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

Acknowledgements

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 rossi* 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 whitefronts 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

We and ca. 70 volunteer ornithologists observed 7,149 foraging flocks of wintering whitefronts at 123 sites across the study area (see Fig. 1a) from autumn until spring (September through April), over 2000 – 2017. Most observations were conducted 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 determined flock age-ratios by counting 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). This formed dataset A. Flocks were 712 strong 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) assessed the family size, i.e., the number of juveniles associated with one or both parents, relying on characteristic behaviour and social interactions; 51,037 families were counted this way, and formed dataset B. The mean family size was 1.78 (range: 1 – 10).

Additionally, we collected observations of neck-banded whitefronts submitted by citizen scientists to the *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 C (see Fig. 1a). In contrast with datasets A and B, this included observations of pairs (which have a family size of 0, i.e., no associated juveniles). Datasets A and B included details on the observer and habitat type, while dataset C did not, and also did not hold information on flock size. Each bird in dataset C 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.

To estimate the effect of autumn migration on family size, we determined family sizes on the breeding grounds on Kolguyev Island, Russia (approx. 69°N, 49°E, Fig. 1B) in August 2016, approximately one month prior to the autumn migration. On Kolguyev Island, 116 observations of families and pairs were collected (see Fig. 1b), forming dataset D, with a mean family size of 2.26 (range: 0 – 6). Kolguyev Island hosts a third of the breeding population of whitefronts, we decided to use it as a proxy for the breeding grounds as a whole (Kruckenberg et al. 2008). 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 madebytheo neck-band integrated devices (weight 35g) in 2016. 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 ≥ 1000m/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 ≥ 1000m in 30 minutes twice each day (range: 0 - 10) and in total 98 times (range: 63 - 367) over the tracking period. 21 split events were recorded, of which 19 were juveniles separating from the family.

Context data

132 To relate our observations to the timing of migration we extracted 90th percentile peaks of 6,266 daily observations of
133 visible overhead migration in the Netherlands (*www.trektellen.nl*; Van Turnhout et al. 2009) to determine yearly
134 whitefront arrival dates in autumn and departure dates in spring. Data were pooled over 84 spring and 180 autumn
135 counting sites. We excluded observations from sites close to night roosts, and observations which did not match the
136 direction of migration appropriate to the season; both in order to avoid bias by local movements. Geese arrived
137 between 26 September and 30 October, and departed between 3 March to 1 April, resulting in an average wintering
138 period of 165 days (range: 124 – 183).

139 To test whether spatial patterns in this population could be explained by environmental effects, we gathered the
140 following daily weather data from 51 sites (Koninklijk Nederlands Meteorologisch Instituut, Netherlands; Deutscher
141 Wetterdienst, Germany): minimum temperature, total precipitation, and mean wind-speed. Sites were on average
142 20km (range: 4 – 83km) from the positions at which flocks were observed.

Analyses

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

152 To place our results in the wider context of migration and the distribution of geese, we examined (5) how flock size
153 was related to distance from the breeding grounds, days since autumn arrival, and temperature, and examined flock-
154 level trends in the following: (6) flock age-ratio, (7) proportion of independent juveniles (a 'juvenile-independence
155 ratio'), and (8) proportion of family-associated birds. Models are summarised in Table 2.

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

Results

Autumn migration and family size (hypothesis 1)

164 Family sizes observed approximately one month prior to goose departure from the breeding area on Kolguyev Island
165 on autumn migration (dataset D) were significantly different from family sizes from flock counts (dataset B) and
166 from neck-banded birds (dataset C) recorded in the first two months following initial goose arrivals on the wintering
167 grounds (model 1: Kruskal-Wallis rank sum test, $\chi^2 = 469.11$, $p < 0.001$). All pairwise differences were significant
168 (Nemenyi post-hoc tests, D-B: $\chi^2 = 17.515$, $p < 0.001$; D-C: $\chi^2 = 248.536$, $p < 0.001$; B-C: $\chi^2 = 436.709$, $p < 0.001$).

169 **Family size and wintering site (hypothesis 2)**

170 We found that family size was not a good predictor of wintering site distance from Kolguyev Island in dataset B
171 (model 2: $\chi^2 = 2.876$, p = 0.089), and in dataset C (model 2: $\chi^2 = 0.0029$, p = 0.957). As expected, days since autumn
172 arrival was a significant predictor in both datasets B and C, with a positive effect (model2, B: $\chi^2 = 116.631$, p < 0.001;
173 C: $\chi^2 = 77.619$, p < 0.001). However, the interaction between family size and days since arrival was a significant
174 predictor of wintering distance in dataset B and had a positive effect (model 2: $\chi^2 = 15.870$, p < 0.001); dataset C did
175 not show this effect ($\chi^2 = 0.251$, p = 0.616).

