Family size dynamics in wintering geese

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Abstract

11

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

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

Acknowledgements

Introduction

Many animals live in groups and animal groups often show age and social structure. Two common examples of social groups are adult individuals bonded to form a breeding pair and pairs, or occasionally single adults, along with their offspring, which form a family (Krause and Ruxton 2002). Animals living in families gain benefits from group-living such as decreased predation risk, while costs such as increased competition are shared with related individuals, increasing inclusive fitness (Hamilton 1964). Many species also spend part of the year in larger aggregations when family groups and independent individuals gather at resource sites (Krause and Ruxton 2002). For example, many large waterfowl such as geese *Anserini* are associated in families over much of the year and these families congregate with pairs without offspring and independent individuals to form often enormous foraging and migratory flocks after the breeding season and during winter. Large flocks allow individuals to access enhanced group-living benefits such as increased anti-predator vigilance and information transfer (Roberts 1996; Krause and Ruxton 2002). Maintaining family bonds in flocks is beneficial as larger social units have been found to be dominant over small ones (Lamprecht 1986; Gregoire and Ankney 1990; Poisbleau et al. 2006). This allows large families to occupy optimal foraging positions in wintertime feeding flocks (Black and Owen 1989; Black et al. 1992).

Due to density dependent effects on the breeding grounds and the fact that many juveniles fail to complete their first autumn migration, reduced family sizes were observed at arrival at wintering sites (Black and Owen 1989; Francis *et al.* 1992; Menu *et al.* 2005). Of the families that arrived to the wintering grounds with their juveniles, smaller-bodied goose species in large flocks seem to dissolve most families in winter (Johnson and Raveling 1988; Jónsson and Afton (Johnson and Raveling 1988; Jónsson and Afton 2008)2008), whereas larger goose species maintain many families through one or more winters (Ely 1979; Warren et al. 1993; Kruckenberg 2005). This suggests that a combination of juvenile condition, competition and dominance in flocks may influence the persistence of goose family bonds (Johnson and Raveling 1988; Jónsson and Afton (Johnson and Raveling 1988; Jónsson and Afton 2008)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), increased levels of being chased away by the parents (Black and Owen 1989; Poisbleau et al. 2008; Scheiber et al. 2013) and higher vulnerability to winter hunting (Madsen et al. 2002; Madsen 2010; Guillemain et al. 2013; Clausen et al. 2017). Still, accidental events, such as the separation of geese from their families during chaotic flock take-offs cannot be ruled out (Prevett and MacInnes 1980). Juvenile geese are also less adept flyers than adults (Green and Alerstam 2000) and may not be able to keep up with their parents leading to separation (Black and Owen 1989; Francis et al. 1992).

Differences in movement capacity and dominance between social classes can lead to differential migration and winter distributions (see Cooke et al. 1975; Cristol et al. 1999). For example, larger, more dominant goose families have displaced smaller social units to sub-optimal southern wintering sites, leading to a latitudinal gradient with more juveniles in northern sites closer to the Arctic breeding grounds (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 and ice (Philippona 1966; Lok *et al.* 1992). Understanding the distribution of different population classes in winter and how it is affected by climatic conditions 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).

Greater White-fronted Geese *Anser a. albifrons*, hereafter white-fronted geese, have distinct family structure and aggregate in large wintering flocks across wide ranges of continental Western Europe (Madsen *et al.* 1999). In addition, it is a species that is hunted, or subject to derogation shooting, during autumn migration and during winter in nearly all countries of its wintering range (except Belgium and the UK; Stroud et al. 2017). Hence, they provide an interesting opportunity to investigate the development of wintering goose family sizes during autumn migration and the concomitant spatio-temporal distributions of different population classes during winter.

We draw on a first set of family size counts from the Russian breeding grounds, long-term age ratio counts in wintering flocks and high frequency GPS tracks of families of white-fronted geese from their wintering grounds in the Netherlands and northern Germany to test the following hypotheses: (1) Family size is reduced after autumn

89 migration, (2) Family size affects wintering site distance from the breeding grounds, (3) Larger families winter in
90 small flocks, (4) Family size decreases over the winter, (5) Family separation events are related to flight frequency.

