over more individuals, and to win contests for access to resources (Hanson 1953; Black and Owen 1989; Black et al. 1992; Loonen et al. 1999).

Yet, variation between species in the maintenance of family bonds in wintering goose flocks is not well understood. Due to density dependent effects on the breeding grounds, many juveniles fail to complete migration, and reduced family sizes are observed immediately after arrival at wintering sites (Black and Owen 1989; Francis et al. 1992). Of the families that do make it, smaller-bodied geese such as Cackling Geese *B. hutchinsii* and Ross' Geese *Anser rossii* that are observed in large flocks seem to dissolve families in winter (Johnson and Raveling 1988; Jónsson and Afton 2008), whereas the large Greater White-fronted Goose *Anser albifrons* may maintain families through one or more winters (Ely 1979; Warren et al. 1993; Kruckenberg 2005). This suggests that a combination of competition and dominance in flocks may influence the persistence of goose family bonds (Johnson and Raveling 1988; Jónsson and Afton 2008). Family size decrease and family dissolution, i.e., the loss of some or all juveniles have been linked to the onset of spring (Prevett and MacInnes 1980; Johnson and Raveling 1988; Black and Owen 1989). In some cases, this results from the intentional chasing away of juveniles by the breeding pair (Black and Owen 1989; Poisbleau et al. 2008; Scheiber et al. 2013). Further, juvenile geese are over-represented in hunting bags, and this may contribute to the loss of juveniles from families where hunting is prevalent (Madsen et al. 2002; Madsen 2010; Guillemain et al. 2013; Clausen et al. 2017). However, accidental events, such as the separation of geese from their families during chaotic flock take-offs cannot be ruled out (Prevett and MacInnes 1980). Finally, juvenile geese are less adept flyers than adults (Green and Alerstam 2000) and may not be able to keep with their parents on long-distance flights, leading to separation (Black and Owen 1989; Francis et al. 1992).

Differences in movement capacity and dominance between population classes can lead to differential migration and winter distribution (see Cooke et al. 1975; Cristol et al. 1999). For example, the winter distribution of Pacific-wintering juvenile Brant Geese *B. bernicla nigricans* follows a latitudinal gradient, with more juveniles seen in northern sites closer to the Arctic breeding grounds. This is hypothesised to be a result of larger, more dominant families displacing smaller social units to sub-optimal southern sites (Schamber et al. 2007). In addition to this 'social dominance effect' (Gauthreaux Jr. 1982), the distribution of wintering geese is dependent on weather; geese avoid conditions that impede foraging such as deep snow (Philippona 1966; Lok et al. 1992). Understanding the distributions of different population classes in winter is important for spatio-temporally targeted management which can help sustain the remarkable recoveries of Western European geese, in which juvenile recruitment is still in long-term decline (Fox and Madsen 2017).

Russian Greater White-fronted Geese *A. a. albifrons*, which have distinct family structure, aggregate in wintering flocks across continental Western Europe (Madsen et al. 1999). This offers an interesting opportunity to investigate the development of wintertime goose family sizes and the concomitant spatio-temporal distributions of different population classes. We draw on long-term field observations of flocks, high frequency GPS tracks of entire families of white-fronted geese from their wintering grounds in the Netherlands and northern Germany, and the first counts of family sizes from the Russian breeding grounds to test the following observational hypotheses: (1) Autumn migration reduces family size, (2) Family size affects wintering site distance from the breeding grounds, (3) Larger families winter in small flocks, (4) Family size decreases over the winter, (5) Family separation events are related to flight frequency and duration.

## Methods

### Age ratios and family size

To estimate the effect of autumn migration on family size, we determined family sizes on the summer breeding grounds on Kolguyev Island, Russia (approx. 69°N, 49°E, Fig. 1B) in August 2016, approximately one month prior to the autumn migration. We directly observed groups of geese, counted the number of individuals, and identified adults and juveniles on the basis of strong and evident differences in size and plumage. We assessed family size, i.e., the number of juveniles associated with one or both parents, relying on characteristic behaviour and social interactions between the juveniles and adults. 116 such observations of families were collected (see Fig. 1b), forming dataset A, with a mean family size of 2.26 (range: 0 – 6). Kolguyev Island hosts a third of the breeding population of white-fronted geese, and we decided to use it as a proxy for the breeding grounds as a whole (Kruckenberg et al. 2008).

In autumn and winter, we and approx. 70 volunteer ornithologists observed 7,149 foraging flocks of wintering white-fronted geese at 123 sites across the study area (The Netherlands and northern Germany, see Fig. 1A) from autumn until spring (September through April), in 2000 – 2017. Most observations were made from October through January (81%), gradually declining through February (11%) and March (7%). April and September had far fewer observations, as most geese had not then arrived, or had already departed. We counted the number of adult and juvenile birds in each flock, using plumage which differs between age classes throughout winter and into spring as a guide (Koffijberg 2006). We calculated the flock's 'age ratio' as the number of juveniles by the flock size, i.e., the total number of individuals. This formed dataset B. Flocks had 712 individual geese on average (range: 2 – 20,000  $P_{95}$  = 2,500), and had a mean age-ratio of 0.18 (range: 0 – 0.87,  $P_{95}$  = 0.35). In a sub-sample of 1,884 flocks at a subset of 65 sites, we ( $n = 17$  of ca. 70 observers) assessed the family size, as on Kolguyev Island, using social interactions as a guide; 51,037 families were counted this way, and formed dataset C. The mean family size was 1.78 (range: 1 – 10).

Additionally, we collected observations of neck-banded white-fronted geese submitted by citizen scientists to the [www.geese.org](http://www.geese.org) portal during the study season in each year of the study period. On average, 626 sightings were reported each year (range: 62 – 1143). We determined family size after filtering out observations of single birds and birds known to be under two years of age; 10,635 observations of 4063 unique geese from 8,416 sites were obtained, forming dataset D (see Fig. 1A). In contrast with datasets B and C, this included observations of pairs (which have a family size of 0, i.e., no associated juveniles). Datasets B and C included details on the observer and habitat type, while dataset D did not, and also did not hold information on flock size. Each bird in dataset D was seen 2.62 times on average (range: 1 – 78), and had a family size of 0.59 (range: 0 – 11). Approximately 71% of observations reported no juveniles associated with the banded bird, and 59% of banded individuals were never observed with juveniles. Datasets are summarised in Table 1.