176 **Flock size, days since arrival, and family size (hypothesis 3 and 4)**

177 Flock size and days since arrival were good predictors of family size, and both had a negative effect in dataset B
178 (model 3: flock size z = -4.288, p < 0.001; days since arrival z = -8.669, p < 0.001), while family size in dataset C
179 also showed a negative effect of days since arrival (model 3: z = -5.018, p < 0.001).

180 **Flight frequency, distance, and split probability (hypothesis 5)**

181 We found a strong correlation between days since arrival and family size as fixed effects (Pearson's r = 0.728). To
182 avoid biasing our model by this multi-collinearity, we chose to omit days since arrival in the final model, reasoning
183 that we had adequately characterised the development of family sizes over the course of winter. Further, including a
184 predictor whose value increased monotonically in the data would imply non-independence of the response (split
185 probability) across days, i.e., that the probability of a family separating on any given day was affected by the
186 probability of splitting on prior days.

187 The daily split probability of families was significantly lower in larger families (model 4: z = -2.644 p = 0.0082).
188 While the number of flights per day was not important (z = -0.355, p = 0.723), the distance travelled each day
189 influenced the likelihood of splitting (z = 2.12, p = 0.027).

190 **Spatio-temporal trends in flocks**

191 Our auxiliary analyses showed that goose flocks were larger at wintering sites which were further from the breeding
192 grounds (model 5: z = 13.22, p < 0.001), and larger later in winter (z = 125.74, p < 0.001), and larger at lower
193 minimum temperatures (z = -68.11, p < 0.001).

194 The age-ratio of flocks was not affected by the distance of the wintering site from the breeding grounds (model 6: z =
195 -1.587, p = 0.113), nor by the days since arrival (z = 1.497, p = 0.134), but was significantly lower in larger flocks (z
196 = -5.902, p < 0.001).

197 Juvenile independence was higher in larger flocks (model 7: z = -6.933, p < 0.001), and later in winter (z = -4.184, p
198 < 0.001), but was not affected by the distance of the wintering site from the breeding grounds (z = -1.154, p = 0.248).

199 The proportion of geese associated in families was lower in larger flocks (model 8: z = -13.118, p < 0.001), and
200 higher in late winter (z = 2.124, p = 0.034), but was insensitive to the distance from the breeding grounds (z = -0.036,
201 p = 0.9713).

202 **Discussion**

203 **Conflict of interest**

204 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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210   **Tables**