91

Methods

Age ratios and family size

94 To estimate the effect of autumn migration on family size, we determined family sizes on the summer breeding
95 grounds on Kolguyev Island, Russia (approx. 69°N, 49°E, Fig. 1B) in August 2016, approximately one month prior
96 to the autumn migration. We directly observed groups of geese, counted the number of individuals, and identified
97 adults and juveniles on the basis of strong and evident differences in size and plumage. We assessed family size, i.e.,
98 the number of juveniles associated with one or both parents, relying on characteristic behaviour and social
99 interactions between the juveniles and adults. 116 such observations of families were collected (see Fig. 1b), forming
100 dataset A, with a mean family size of 2.38 (range: 1 – 6). Kolguyev Island hosts a third of the Western Palearctic
101 population of white-fronted geese, and we decided to use it as a proxy for the breeding grounds as a whole
102 (Kondratyev and Zaynagutdinova 2008; Kruckenberg et al. 2008), also when calculating distances between breeding
103 and wintering areas.

104 In autumn and winter, approx. 70 volunteer ornithologists observed 7,149 foraging flocks of wintering white-fronted
105 geese at 123 sites across the study area in The Netherlands and northern Germany (see Fig. 1A), constituting the core
106 wintering area of the species (Madsen *et al.* 1999). Field observations were carried out from arrival in September
107 until departure in April, in 2000 – 2017. Most observations were made from October through January (81%),
108 gradually declining through February (11%) and March (7%). April and September had far fewer observations, as
109 most geese had not then arrived, or had already departed. We counted the number of adult and juvenile birds in each
110 flock, or a sample within especially large flocks, using plumage characteristics and moult patterns throughout the
111 wintering season. (Koffijberg 2006). We calculated the flock's age ratio as the proportion of juveniles within the
112 sampled part of the flock. For all observations, we also counted the total number of individuals within each flock (i.e.
113 total flock size), leading to a difference between total flock size and sampled size; the latter was used to determine
114 age ratio. This formed dataset B. Total flock size was 712 individual geese on average (range: 2 – 20,000 P_{95} =
115 2,500), and had a mean age ratio of 0.18 (range: 0 – 0.87, P_{95} = 0.35). In a subsample of 1,884 flocks at a subset of 65
116 sites, a specific group of 17 expert observers assessed goose family size using the same method and same definitions
117 as on Kolguyev Island (see above). As a result, 51,037 families were counted, and formed dataset C. The mean
118 family size in wintering flocks was 1.78 (range: 1 – 10).

119 Additionally, we derived information on family size from observations of neckbanded white-fronted geese submitted
120 by citizen scientists to the *www.geese.org* portal during the study season in each year of the study period. On average,
121 626 sightings were reported each year (range: 62 – 1143). We assessed family size after filtering out observations of
122 single birds and birds known to be under two years of age, thus not actively taking part in the breeding population;
123 10,635 observations of 4063 unique geese from 8,416 sites were obtained, forming dataset D (see Fig. 1A). In
124 contrast with datasets B and CB, this included observations of pairs or single adults without associated juveniles, i.e.
125 a family size of 0. Datasets B and C included details on the observer and habitat type, while dataset D did not, and
126 also did not hold information on total flock size. Each bird in dataset D was seen 2.62 times on average (range: 1 –
127 78), and had a family size of 0.59 (range: 0 – 11). Approximately 71% of observations reported no juveniles
128 associated with the banded bird, and 59% of banded individuals were never observed with juveniles. Datasets are
129 summarised in Table 1.

Family tracking

131 We caught and fitted 13 complete goose families (26 adults, 38 juveniles) with GPS transmitters in The Netherlands
132 between November and January in 2013 (n = 3 families), 2014 (n = 4), and 2016 (n = 6). In 2013 and 2014 we used

133   e-obs GmbH backpacks with teflon harness (weight 45g), and in 2016 madebytheo neck-band integrated devices
134   (weight 35g). Transmitters reported positions at 30-minute intervals. These selectively large families were tracked
135   within the study area (2 – 10°E, 50 – 54°N) during winter (before 1 April) for 34 – 135 days. The parent with the
136   greater number of GPS fixes was chosen the reference bird for each family.