### Family tracking

We caught and fitted 13 complete goose families (26 adults, 38 juveniles) with GPS transmitters in the Netherlands between November and January in 2013 ( $n = 3$  families), 2014 ( $n = 4$ ), and 2016 ( $n = 6$ ). In 2013 and 2014 we used e-obs GmbH backpacks with teflon harness (weight 45g), and in 2016 made by the neck-band integrated devices (weight 35g). Transmitters reported positions at 30-minute intervals. These selectively large families were tracked within the study area (2 – 10°E, 50 – 54°N) during winter (before 1 April) for 34 – 135 days. The parent with the greater number of GPS fixes was chosen the reference bird for each family.

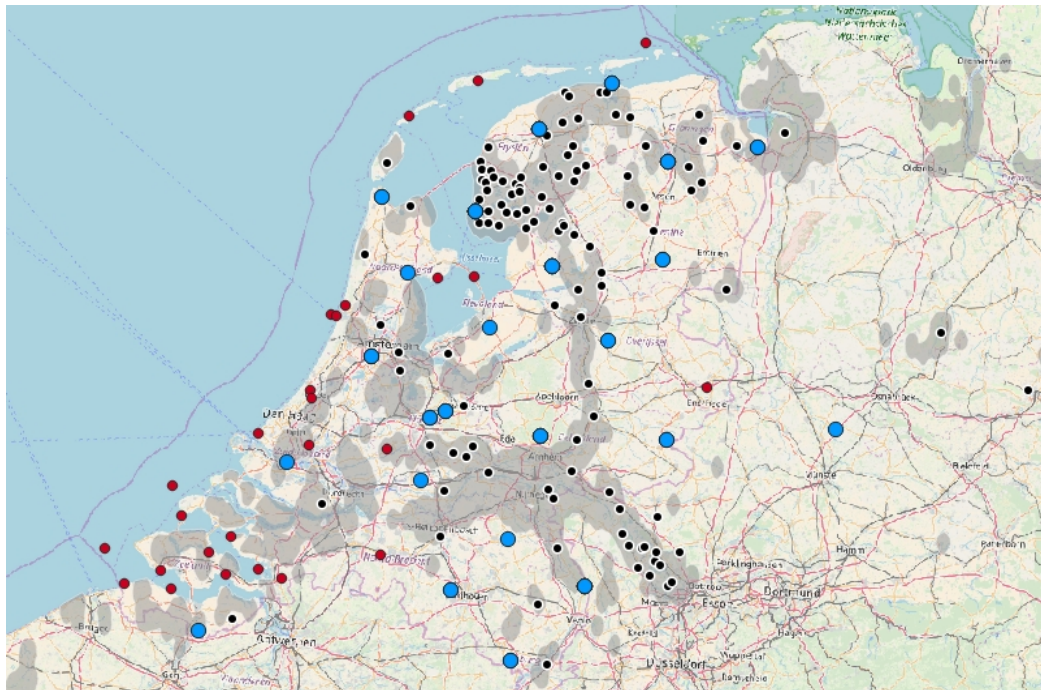
We identified the day and position where a decrease in the number of family members within 1000m of the reference bird relative to the previous day was recorded (Fig. 1a), and termed this a split. We determined the daily split probability by a binomial fit on the classification of each day as a success or failure (1 or 0) depending on whether a split occurred or not. To relate the probability of a split to goose flight, we summed the distance travelled by a family each day, and identified and counted the number of displacements with a speed  $\geq 1000\text{m}/30$  minutes. This constituted dataset E.

Families travelled on average 11 km each day over the tracking period (range: 0 – 306km). On average, they travelled a distance  $\geq 1000\text{m}$  in 30 minutes twice each day (range: 0 - 10). 21 split events were recorded, of which 19 were juveniles separating from the family.

## Context data

To relate our observations to the average timing of migration we extracted 90<sup>th</sup> percentile peaks of 6,266 daily observations of visible overhead migration in the Netherlands ([www.trektellen.nl](http://www.trektellen.nl); Van Turnhout et al. 2009) to determine yearly white-fronted goose arrival dates in autumn and departure dates in spring. Data were pooled over 84 spring and 180 autumn counting sites. We excluded observations from sites close to night roosts, and observations which did not match the direction of migration appropriate to the season; both in order to avoid bias by local movements. Geese arrived between 26 September and 30 October, and departed between 3 March to 1 April, resulting in an average wintering period of 165 days (range: 124 – 183). Roughly following Madsen et al. 2002, we refer to the period 0 – 90 days after arrival in each year (ending approximately 31<sup>st</sup> December) as autumn, and the period 91 – 180 days (ending approximately 31<sup>st</sup> March) as winter.

To test whether spatial patterns in this population could be explained by environmental effects, we gathered the daily minimum temperature from 51 meteorological stations in the Netherlands and northern Germany (Koninklijk Nederlands Meteorologisch Instituut, Netherlands,  $n = 50$ ; Deutscher Wetterdienst, Germany,  $n = 1$ ). Meteorological stations were on average 19km (range: 4 – 61km) from the positions at which flocks (datasets B, C) were observed, and 21km (range: 0.42 – 172) km from locations of at which neckbanded individuals (dataset D) were resighted.