211

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

[a]Half-hourly family positions, [b]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	B, C, D	Family size	Dataset	–	
2	LMM	B, C	Distance to breeding grounds	1, 3	7, 8[B], 9[B], 10[C]	
3	Poisson GLMM	B, C	Family size	2, 3	7, 8[B], 9[B], 10[C]	
4	Binomial GLMM	E	Daily split probability	3, 12, 13, 14	11	
			Context trends			
5	Poisson GLMM	A	Flock size	3, 4, 5	7, 8, 9	
6	Binomial GLMM	A	Juvenile proportion of flock	2, 3, 4, 5	7, 8, 9	
7	Binomial GLMM	A	Proportion of independent juveniles	2, 3, 4, 5	7, 8, 9	
8	Binomial GLMM	A	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
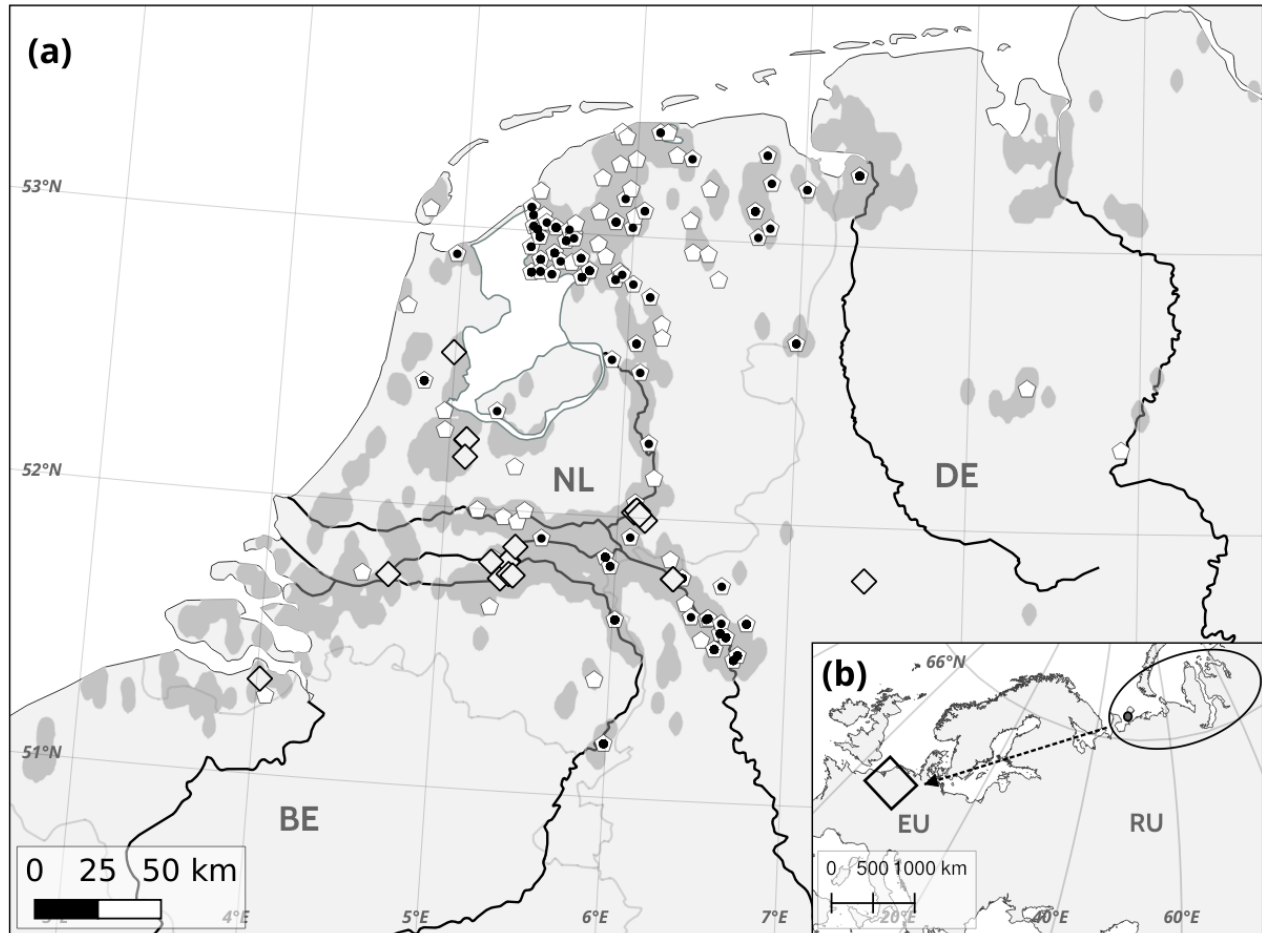
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217   **Figures**