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

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

146   **Context data**

147   In order to analyse changes in age ratios and family sizes relative to arrival and departure on the wintering grounds,
148   we extracted 90th percentile peaks of 6,266 daily observations of visible overhead migration in the Netherlands
149   (*www.trektellen.nl*; Van Turnhout et al. 2009) as a proxy for annual arrival and departure dates. Data were pooled
150   over 84 spring and 180 autumn counting sites. We excluded observations from sites close to night roosts, and
151   observations which did not match the direction of migration appropriate to the season; both in order to avoid bias by
152   local movements. Geese arrived between 26 September and 30 October, and departed between 3 March to 1 April,
153   resulting in an average wintering period of 165 days (range: 124 – 183). Roughly following Madsen et al. 2002, we
154   refer to the period 0 – 90 days after arrival in each year (ending approximately 31st December) as the autumn season,
155   and the period 91 – 180 days (ending approximately 31st March) as the winter season.

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

162   **Analyses**

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

171   In order to seek explanatory variables for our observations, we examined (5) how flock size was related to distance
172   from the breeding grounds, days since autumn arrival, temperature, and changes during winter in the following flock
173   attributes, using dataset B: (6) age ratio, (7) proportion of independent juveniles, which we call the juvenile

174   independence ratio, which we calculated as $1 - \dfrac{\sum\limits_{x=1}^{x=n} \text{family size}_i}{\text{number of juveniles}}$ defined as 1 – the sum of all family sizes in

175   a flock (family-associated juveniles) divided by the total number of juveniles in the flock, and (8) the proportion of

176   family-associated birds, which we calculated as $1 - \dfrac{\sum\limits_{x=1}^{x=n} \text{family size}_i + 2\,n}{\text{flock size}}$, i.e., the sum of all family sizes plus

177   twice the number of families divided by the total flock size. Models are summarised in Table 2.

178   We used a one-way Kruskal-Wallis test with a Nemenyi post-hoc for model 1, a Poisson generalised linear mixed
179   models (GLMMs) for models 2, 3, & 4, and binomial-error GLMMs for models 5, 6,7, and 8. In each model, we
180   included the breeding year, the observer identity, and the goose identity as independent random effects, if available in
181   the relevant data (see Tab. 2). Analyses and data handling were performed in the R environment (R Core Team
182   2017), using the packages: *lme4* (Bates et al. 2015) and *move* (Kranstauber and Smolla 2016).

183   **Results**

184   **Autumn migration and family size**

185   Family sizes observed on the breeding area on Kolguyev Island approximately prior to onset of autumn migration
186   (dataset A, mean ± 95% confidence interval = 2.38 ± 0.25 juveniles) were significantly higher than family sizes from
187   flock counts (dataset C, mean ± 95% confidence interval = 1.72 ± 0.0398) and from neck-banded birds (dataset D,
188   mean ± 95% confidence interval = 0.46 ± 0.124) recorded in the first two months following initial goose arrivals on
189   the wintering grounds, indicating the average loss of approximately 0.5 (dataset C) and 1.8 juveniles (dataset D)
190   respectively along the migration route (model 1: Kruskal-Wallis rank sum test, $\chi^2 = 469.11$, $p < 0.001$; see Fig. 2). All
191   pairwise differences were significant (Nemenyi post-hoc tests, D-B: $\chi^2 = 17.515$, $p < 0.001$; D-C: $\chi^2 = 248.536$, $p <$
192   0.001; B-C: $\chi^2 = 436.709$, $p < 0.001$).

193   **Family size and wintering site**

194   We found that family size alone was not a good predictor of wintering site distance from the breeding area in dataset
195   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
196   to be a significant predictor of wintering distance in dataset C (model 2: z = -0.683, p = 0.495), but was a significant
197   effect in dataset D (model 2: z = 3.391, p < 0.01). However the minimum daily temperature explained observed
198   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
199   the trends ran counter to each other. Interestingly, the interaction term of family size and season was found to
200   influence wintering site distance only in winter, but not in autumn in dataset C (model 2: z = 4.009, p < 0.01; Fig.
201   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
202   2 juveniles would be found 4 km further from the breeding grounds in winter as opposed to autumn, while a large
203   family of 7 juveniles would be 26 km further away.