## Analyses

We first tested (1) whether family size was different on the breeding grounds of Kolguyev Island one month prior to migration, and on the wintering grounds up to two months following the first arrivals of geese (hypothesis 1; dataset A). We then ran models to test (2) whether the distance from the breeding grounds at which a family was observed was explained by the family's size and the days since autumn arrivals (hypothesis 2; dataset C, D), and whether (3) family size was explained by flock size and the number of days since autumn arrival of geese (hypotheses 3, 4; dataset C, D). Model 3 also included distance from the breeding grounds as a predictor. Finally, we tested (4) whether the daily probability of a family splitting was explained by the days since goose arrivals, the daily distance travelled, the daily number of take-offs, and the daily family size (hypothesis 5; dataset E).

To place our observations in the wider context of migration to and from the summer range, and to account for plausible environmental factors affecting the winter distribution of geese, we examined (5) how flock size was related



to distance from the breeding grounds, days since autumn arrival, and temperature, and examined the trends over winter in the following flock attributes, using dataset B: (6) flock age-ratio, (7) proportion of independent juveniles, defined as the inverse of the sum of all family sizes in a flock (family-associated juveniles) divided by the total number of juveniles in the flock, and (8) proportion of family-associated birds, i.e., the sum of family sizes plus twice the number of families divided by the total flock size. Models are summarised in Table 2.

We used a one-way Kruskal-Wallis test with a Nemenyi post-hoc for model 1, a Poisson generalised linear mixed models (GLMMs) for models 2, 3, & 4, and binomial-error GLMMs for models 5, 6, 7, and 8. In each model, we included the breeding year, the observer identity, and the goose identity as independent random effects, if available in the relevant data (see Tab. 2). Analyses and data handling were performed in the R environment (R Core Team 2017), using the packages: *lme4* (Bates et al. 2015) and *move* (Kranstauber and Smolla 2016).

## Results

### Autumn migration and family size

Family sizes observed approximately one month prior to goose departure from the breeding area on Kolguyev Island on autumn migration (dataset A, mean  $\pm$  95% confidence interval =  $2.26 \pm 0.25$  juveniles) were significantly higher than family sizes from flock counts (dataset C, mean  $\pm$  95% confidence interval =  $1.72 \pm 0.0398$ ) and from neck-banded birds (dataset D, mean  $\pm$  95% confidence interval =  $0.46 \pm 0.124$ ) recorded in the first two months following initial goose arrivals on the wintering grounds, indicating the average loss of approximately 0.5 (dataset C) and 1.8 juveniles (dataset D) respectively along the migration route (model 1: Kruskal-Wallis rank sum test,  $\chi^2 = 469.11$ ,  $p < 0.001$ ; see Fig. 2). All pairwise differences were significant (Nemenyi post-hoc tests, D-B:  $\chi^2 = 17.515$ ,  $p < 0.001$ ; D-C:  $\chi^2 = 248.536$ ,  $p < 0.001$ ; B-C:  $\chi^2 = 436.709$ ,  $p < 0.001$ ).

### Family size and wintering site

We found that family size alone was not a good predictor of wintering site distance from Kolguyev Island in dataset C (model 2:  $z = 1.806$ ,  $p = 0.071$ ), and in dataset D (model 2:  $z = 0.516$ ,  $p = 0.606$ ). The season alone, did not appear to be a significant predictor of wintering distance in dataset C (model 2:  $z = -0.683$ ,  $p = 0.495$ ), but was a significant effect in dataset D (model 2:  $z = 3.391$ ,  $p < 0.01$ ). However the minimum daily temperature explained observed variation well in both dataset C (model 2:  $z = 3.698$ ,  $p < 0.01$ ), and dataset D (model 2:  $z = -9.346$ ,  $p < 0.01$ ), though the trends ran counter to each other. Interestingly, the interaction term of family size and season was found to influence wintering site distance only in winter, but not in autumn in dataset C (model 2:  $z = 4.009$ ,  $p < 0.01$ ; Fig. 3A), and not at all in dataset D (model 2:  $z = -1.851$ ,  $p = 0.064$ ; Fig. 3B). Thus, on average in dataset C, a family with 2 juveniles would be found 4 km further from the breeding grounds in winter as opposed to autumn, while a large family of 7 juveniles would be 26 km further away.

### Flock size, days since arrival, and family size

Flock size and days since arrival were good predictors of family size, and both had a negative effect in dataset C (model 3: flock size  $z = -4.288$ ,  $p < 0.001$ ; days since arrival  $z = -8.669$ ,  $p < 0.001$ ; see Fig. 4). On average, families in this data had 2 juveniles in the first 10 days after arrival, which decreased linearly to 1.49 juveniles per family 180 days after arrival, i.e., just prior to departure. Similarly, families in flocks of up to 100 geese had 1.91 juveniles, but only 1.67 juveniles in flocks of between 3900 – 4000 geese. Family size in dataset D also showed a negative effect of days since arrival (model 3:  $z = -5.018$ ,  $p < 0.001$ ; Fig. 4), with families of a mean 0.593 juveniles in the first ten days after arrival, and 0.497 juveniles 180 days after arrival.

### Flight frequency, distance, and split probability

We found a strong correlation between days since arrival and family size as fixed effects (Pearson's  $r = 0.728$ ). To avoid biasing our model by this multi-collinearity, we chose to omit days since arrival in the final model, reasoning that we had adequately characterised the development of family sizes over the course of winter. The daily split probability of families was significantly lower in larger families (model 4:  $z = -2.644$ ,  $p = 0.0082$ ); for example, the smallest families with 1 juvenile ( $p_{\text{split}} = 0.026$ ) were nearly 5 times more likely to split on average than a family with 5 juveniles ( $p_{\text{split}} = 0.00542$ ); see Fig. 5A. While the number of flights per day was not important ( $z = -0.355$ ,  $p =$

0.723), the distance travelled per day increased the likelihood of splitting ( $z = 2.12$ ,  $p = 0.027$ ); a family covering up to 80 km/day had a split probability ( $p_{\text{split}} = 0.092$ ) around 5.6 times that of a family travelling only 10 km/day ( $p_{\text{split}} = 0.016$ ); see Fig. 5B.