Fig. 1 (a) Wintering grounds of greater white-fronted geese *Anser a. albifrons* in the Netherlands and northern Germany, showing 123 sites (pentagons) where the age-ratio of 7,149 flocks was determined, a subset of 65 sites (black dots) where 51,037 successful families were recorded in 1,884 flocks. Shaded area bounds 10,635 neckband-resightings. 21 split events (diamonds) were observed in 13 GPS tracked families. Observations correspond well with major rivers and marked as black lines. Data were collected from 2000 - 2017. **(b)** Breeding grounds (ellipse) in Russia with Kolguyev island (dot) and general flyway (arrow) to wintering area (rectangle) (adapted from Madsen et al. 1999)
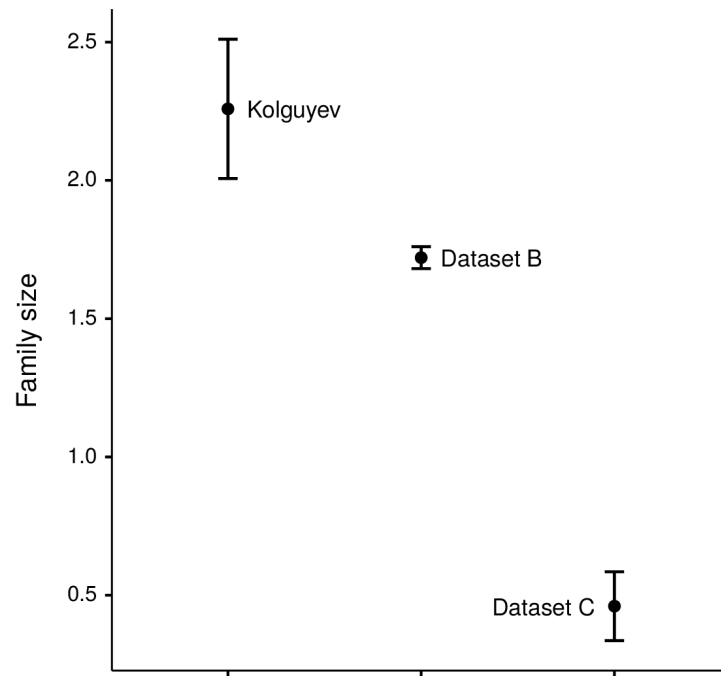