204   **Flock size, days since arrival, and family size**

205   Total flock size and days since arrival were good predictors of family size, and both had a negative effect in dataset C
206   (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
207   in this data had 2 juveniles in the first 10 days after arrival, which decreased linearly to 1.49 juveniles per family 180
208   days after arrival, i.e., just prior to departure. Similarly, families in flocks of up to 100 geese had 1.91 juveniles, but
209   only 1.67 juveniles in flocks of between 3900 – 4000 geese. Family size in dataset D also showed a negative effect of
210   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
211   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_{split} = 0.026) were nearly 5 times more likely to split on average than a family with 5 juveniles (p_{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_{split} = 0.092) around 5.6 times that of a family travelling only 10 km/day (p_{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°C and 1°C, growing to 680 birds when temperatures were -13°C – -11°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 in late summer on the breeding grounds and after autumn migration in their wintering areas, calculated flock age-ratios, and connected hypotheses regarding different scales of social organisation to better connect 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

257 breeding grounds in winter, where goose flocks are also smaller. This leads to the observation that larger flocks have
258 smaller families. Over the winter, families get smaller, but larger families, and more sedentary families are less likely
259 to lose juveniles accidentally. The age-ratio of flocks increases significantly through the winter, with a marked
260 increase in the proportion of independent juveniles, and also in the proportion of family-associated birds in flocks.

261 **Autumn migration and family size**

262 Our result that families were significantly larger on the breeding sites at Kolguyev Island shortly prior to migration
263 than in the first two months on the wintering grounds confirms our first hypothesis, and is in line with previous
264 findings of high autumn migration mortality in juvenile Arctic geese (Owen and Black 1989; Francis *et al.* 1992;
265 Menu *et al.* 2005). These studies concluded that autumn migration-related mortality in Arctic goose populations is
266 mainly due to strong density-driven competition for resources prior to autumn migration itself, which leads to
267 juveniles being under-fueled for the journey and thus unsuccessful. The juvenile summertime survival of Arctic-
268 breeding birds including geese has earlier been strongly linked to the cyclical abundance of, and concomitant levels
269 of predation on Arctic rodents *Arvicolinae* in the 'Alternative Prey Hypothesis' (see Summers and Underhill 1987).
270 However, Kolguyev Island lacks lemmings and their associated cycle (Kondratyev and Zaynagutdinova 2008;
271 Kruckenberg et al. 2008), making it unlikely that we sampled in a year with especially high or low predation. The
272 young of white-fronted geese form the major prey base of most predators on Kolguyev Island (Pokrovsky et al.
273 2015); this results in a family size decrease between hatching (early July; mean ≈ 3) and fledging (end July; mean ≈
274 2; see Kondratyev and Zaynagutdinova 2008). We report nearly the same mean family size pre-migration (mid-
275 August; mean = 2.38) as at fledging, suggesting both that we sampled in a year with typical predation levels, and that
276 most juveniles in August were sufficiently grown to avoid all but the largest predators (such as Arctic fox *Vulpes*
277 *lagopus,* Rough-legged buzzard *Buteo lagopus*, and Glaucous gull *Larus hyperboreus*). Finally, the adults of large
278 goose species are effective at countering predation attempts (Thompson and Raveling 1987), leading us to conclude
279 that reductions in family size likely occurred on autumn migration, rather than between our sampling and the start of
280 migration.

281 **Temporal dynamics of family size**

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

293 Juvenile independence from parents should result in a consequently steady reduction in the proportion of family-
294 associated birds in flocks over the winter, but our findings went against this expectation. We suggest two possible
295 explanations, first, that most pairs do not dissociate from all their young over a single winter, i.e., that split events are
296 accidental rather than triggered by the parents (Prevett and MacInnes 1980). Second, families with juveniles likely
297 begin spring migration later than pairs without young, mirroring their differential autumn migration arrival, which is
298 later than that of single and paired geese (Jongejans et al. 2015). This proposed differential migration is further
299 supported by the strong temporal increases in proportions of juveniles in foraging flocks. We hypothesise that in
300 spring, single and paired geese leave the wintering grounds for Arctic breeding sites first, followed by families with
301 young and thatindependent juveniles are the last to leave the wintering grounds. While this is contrary to previous
302 work on the spring migration of pink-footed geese (Madsen 2001), it is interestingly similar to the migration of some

303   juvenile snow geese, which, having separated from their parents, appear to arrive somewhat later that adults to the
304   spring breeding grounds (Prevett and MacInnes 1980).