### Spatio-temporal trends in flocks

Our auxiliary analyses showed that goose flocks were larger at wintering sites which were closer to the breeding grounds (model 5:  $z = -100.61$ ,  $p < 0.001$ ), and larger later in the wintering period ( $z = 77.20$ ,  $p < 0.001$ ), and larger at lower minimum temperatures ( $z = -31.32$ ,  $p < 0.001$ ). Thus the average flock at the eastern margins of the study area, 2760 – 2790 km from breeding sites, comprised 543 individuals, and was 1.45 times larger than flocks furthest away (3040 – 3070 km) with 374 geese, while the average late winter flock (170 – 180 days after arrivals) held 458 geese and was thus 1.22 times the size of the average early autumn flock (0 – 10 days) of 376 geese. Flocks had on average 582 geese on days when the minimum temperature was between  $-1^{\circ}\text{C}$  and  $1^{\circ}\text{C}$ , growing to 680 birds when temperatures were  $-13^{\circ}\text{C}$  –  $-11^{\circ}\text{C}$ .

The proportion of geese associated in families was lower in larger flocks: flocks of 2900 – 3000 geese had a mean family-associated proportion of only 0.102, while flocks in the 1400 – 1500 range, and the much lower 0 – 100 range had family-associated proportions of 0.163 and 0.469, respectively (model 8:  $z = 13.117$ ,  $p < 0.001$ ; Fig. 6A). It increased through the winter, such that on average, a flock just after the beginning of arrivals (0 – 10 days) had a family-associated proportion of 0.264, whereas the same for a flock in late winter (170 – 180 days) was 0.367 ( $z = 2.124$ ,  $p = 0.034$ ; Fig. 6B). However, it was insensitive to the distance from the breeding grounds at which flocks were seen ( $z = -0.036$ ,  $p = 0.9713$ ).

The proportion of independent juveniles increased with flock size, such that the average small flock (0 – 100 geese) had a juvenile independence ratio of 0.037, while flocks of intermediate (1400 – 1500 geese) and large sizes (2900 – 3000 geese) had ratios of 0.143 and 0.232, respectively (model 7:  $z = -8.063$ ,  $p < 0.001$ ; Fig. 6C). This proportion rose through winter, with early autumn just after goose arrivals (0 – 10 days; mean value = 0.034) contrasting strongly with late winter, just prior to migration (160 – 170 days; mean value = 0.273) ( $z = -4.315$ ,  $p < 0.001$ ; Fig. 4A). We found that the proportion of independent juveniles was not affected by the distance of the wintering site from the breeding grounds ( $z = -1.267$ ,  $p = < 0.001$ ).

The overall age-ratio of flocks was not affected by the distance of the wintering site from the breeding grounds (model 6:  $z = -1.3460.965$ ,  $p = 0.178335$ ). However, it was significantly higher later in the wintering period ( $z = 1.2073.218$ ,  $p = 0.2270013$ ); for example, flocks seen between 0 – 10 days after arrival had an average age-ratio of 0.157, while flocks in late winter (170 – 180 days) had a mean age-ratio of 0.256 (see Fig. 6D). Larger flocks also had a significantly lower age-ratio, from a high of 0.224 in flocks 0 – 100 large, to a low of 0.135 in extremely large flocks of 2900 – 3000 geese ( $z = -4.227$ ,  $p < 0.001$ ).

## Discussion

We quantified family and flock sizes of white-fronted geese on the summer breeding grounds and in their wintering area, and connected hypotheses regarding different scales of social organisation to better spatio-temporal patterns in the context of migration and winter conditions. In support of our hypotheses, we found that autumn migration takes a significant toll on goose families. On the wintering grounds, families leverage their social dominance to occupy climatically milder sites further from the breeding grounds in winter, where goose flocks are also smaller. This leads to the observation that larger flocks have smaller families. Over the winter, families get smaller as juveniles become independent, but larger families, and more sedentary families are less likely to lose juveniles accidentally. The age-ratio of flocks increases significantly through the winter, with a marked increase in the proportion of independent juveniles, and also in the proportion of family-associated birds in flocks.

### Autumn migration and family size

Our result that families were significantly larger on Kolguyev Island shortly prior to migration than in the first two months on the wintering grounds confirms our first hypothesis, and is in line with previous findings of high autumn migration mortality in juvenile Arctic geese (Owen and Black 1989, Francis et al. 1992). As in these prior studies, we suspect that mortality in our population is mainly due to strong density-driven competition for resources prior to and

during autumn migration, that leads to juveniles being under-fueled for the journey and thus unsuccessful. The juvenile summertime survival of Arctic-breeding birds including geese has earlier been strongly linked to – among other factors such as snow cover – the cyclical abundance of, and concomitant levels of predation on Arctic rodents *Arvicolinae* in the ‘alternative prey hypothesis’ (see Summers and Underhill 1987). However, Kolguyev Island lacks lemmings and their associated cycle (Kruckenberg et al. 2008), making it unlikely that we sampled in a year with especially high or low predation. Moreover, most juveniles in August were sufficiently grown to avoid all but the largest predators (such as Arctic fox *Vulpes lagopus* and Glaucous gull *Larus hyperboreus*), and the adults of large goose species are effective at countering predation attempts (Thompson and Raveling 1987), leading us to conclude that reductions in family size likely occurred on autumn migration, rather than between our sampling and the start of migration.

### Temporal dynamics of family size

Family size continues to decrease after arrival on the wintering grounds pointing to a steady reduction in the number of juveniles associated in families, as expected in hypothesis 4. There is however high variation in the age of juvenile independence; some young geese may be found with parents even in their second or third winter (Ely 1979, Warren et al. 1993, Kruckenberg 2005). Hunting takes a toll on geese, and on waterfowl more generally, and there is good evidence from both our study area and across Europe that juveniles and families are over-represented in hunting ‘bags’ (Madsen 2010; Guillemain et al. 2013; Clausen et al. 2017). While this presents itself as a simple explanation for observed family size reductions, the simultaneously increasing proportion of independent juveniles in flocks suggests that though hunting may be a leading cause of juvenile autumn mortality (most hunting seasons end with the year, i.e., as winter begins), young geese likely become independent rather than being culled from the population. This is in line with the finding that juvenile mortality is unrelated to hunting in the similar pink-footed goose *A. brachyrhynchus* which also winters in the area (Madsen et al. 2002).