Fig. 2 Mean family size on the core breeding grounds on Kolguyev Island in August 2016, one month prior to migration, and in the core wintering range in the Netherlands and Northern Germany from two different datasets, observed within the first 60 days of goose autumn arrivals in 2016
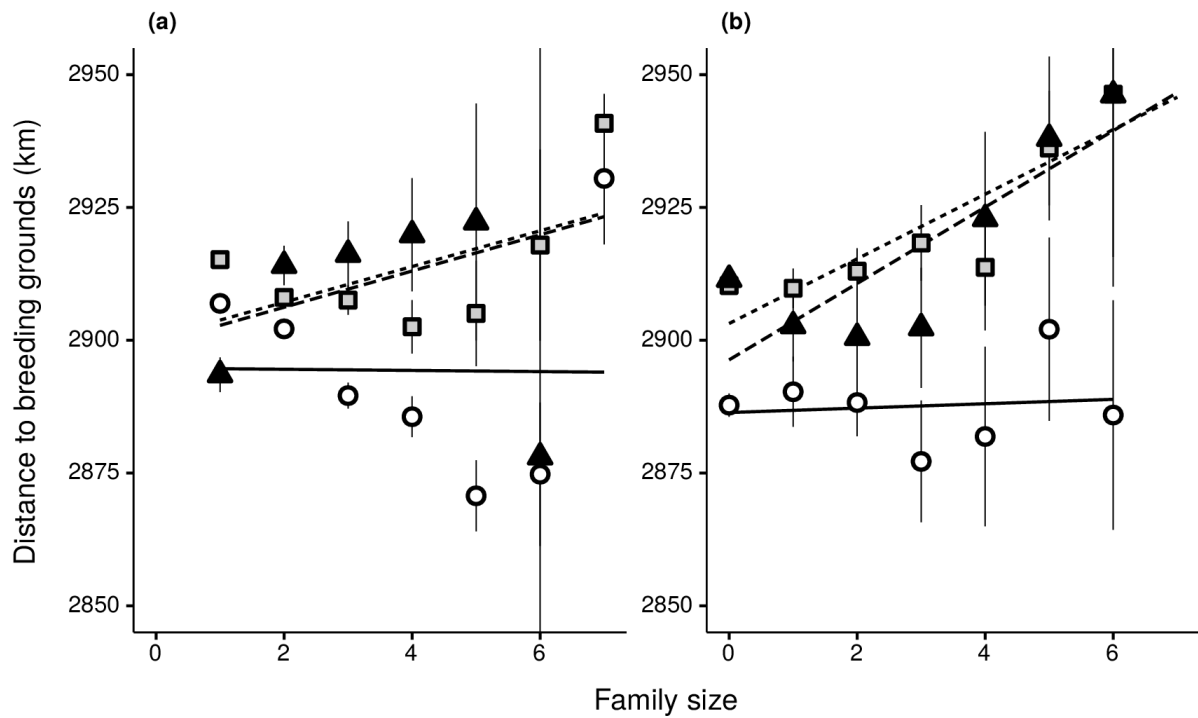
Fig. 3 LMM fits (lines), and mean distance of wintering sites from Kolguyev Island (symbols) per family size for **(a)** family size counts (dataset B) and **(b)** neckband-resightings (dataset C). Data and fit are separated by number of days since arrival to the wintering grounds: 0 – 60 days (solid lines, circles), 61 – 120 days (dashed line, triangles), and 121 – 180 days (dotted line, squares). Vertical lineranges represent 95% confidence intervals at each data point
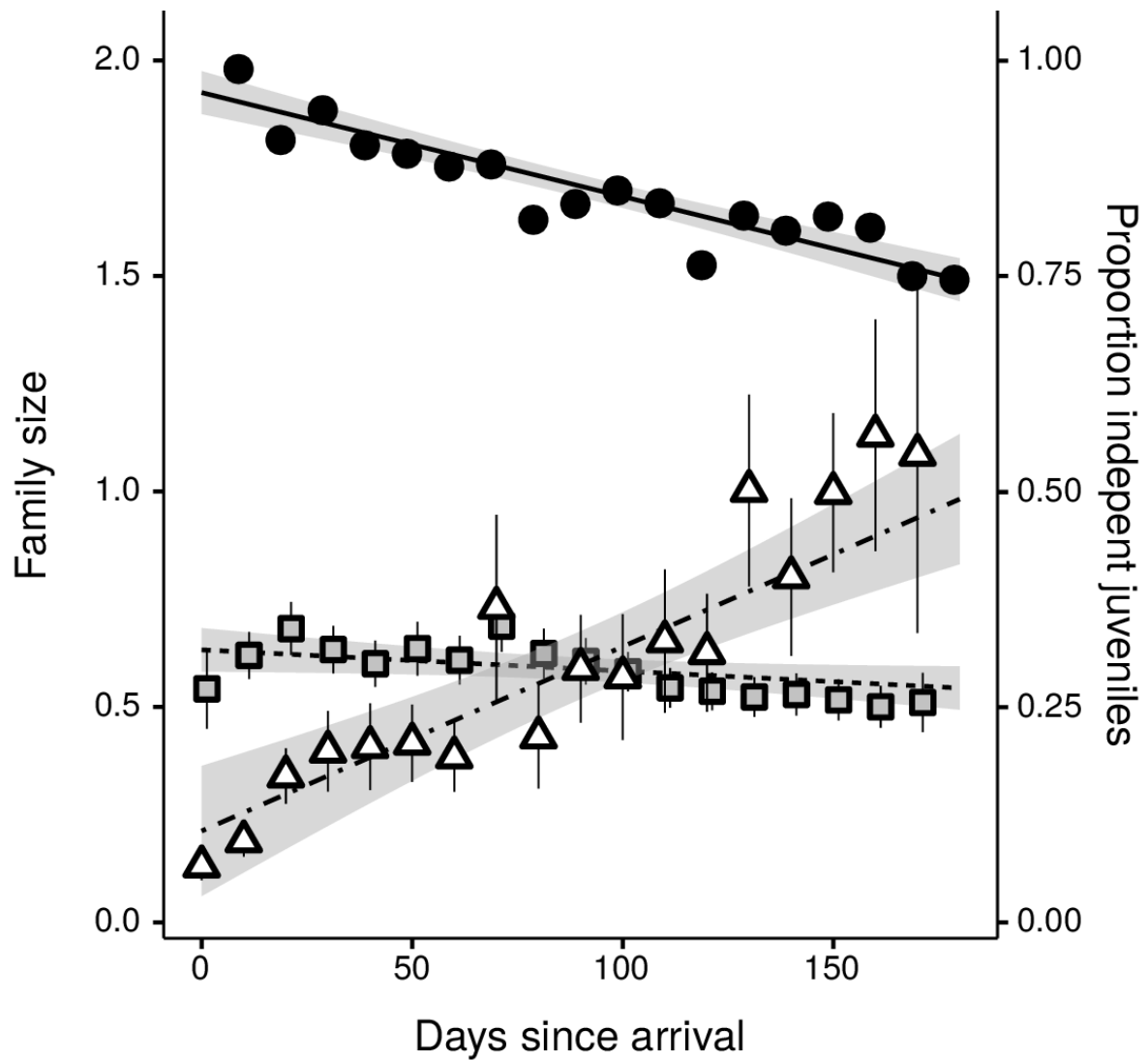
