Family size dynamics in wintering geese

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Abstract

Many bird populations are made up of social units with differences in size and social 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 populations, as well as the events leading to juvenile independence are not well understood. We focus on family size dynamics of the Baltic-North Sea flyway population of 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 social status and family size affected wintering site choice and migration timing as well as how and why family sizes decreased. We found that family size decreased strongly during autumn migration, likely from juvenile death due to insufficient fuelling. It further decreased through the winter, here seemingly by juveniles accidentally splitting off during strong disturbance events. Different from previous findings, a large proportion of juveniles became independent during winter. Large families generally arrived later to the wintering grounds, wintered further from the breeding grounds and departed later for spring migration than adults without young. Independent young left for spring migration last. Thus, white-fronted geese are differential migrants by social status. In combination with the observation of low breeding success in this population in recent years, our findings improve the understanding of its spatial and temporal patterns during winter, and their apparent changes. This can support conservation and management decisions for both white-fronted geese as well as other large migrants with complex age and social structure.

Zusammenfassung

Die Populationen der meisten Vogelarten setzen sich aus Individuen verschiedener Größe und sozialem Status zusammen. Gänsefamilien und -schwärme gehören dabei zu den besser bekannten. Wie jedoch der Verband von juvenilen Gänsen mit ihren Eltern als Familie Zugtiming und Raumnutzung der Popualtion bestimmen und welche Ereignisse zur Unabhängigkeit von Juvenilen führen, ist bisher nicht ganzheitlich verstanden. Wir haben hier betrachtet, wie Familiengrößen von Blessgänsen *Anser a. albifrons* sich in ihren Überwinterungsgebieten in den Niederlanden und Norddeutschland entwickeln, wo wir 17 Jahre Beobachtungsdaten an fressenden Gänseschwärmen gesammelt haben und 13 vollständige Familien mit GPS-Sendern verfolgen konnten. Es wurde untersucht, wie sozialer Status und Familiengröße sich auf die Wahl des Überwinterungsgebietes und Zugtiming auswirken, und wie und warum Familien sich trennen. Wir konnten zeigen, dass Familiengrößen während des Herbstzuges stark abnehmen, vermutlich durch Tod der Juvenilen aufgrund ungenügender Fettreserven. Sie nimmt durch den Winter weiter ab, hier möglicherweise durch unabsichtliche Trennung während starker Störungsereignisse. Entgegen früherer Erkenntnisse, sind ein Großteil der Juvenilen im Winter so unabhängig geworden. Große Familien sind im allgemeinen später in den Überwinterungsgebieten angekommen, haben weiter von den Brutgebieten überwintert und sind im Frühjahr später abgezogen als Adultvögel ohne Jungtiere. Unabhängige Juvenile haben den Frühjahrszug als letzte begonnen. Folglich sind Blessgänse differentielle Migranten durch verschiedene soziale Status. In Kombination mit der Beobachtung, dass diese Population seit einigen Jahren sehr geringen Bruterfolg hat, verbessern unsere Ergebnisse das Verständnis der räumlichen und zeitlichen Populationsmuster im Wintergebiet und ihre anscheinenden Änderungen. Dies kann Artenschutz- und Managemententscheidungen zu Blessgänsen und auch anderen großen Migranten mit komplexer Alters- und sozialen Struktur unterstützen.

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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 and offset by increased 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 in the non-breeding season. 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 are observed on arrival at wintering sites (Black and Owen 1989; Francis et al. 1992; Menu et al. 2005). Of the families that arrive on 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 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 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 parental aggression toward juveniles (Black and Owen 1989; Poisbleau et al. 2008; Scheiber et al. 2013) and the higher vulnerability of families 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 been hypothesised to displace 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, of the Baltic-North Sea flyway population have distinct family structure and aggregate in large wintering flocks across large parts 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 one of the few sets 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

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

Methods

Age ratios and family size

124 To estimate the effect of autumn migration on family size, we determined family sizes on the summer breeding
125 grounds on Kolguyev Island, Russia (approx. 69°N, 49°E, Fig. 1b) in August 2016, approximately one month prior to
126 the autumn migration. We directly observed groups of geese, counted the number of individuals, and identified adults
127 and juveniles on the basis of evident differences in size and plumage. We assessed family size, i.e., the number of
128 juveniles associated with one or both parents, relying on characteristic behaviour and social interactions between the
129 juveniles and adults. 116 such observations of families and pairs without juveniles were collected, forming dataset A
130 (Table 1), with a mean family size of 2.26 (range: 0-6) when including the few families without young, and 2.38
131 (range: 1 – 6) excluding pairs without young. As the two values do not differ much, we used only the latter for further
132 analyses. Kolguyev Island hosts a third of the Western Palearctic population of white-fronted geese, and we consider
133 it representative of the breeding grounds as a whole (Kondratyev and Zaynagutdinova 2008; Kruckenberg et al.
134 2008), especially when calculating distances between breeding and wintering areas.