Juvenile independence from parents should result in a consequently steady reduction in the proportion of family-associated birds in flocks over the winter, but our findings went against this expectation. We suggest two possible explanations, first, that most pairs do not dissociate 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). Second, families with juveniles likely begin spring migration later than pairs without young, mirroring their differential autumn migration arrival, which is later than that of single and paired geese (Jongejans et al. 2015). This proposed differential migration is further supported by the strong temporal increases in proportions of juveniles in foraging flocks. We hypothesise that in spring, single and paired geese leave the wintering grounds for Arctic breeding and moulting sites, followed by families with young, with independent juveniles bringing up the rear. While this is contrary to previous studies on the spring migration of pink-footed and snow geese (Bêty et al. 2001), it is interestingly similar to the migration of juvenile snow geese, which appear to arrive somewhat later than adults on the spring breeding grounds (Prevett and MacInnes 1980).

Data from our 13 GPS-tracked goose families support the hypothesis that winter dissociation of first-year juveniles from their families is 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.

### Flocks, families, and wintering site choice

Our results showed that flock sizes are smaller further from the breeding grounds, which can be explained by the metabolic constraints that determine maximum flight distance and duration on migration (Klaassen 1996). Indeed though the centre of the white-fronted goose wintering area had already shifted south between the 1960s and 1980s (from the Dollard ~ 7.1°E 53°N to the Lower Rhine along the Dutch-German border ~ 6.7°E, 51°N, ~ 190 km; see Mooij 1982), autumn migration tracks in 2016 from Kolguyev Island (*unpublished data*) indicate no real increase in

the distance travelled by geese – which stop-over briefly in Poland – to either of these areas. This interpretation is supported by the fact that family sizes do not vary spatially in autumn (i.e., 0 – 90 days after arrival).

However in winter, once all geese have arrived and foraging sites are saturated, food becomes more limited and less accessible due to lower temperatures, which promote snow cover. It seems that large, socially dominant families then make further movements to occupy climatically milder sites which are more favourable as expected from previous work (Vangilder and Smith 1985, Schamber et al. 2007) and supports both our second hypothesis and the earlier suggestion of differential use of wintering sites according to social status (Jongejans et al. 2015). This is also in line with current knowledge of goose foraging preferences (Fox and Madsen 2017). Geese tolerate snow depths of about 15 cm before relocating to areas with better access to forage (Philippona 1966). Such conditions have become rare in the study area over the past decade, and usually do not occur before winter. This might explain why spatial differences in family size are only observed in winter, and not autumn. Limited habitat availability in the western 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.

### **Flock composition in space and time, and thoughts on management**

As would be expected then, larger families were associated with smaller flocks, confirming our third hypothesis. These family-size dependent spatial differences in wintering areas could lead to the finding that larger flocks have a lower proportion of juveniles overall (Jongejans et al. 2015). However, large flocks had a higher proportion of independent juveniles, and a correspondingly lower proportion of geese associated in families, suggesting that as juveniles separate from their parents, they gather in larger flocks to gain group-living benefits. However, contrary to expectations that both the above proportions would be well predicted by distance to the breeding grounds, no such trends were found. This could be linked to population movements in late winter, when geese travel to the eastern extent of our study area to prepare for the spring migration.

Based on the spatial and temporal patterns of wintering goose families and flocks in our study area, we suggest that management actions such as culling, deterrence shooting, or even passive measures such as designating foraging areas (Stroud et al. 2017) must consider that goose populations can be differentially migratory. It is crucial to distinguish between adult survival and juvenile recruitment for population control (Madsen 2010) and conservation. While our data suggest that large numbers of juveniles do reach independence each winter, we caution that the population's adaptability to changing environmental conditions could be affected by future actions that either inadvertently or deliberately target population classes (Clausen et al. 2017) that contribute to population recruitment and the maintenance of flyways through the cultural transmission of space use.

### **Conflict of interest**

The authors declare that they have no conflict of interest.

### **Ethical approval**

Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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Tables

Dataset name	Dataset description	Observations	Sites	Spatial extent
A	Family sizes on Kolguyev Island	116	26	49°E, 69°N
B	Flock census with age-ratio	7,149	123	4.0° - 8.8°E, 51.1° - 53.4°N
C	Family size counts in flocks	51,037	65	4.8° - 7.3°E, 51.1° - 53.4°N
D	Neck-banded individual resightings	10,635	8,416	2.7° - 9.7°E, 50.9° - 53.9°N
E	GPS tracking of entire families	32,630 <sup>a</sup> , 13 <sup>b</sup>	32,630	3.9° - 7.9°E, 51.3° - 54.3°N
<sup>a</sup> Half-hourly family positions, <sup>b</sup> Number of families tracked				

Tab. 1 Summary of field observations and satellite telemetry

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Model	Type	Dataset	Response	Fixed effects	Random effects	Records used
Main hypotheses						
1	Kruskall-Wallis + Nemenyi post-hoc	A, C, D	Family size	Dataset	–	
2	Poisson GLMM	C, D	Distance to breeding grounds	1, 3	7, 8 <sup>B</sup> , 9 <sup>B</sup> , 10 <sup>C</sup>	
3	Poisson GLMM	C, D	Family size	2, 3	7, 8 <sup>B</sup> , 9 <sup>B</sup> , 10 <sup>C</sup>	
4	Binomial GLMM	E	Daily split probability	3, 12, 13, 14	11	
Context trends						
5	Poisson GLMM	B	Flock size	3, 4, 5	7, 8, 9	
6	Binomial GLMM	B	Juvenile proportion of flock	2, 3, 4, 5	7, 8, 9	
7	Binomial GLMM	B	Proportion of independent juveniles	2, 3, 4, 5	7, 8, 9	
8	Binomial GLMM	B	Proportion of geese in families	2, 3, 4, 5	7, 8, 9	
Effects: 1: Number of juveniles per family, 2: Flock size, 3: Days since autumn arrival, 4: Minimum temperature, 5: Distance to breeding grounds, 6: Mean daily windspeed, 7: Breeding year, 8: Observer, 9: Zone, 10: Goose identity, 11: Family identity, 12: Daily distance travelled, 13: Daily number of take-offs, 14: Family size + present pair						
a: ≤ 60 days after arrival, b: ≥ 60 days after arrival						