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

312   **Flocks, families, and wintering site choice**

313   Our results showed that flock sizes are smaller further from the breeding grounds, which can be explained by the
314   metabolic constraints that determine maximum flight distance and duration on migration (Klaassen 1996). The centre
315   of the white-fronted goose wintering area had already shifted south between the 1960s and 1980s (from the Dollard ~
316   7.1°E 53°N to the Lower Rhine along the Dutch-German border ~ 6.7°E, 51°N; ~190 km further south; see Mooij
317   1982), and this flexibility might call into question the strictness of energetic constraints faced by geese in wintering
318   site choice. However, GPS tracked geese migrating in autumn 2016 from Kolguyev Island made brief stop-overs in
319   Poland before continuing on to the study area (*unpublished data,* but see also Kölzsch et al. 2016). The distance from
320   this habitual stop-over to the Dollard (~420 km) is nearly the same as to the Lower Rhine (~455 km), indicating
321   restrictions in how far geese can travel on migration. This interpretation is supported by the fact that family sizes do
322   not vary spatially in autumn (i.e., 0 – 90 days after arrival).

323   However in winter, once all geese have arrived and foraging sites become saturated, food becomes more limited and
324   is eventually also limited by snow cover. It seems that large, socially dominant families then make further
325   movements to occupy climatically milder sites which are more favourable as expected from previous work
326   (Vangilder and Smith 1985, Schamber et al. 2007) and supports both our second hypothesis and the earlier suggestion
327   of differential use of wintering sites according to social status (Jongejans et al. 2015). This is also in line with current
328   knowledge of goose foraging preferences (Fox and Madsen 2017). Geese tolerate snow depths of about 15 cm before
329   relocating to areas with better access to forage (Philippona 1966). Such conditions have become rare in the study area
330   over the past decade, and usually do not occur before winter. This might explain why spatial differences in family
331   size are only observed in winter, and not autumn. Limited habitat availability in the western Netherlands and Belgium
332   — combined with high hunting pressure in France, and the high energetic costs of long flights — seems to lead to
333   geese aggregating in large flocks on the remaining accessible grassland sites on cold, snowy days.

334   As would be expected then, larger families were associated with smaller flocks, confirming our third hypothesis.
335   These family-size dependent spatial differences in wintering areas could lead to the finding that larger flocks have a
336   lower proportion of juveniles overall (Jongejans et al. 2015). However, large flocks had a higher proportion of
337   independent juveniles, and a correspondingly lower proportion of geese associated in families, suggesting that as
338   juveniles separate from their parents, they gather with other juveniles and pairs of adults in flocks to gain group-
339   living benefits (Prevett and MacInnes 1980). However, contrary to expectations that both the above proportions
340   would be well predicted by distance to the breeding grounds, no such trends were found. This could be linked to
341   population movements in late winter and early spring, when geese spread out across the study area to prepare for the
342   spring migration (Kölzsch et al. 2016). Overall, our data suggest that large numbers of white-fronted goose juveniles
343   reach independence each winter and contribute to the species' meteoric rise in abundance (Fox and Madsen 2017),
344   yet we caution that the population's adaptability to changing environmental conditions could be affected by future
345   actions that either inadvertently or deliberately affect (for examples see Stroud et al. 2017; Clausen et al. 2017)
346   population recruitment and the maintenance of flyways through the cultural transmission of space use.