Fig. 4 Mean family size every 10 days since goose autumn arrival (symbols) in flock counts (dataset B, circles), and neckband-resightings (dataset C, squares), and GLMM fits (lines) for model 3. Triangles and dot-dash line represents the mean proportion of first winter juvenile geese observed in flock counts (dataset B) 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
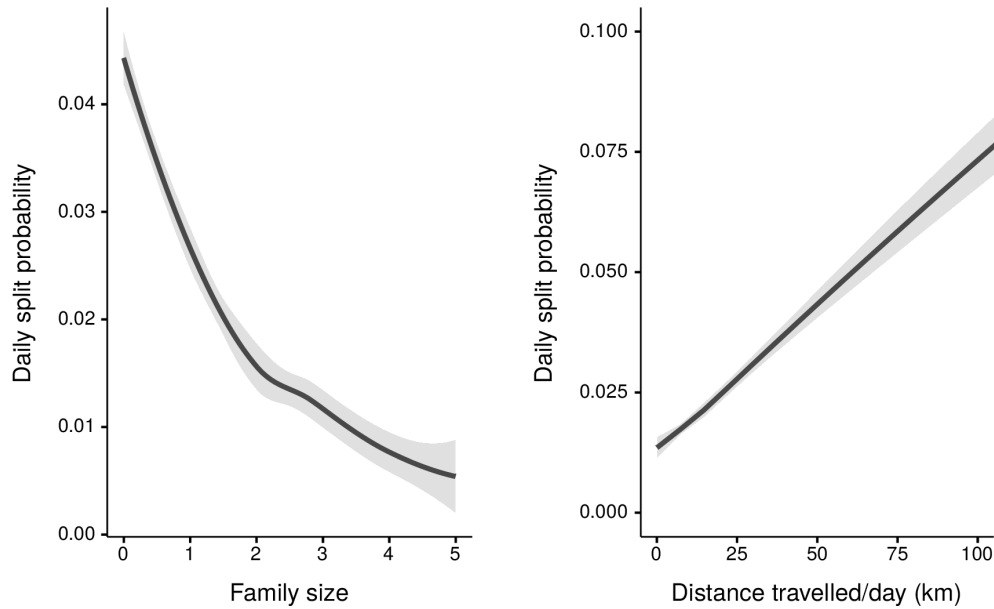
Fig. 5 GLMM fits (lines) for split probability in relation to **(a)** family size, and **(b)** daily distance travelled, with confidence intervals (shaded regions)
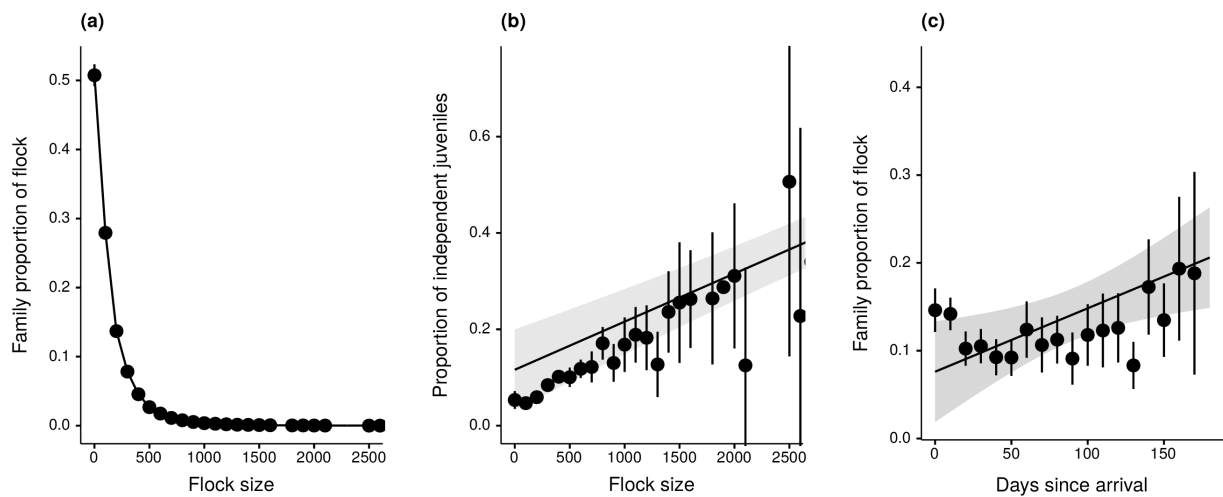

Fig. 6 Mean values (symbols) and GLMM fits (lines) for **(a)** the proportion of flocks composed of family-associated geese, and **(b)** the proportion of flock juveniles not associated in a family as a function of flock size. **(c)** The proportion of family-associated birds in a flock as a function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