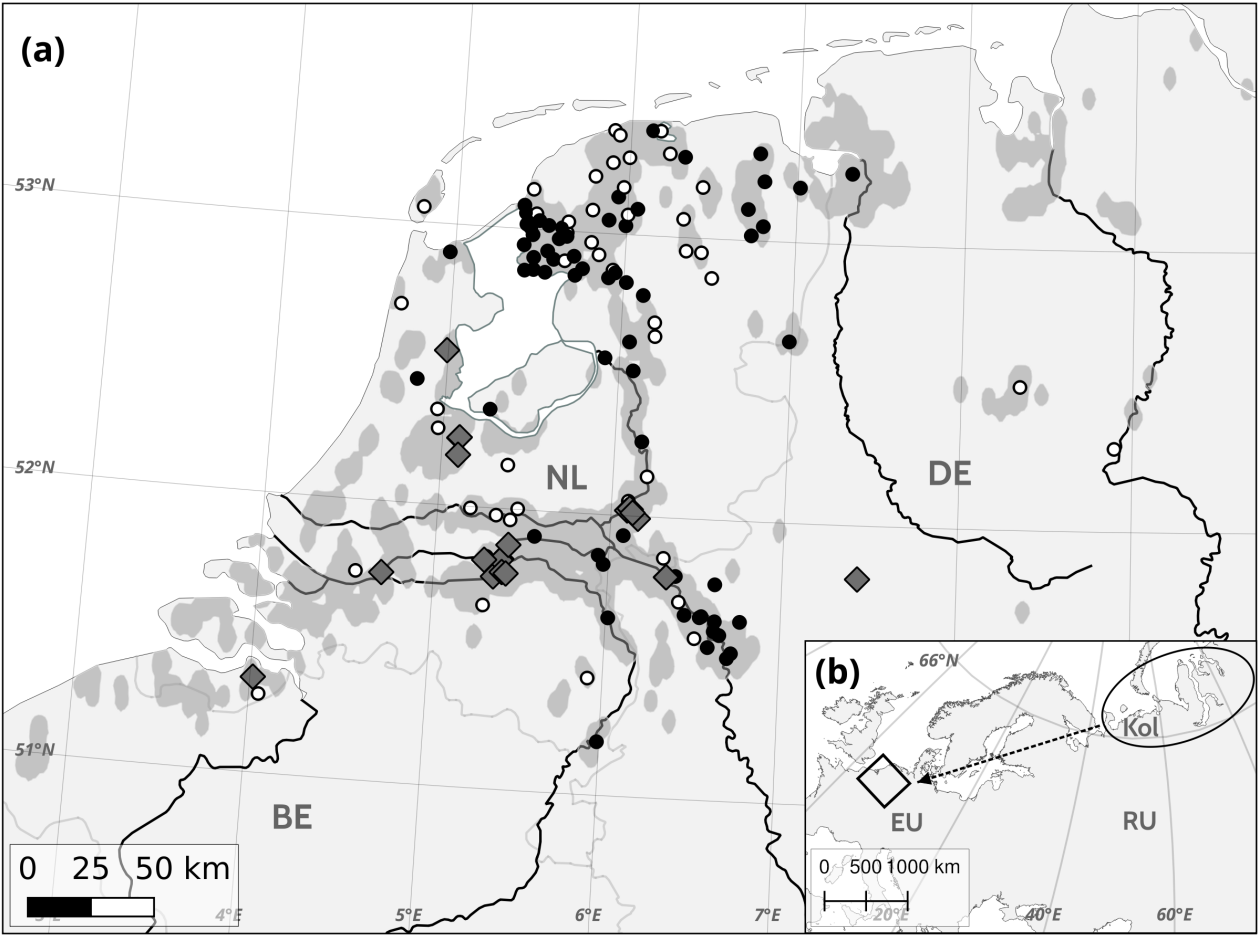
Tab. 2 Summary of analyses

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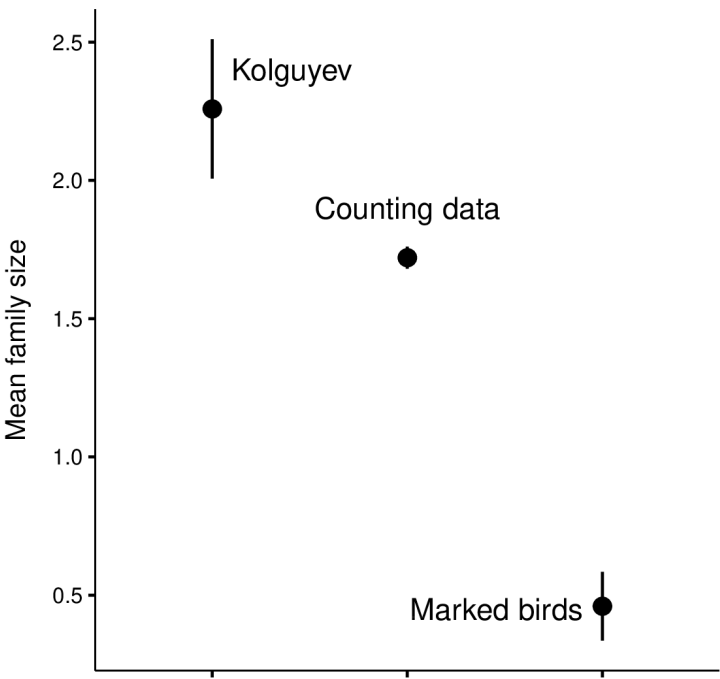
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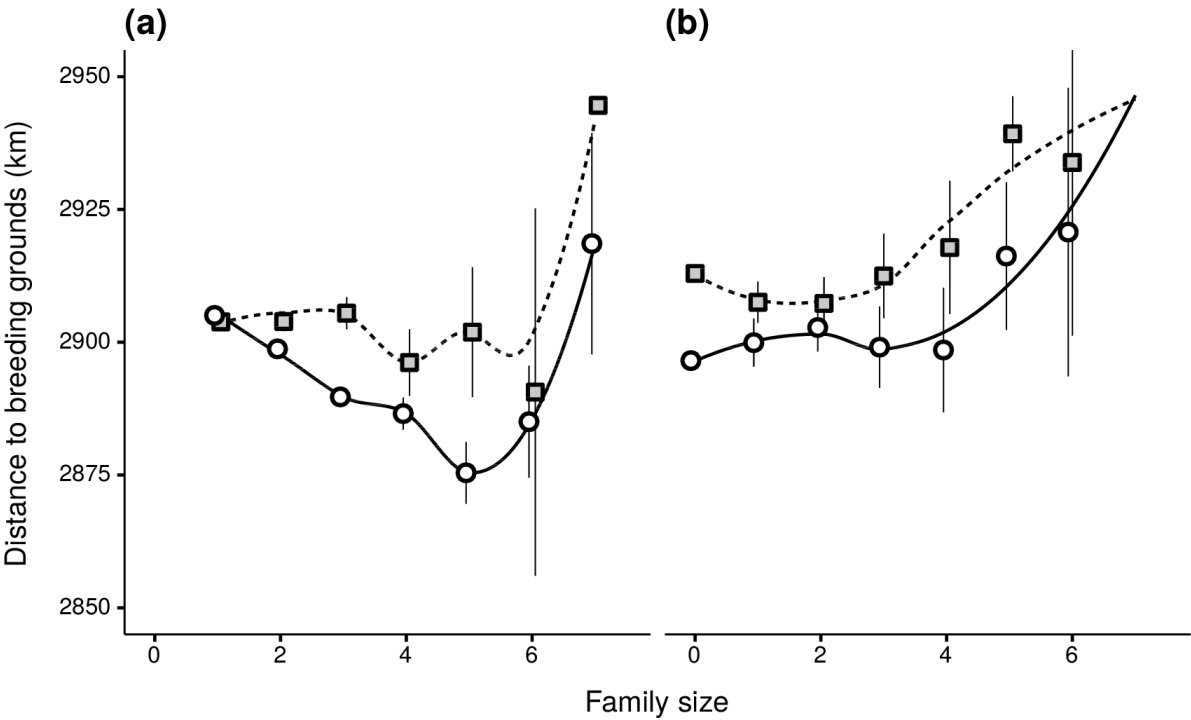




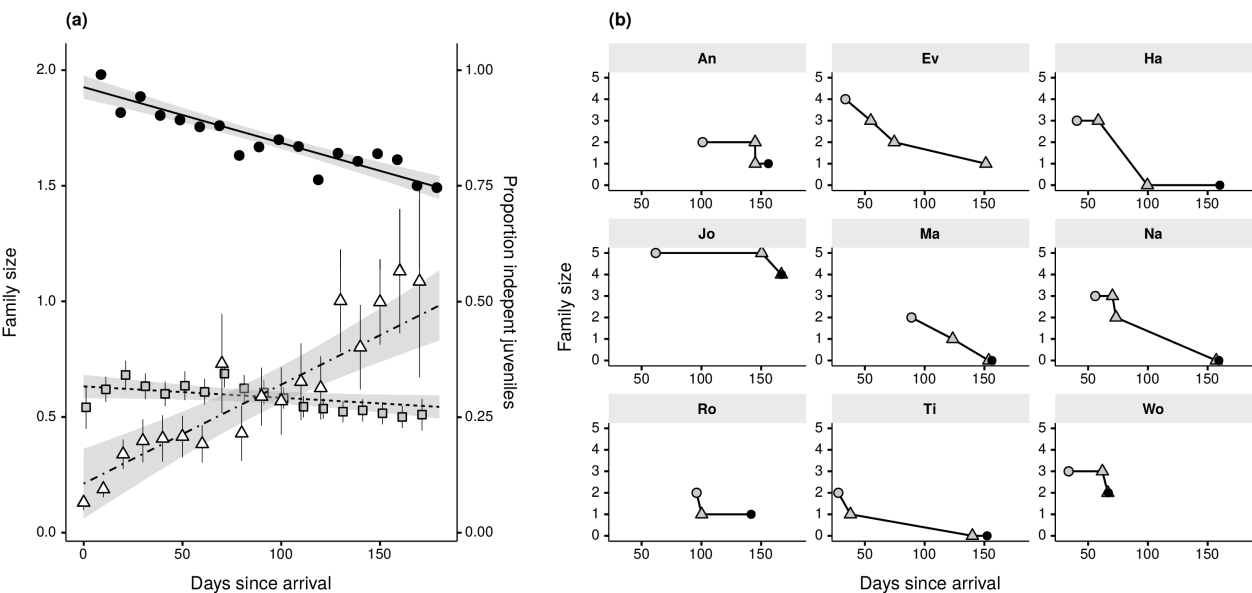
**Fig. 1 (a)** Wintering grounds of greater white-fronted geese *Anser a. albifrons* in the Netherlands and northern Germany, showing 123 sites ( filled and open circles) where the age-ratio of 7,149 flocks was determined (dataset B), and the subset of 65 sites (filled black circles) where 51,037 successful families were recorded in 1,884 flocks (dataset C). Shaded grey area bounds 10,635 neckband-resightings (dataset D). 21 split events (diamonds) were observed in 13 GPS tracked families (from dataset E). Observations correspond well with major rivers (marked as black lines). Data were collected from 2000 - 2017. **(b)** Breeding grounds (ellipse) in Russia with Kolguyev island (marked “Kol”) and general flyway (arrow) to wintering area (rectangle) (adapted from Madsen et al. 1999)