347   **Conflict of interest**

348   The authors declare that they have no conflict of interest.

349 **Ethical approval**

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

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354   **Tables**

355

Dataset name	Dataset description	Observations	Sites	Spatial extent
A	Family sizes on Kolguyev Island	116	26	49ºE, 69ºN
B	Flock census with age-ratio	7,149	123	4.0º - 8.8ºE, 51.1º - 53.4ºN
C	Family size counts in flocks	51,037	65	4.8º - 7.3ºE, 51.1º - 53.4ºN
D	Neck-banded individual resightings	10,635	8,416	2.7º - 9.7ºE, 50.9º - 53.9ºN
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

356   **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^B, 9^B, 10^C	
3	Poisson GLMM	C, D	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	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

360   **Tab. 2 Summary of analyses**

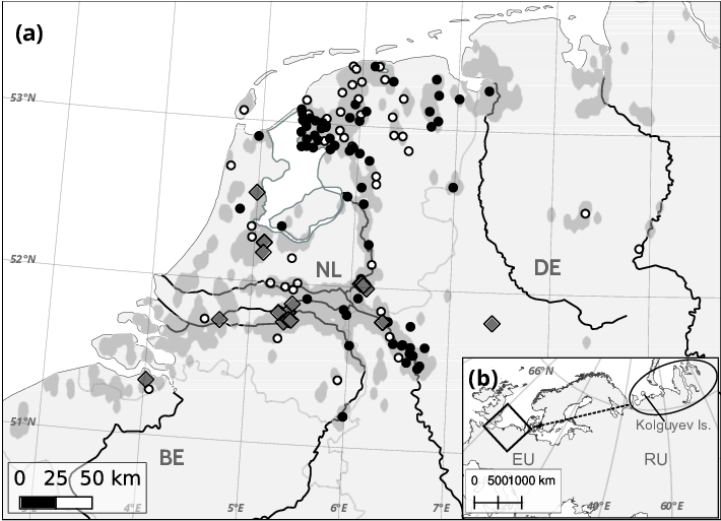361

362

363 **Figures**

365   **Fig. 1 (a) Wintering grounds of greater white-fronted geese *Anser a. albifrons* in the Netherlands and northern**
366   **Germany, showing 123 sites (filled and open circles) where the age-ratio of 7,149 flocks was determined**
367   **(dataset B), and the subset of 65 sites (filled black circles) where 51,037 successful families were recorded in**
368   **1,884 flocks (dataset C). Shaded grey area bounds 10,635 neckband-resightings (dataset D). 21 split events**
369   **(diamonds) were observed in 13 GPS tracked families (from dataset E). Observations correspond well with**
370   **major rivers (marked as black lines). Data were collected from 2000 - 2017. (b) Breeding grounds (ellipse) in**
371   **Russia with Kolguyev Island and general flyway (arrow) to wintering area (rectangle) (adapted from Madsen**
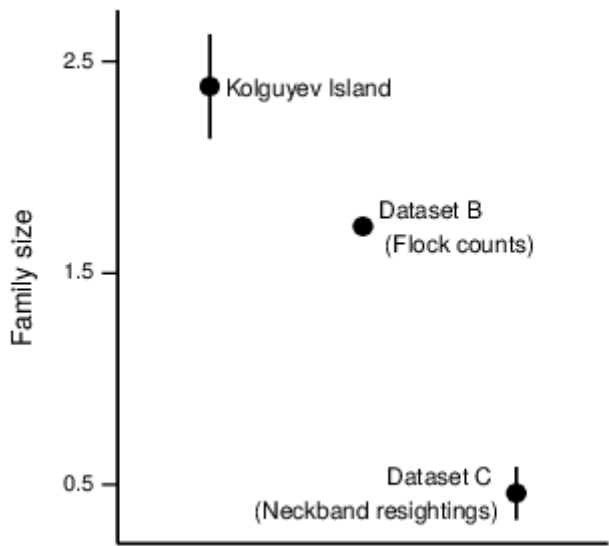372   **et al. 1999)**