135 In autumn and winter, approx. 70 volunteer ornithologists observed 7,149 foraging flocks of wintering white-fronted
136 geese at 123 sites across the study area in the Netherlands and northern Germany (see Fig. 1a), constituting the core
137 wintering area of the species (Madsen *et al.* 1999). Field observations were carried out from goose arrival in
138 September until goose departure in April, in 2000 – 2017. Most observations were made from October through
139 January (81%), gradually declining through February (11%) and March (7%). September and April had far fewer
140 observations, as most geese had not then arrived, or had already departed, respectively. The number of adult and
141 juvenile birds in each flock, or a sample within especially large flocks was counted, using plumage characteristics
142 and moult patterns throughout the wintering season (Koffijberg 2006). We calculated the flock's age ratio as the
143 proportion of juveniles within the sampled part of the flock. For all observations, we also counted the total number of
144 individuals within each flock (i.e. total flock size), leading to a difference between total flock size and sampled size;
145 the latter was used to determine age ratio. This formed dataset B (Table 1). Total flock size was 712 individual geese
146 on average (range: 2 – 20,000, 95th percentile $P_{95} = 2,500$), and had a mean age ratio of 0.18 (range: 0 – 0.87, $P_{95} = $
147 0.35). In a subsample of 1,884 flocks at a subset of 65 sites, a specific group of 17 expert observers assessed goose
148 family size using the same method and definitions as on Kolguyev Island (see above). As a result, 51,037 families
149 were counted, and formed dataset C (Table 1). The mean family size in wintering flocks was 1.78 juveniles (range: 1
150 – 10).

151 Additionally, we derived information on family size from observations of wintering neckbanded white-fronted geese
152 submitted by citizen scientists to the *www.geese.org* portal during the study period. On average, 626 sightings were
153 reported each year (range: 62 – 1143). We assessed family size after filtering out observations of single birds without
154 young, and birds known to be under two years of age, thus not actively taking part in the breeding population. 10,635
155 observations of 4,063 unique geese from 8,416 sites were obtained, forming dataset D (Table 1, Fig. 1a). In contrast
156 with datasets B and C, this included observations of pairs without associated juveniles, i.e. a family size of 0.
157 Datasets B and C included details on the observer and habitat type, while dataset D did not; dataset D also did not
158 hold information on total flock size. Each bird in dataset D was seen 2.62 times on average over the study period
159 (range: 1 – 78), and had a family size of 0.59 (range: 0 – 11). Approximately 71% of observations reported no
160 juveniles associated with the banded bird, and 59% of banded individuals were never observed with juveniles over
161 the entire study period.

Family tracking

163 We caught and fitted 13 complete goose families, (26 adults, 38 juveniles) with GPS transmitters in the Netherlands
164 between November and January in 2013/14 (n = 3 families), 2014/15 (n = 4), and 2016/17 (n = 6). Large families

167   were preferentially selected for tagging. In 2013/14 and 2014/15 we used e-obs GmbH backpacks with teflon harness
168   (weight 45g), and in 2016/17 madebytheo neck-band integrated devices (weight 35g). Transmitters reported positions
169   at 30-minute intervals. Families were tracked within the study area (2 – 10°E, 50 – 54°N) during autumn and winter
170   (tagging date – 1 April) for 34 – 135 days.

171   We identified the day and position where a decrease in the number of family members within 1000m of a reference
172   bird relative to the previous day was recorded (Fig. 1a), and termed this a split. As reference bird for each family, we
173   chose the parent with the greater number of GPS fixes. We determined the daily split probability by a binomial fit on
174   the classification of each day as a success or failure (1 or 0) depending on whether a split occurred or not. To relate
175   the probability of a split to goose flight, we summed the distance travelled by each family each day, and identified
176   and counted the number of displacements with a speed ≥ 1000 m/ 30 minutes. This constituted dataset E (Table 1).
177   Families travelled on average 11 km each day over the tracking period (range: 0 – 306 km). On average, they
178   travelled a distance ≥ 1000 m in 30 minutes twice each day (range: 0 - 10). 21 split events were recorded, of which 19
179   were juveniles separating from the family.