**Fig. 2 Mean family size on the core breeding grounds on Kolguyev Island in August 2016 (dataset A), one month prior to migration, and in the core wintering range in the Netherlands and Northern Germany from two different datasets (counting data = dataset C, marked birds = dataset D), observed within the first 60 days of goose autumn arrivals in 2016**

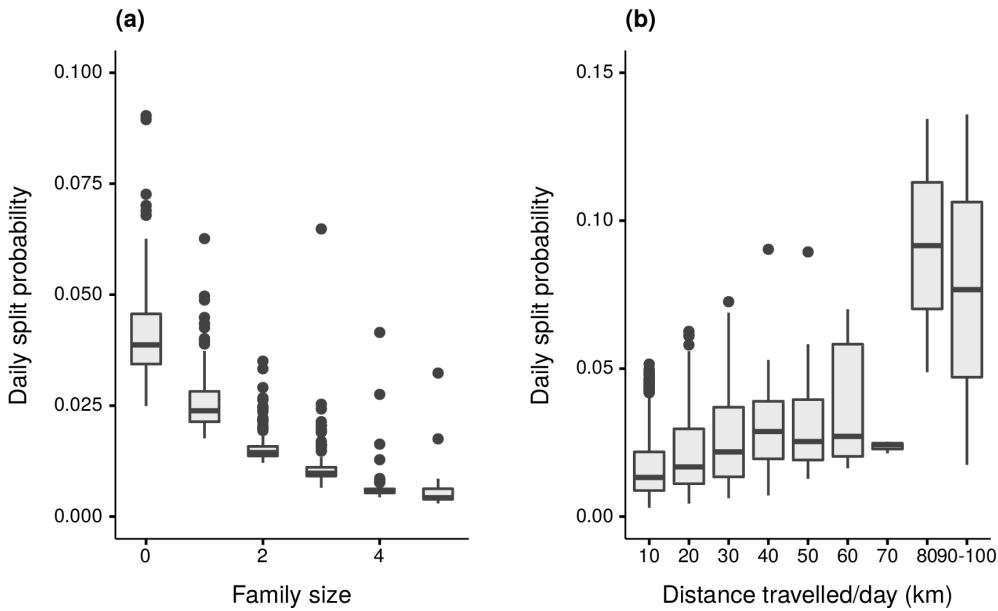


**Fig. 3 GLMM fits (lines), and mean distance of wintering sites from Kolguyev Island (symbols) per family size for (a) family size counts (dataset C) and (b) neckband-resightings (dataset D). Data and fit are separated by number of days since arrival to the wintering grounds: 0 – 90 days (solid lines, circles), 91 – 180 days (dashed line, squares). Vertical lineranges represent 95% confidence intervals at each data point**

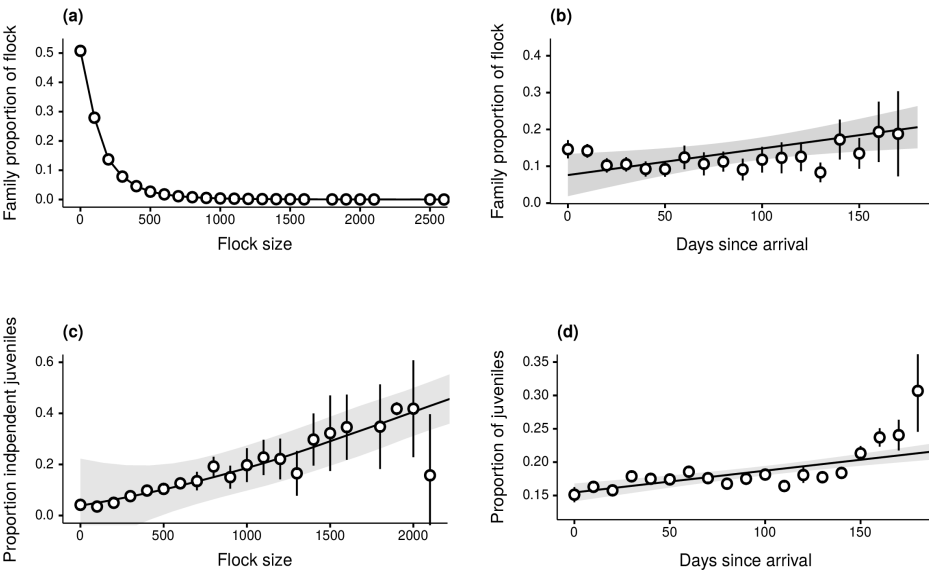


**Fig. 4 (a)** Mean family size every 10 days since goose autumn arrival (symbols) in flock counts (dataset C, circles), and neckband-resightings (dataset D, squares), and GLMM fits (lines) for model 3. Triangles and dot-dash line represents the mean proportion of first winter juvenile geese observed in flock counts (dataset C) which are not associated with parents, and GLMM fit for model 7. Vertical lineranges and shaded grey areas represent 95% confidence intervals at each point. **(b)** Family size development in 9 of 13 GPS tracked families (family identity in header bar). Symbols represent start of tracking (grey circle), juvenile separation (grey triangle), and exit of the family from the study area or end of winter (> 8°E or > 1 April). Symbols overlap when events are temporally proximate.





**Fig. 5** Boxplots of daily predicted split probability in relation to (a) family size, and (b) daily distance travelled



**Fig. 6** Mean values (symbols) and GLMM fits (lines) for (a) the proportion of flocks composed of family-associated geese at different flock sizes, and (b) the proportion of family-associated birds in a flock as a function of the days since autumn arrivals, (c) the proportion of flock juveniles not associated in a family as a function of flock size, and (d) the overall juvenile proportion of flocks as a function of days since autumn arrivals. Vertical lineranges and shaded grey areas show 95% confidence intervals in all cases