374

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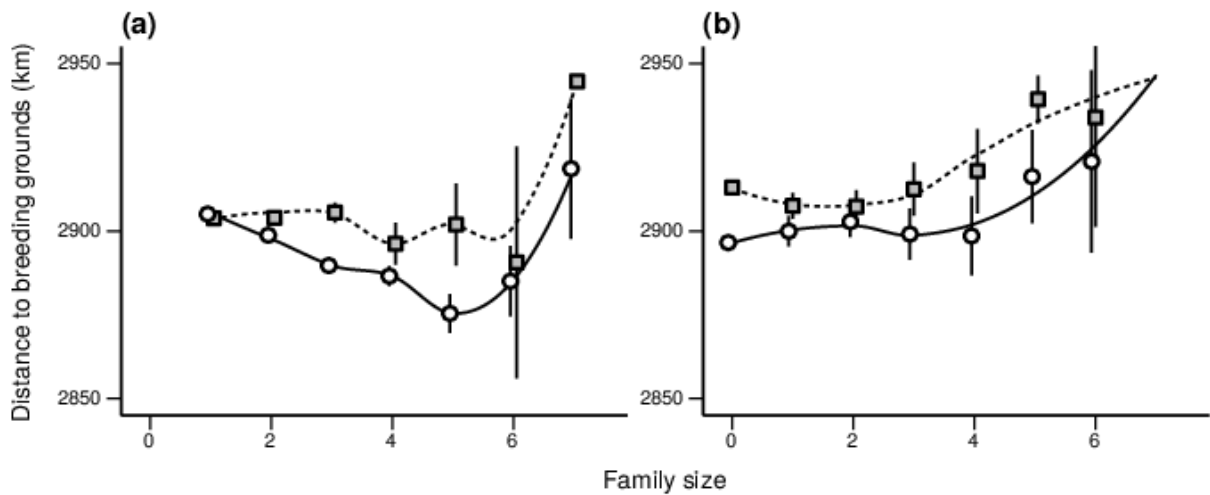378   **of goose autumn arrivals in 2016**

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380

382 **Fig. 3 GLMM fits (lines), and mean distance of wintering sites from Kolguyev Island (symbols) per family size**
383 **for (a) family size counts (dataset C) and (b) neckband-resightings (dataset D). Data and fit are separated by**
384 **number of days since arrival to the wintering grounds: 0 – 90 days (solid lines, circles), 91 – 180 days (dashed**
385 **line, squares). Vertical lineranges represent 95% confidence intervals at each data point**
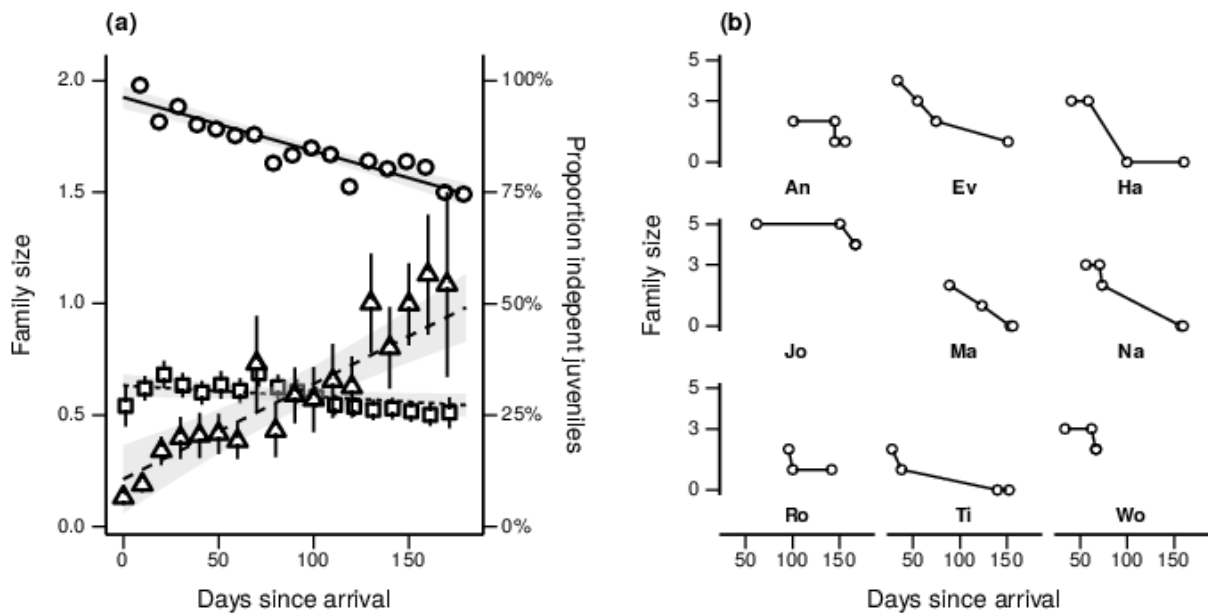
386