Context data

181   In order to analyse changes in age ratios and family sizes relative to the inter-anually variable date of goose arrival on
182   and departure from the wintering grounds, we extracted the first and last 90th percentile peaks in each year from 6,266
183   daily observations of visible overhead migration in the Netherlands (*www.trektellen.nl*; Van Turnhout et al. 2009) as
184   a proxy for annual arrival and departure dates. Data were pooled over 84 spring and 180 autumn counting sites. We
185   excluded observations from sites close to night roosts, and observations which did not match the direction of
186   migration appropriate to the season in order to avoid bias by local movements. Geese arrived between 26 September
187   and 30 October, and departed between 3 March to 1 April, resulting in an average wintering period of 165 days
188   (range: 124 – 183). Following Madsen et al. (2002), we refer to the period 0 – 90 days after arrival in each year
189   (ending approximately 31st December) as the autumn season, and the period 91 – 180 days (ending approximately 31st
190   March) as the winter season.

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

Analyses

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

205   In order to seek explanatory variables for our observations, we examined (5) how flock size was related to days since
206   autumn arrival, temperature and distance from the breeding grounds. Further, using dataset B, we explored (6) flock
207   age ratio, (7) proportion of independent juveniles in a flock (called 'juvenile independence ratio') and (8) the
208   proportion of family-associated birds in relation to flock size, days since autumn arrival, temperature and distance
209   from the breeding grounds. The juvenile independence ratio was calculated as one minus the sum of all family sizes

210   in a flock (family-associated juveniles) divided by the total number of juveniles in the flock:

211
$$1 - \frac{\sum_{x=1}^{x=n} \text{family size}_i}{\text{total number of juveniles}}$$

212   We calculated the different, but related proportion of family-associated birds as one minus the sum of all family sizes
213   plus twice the number of families divided by the total flock size:

214
$$1 - \frac{\sum_{x=1}^{x=n} \text{family size}_i + 2n}{\text{flock size}}$$

215   Models and variables are summarised in Table 2.

216   We used a one-way Kruskal-Wallis test with a Nemenyi post-hoc for model 1, Poisson generalised linear mixed
217   models (GLMMs) for models 2, 3, & 4, and binomial-error GLMMs for models 5, 6,7, and 8. In each model, we
218   included the breeding year, the observer identity, and the goose identity as independent random effects, if available in
219   the relevant data (see Table 2). Analyses and data handling were performed in the R environment (R Core Team
220   2017), using the packages *lme4* (Bates et al. 2015), *mgcv* (Wood 2013) and *move* (Kranstauber and Smolla 2016).

Results

Autumn migration and family size

223   Family sizes observed on the breeding grounds on Kolguyev Island (dataset A, mean ± 95% confidence interval =
224   2.38 ± 0.25 juveniles) were significantly higher than family sizes from flock counts (dataset C, mean ± 95%
225   confidence interval = 1.72 ± 0.0398) and neck-banded birds (dataset D, mean ± 95% confidence interval = 0.46 ±
226   0.124) recorded in the first two months following initial goose arrivals on the wintering grounds. This indicates an
227   average loss of approximately 0.5 (dataset C) and 1.8 juveniles (dataset D) respectively along the migration route
228   (model 1: Kruskal-Wallis rank sum test, $\chi^2 = 469.11$, $P < 0.001$; see Fig. 2). All pairwise differences were significant
229   (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

231   We found that family size alone was not a good predictor of wintering site distance from the breeding area in dataset
232   C (model 2: $z = 1.806$, $P = 0.071$), and in dataset D (model 2: $z = 0.516$, $P = 0.606$). The season (i.e. autumn or
233   winter) alone did not appear to be a significant predictor of wintering distance in dataset C (model 2: $z = -0.683$, $P =$
234   0.495), but was a significant effect in dataset D (model 2: $z = 3.391$, $P < 0.01$). However, the minimum daily
235   temperature explained observed variation well in both dataset C (model 2: $z = 3.698$, $P < 0.01$), and dataset D (model
236   2: $z = -9.346$, $P < 0.01$), though the trends ran counter to each other. Interestingly, the interaction term of family size
237   and season was found to influence wintering site distance only in winter, but not in autumn in dataset C (model 2: $z =$
238   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
239   dataset C, a family with 2 juveniles would be found 4 km further from the breeding grounds in winter as opposed to
240   autumn, while a large family of 7 juveniles would be 26 km further away.