387

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.
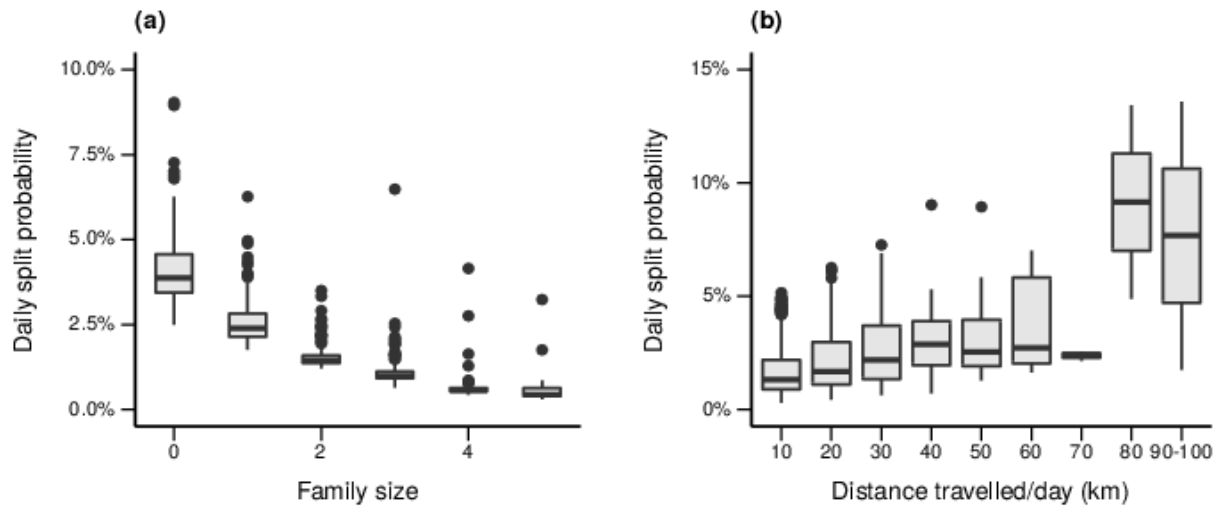
400   **Fig. 5 Boxplots of daily predicted split probability in relation to (a) family size, and (b) daily distance travelled**
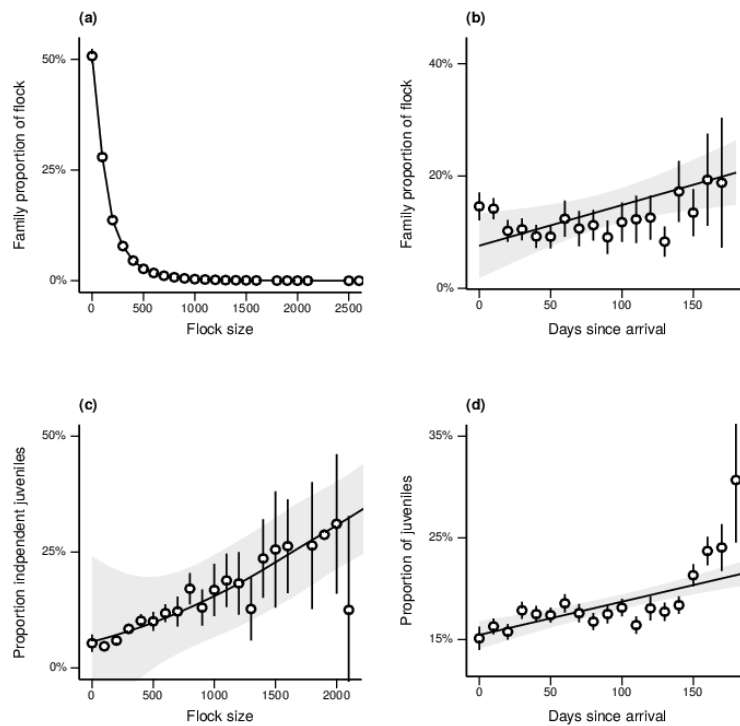401

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