Flock size, days since arrival and family size

242   Total flock size and days since arrival were good predictors of family size and both had a negative effect in dataset C
243   (model 3: flock size $z = -4.288$, $P < 0.001$; days since arrival $z = -8.669$, $P < 0.001$; see Fig. 4a). On average, families

244   in this dataset had 2 juveniles in the first 10 days after arrival, which decreased linearly to 1.49 juveniles per family
245   180 days after arrival, i.e., just prior to departure. Similarly, families in flocks of up to 100 geese had 1.91 juveniles,
246   but only 1.67 juveniles in flocks of between 3900 – 4000 geese. Family size in dataset D showed no relation with
247   total flock size, but was negatively effected by days since arrival (model 3: $z = -5.018$, $P < 0.001$; Fig. 4a), with
248   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

250   We found a strong correlation between days since arrival and family size in dataset E (Pearson's $r = 0.728$; Fig. 4b).
251   To avoid biasing our model by this multi-collinearity, we chose to omit days since arrival in the final model,
252   reasoning that we had adequately characterised the development of family sizes over the course of winter. The daily
253   split probability of families was significantly lower in larger families (model 4: $z = -2.644$ $P = 0.0082$); for example,
254   the smallest families with 1 juvenile ($P_{split} = 0.026$) were on average 5 times more likely to split than a family with 5
255   juveniles ($P_{split} = 0.00542$; Fig. 5a). While the number of flights per day seemed to have no effect ($z = -0.355$, $P =$
256   0.723), the distance travelled per day increased the likelihood of splitting ($z = 2.12$, $P = 0.027$); a family covering up
257   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}
258   $= 0.016$; Fig. 5b).

Spatio-temporal trends in flocks

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

268   The overall age ratio of flocks was not affected by the distance of the wintering site from the breeding grounds
269   (model 6: $z = -1.3460.965$, $P = 0.178335$). However, it was significantly higher later in the wintering period ($z =$
270   1.2073.218, $P = 0.2270013$); for example, flocks seen between 0 – 10 days after arrival had an average age ratio of
271   0.157 juveniles in the flock, while flocks in late winter (170 – 180 days) had a mean age ratio of 0.256 (see Fig. 6d).
272   Larger flocks also had a significantly lower age ratio, from 0.224 in flocks of size 0 – 100 geese, to 0.135 in
273   extremely large flocks of size 2900 – 3000 geese ($z = -4.227$, $P < 0.001$).

274   The proportion of geese associated in families was lower in larger flocks: flocks of 2900 – 3000 geese had a mean
275   family-associated proportion of only 0.102, while flocks in the range of 1400 – 1500 and 0 – 100 had family-
276   associated proportions of 0.163 and 0.469, respectively (model 8: $z = 13.117$, $P < 0.001$; Fig. 6a). It increased
277   through the winter, such that on average, a flock just after the beginning of arrivals (0 – 10 days) had a family-
278   associated proportion of 0.264, whereas the same for a flock in late winter (170 – 180 days) was 0.367 ($z = 2.124$, P
279   $= 0.034$; Fig. 6b). However, it was insensitive to the distance from the breeding grounds at which flocks were seen (z
280   $= -0.036$, $P = 0.9713$).

281   The proportion of independent juveniles increased with flock size, such that the average small flock (0 – 100 geese)
282   had a juvenile independence ratio of 0.037, while flocks of intermediate (1400 – 1500 geese) and large sizes (2900 –
283   3000 geese) had ratios of 0.143 and 0.232, respectively (model 7: $z = -8.063$, $P < 0.001$; Fig. 6c). This proportion
284   rose through winter, with early autumn just after goose arrivals (0 – 10 days; mean value = 0.034) contrasting
285   strongly with late winter (160 – 170 days; mean value = 0.273; $z = -4.315$, $P < 0.001$; Fig. 4a). We found that the
286   proportion of independent juveniles was not affected by the distance of the wintering site from the breeding grounds
287   ($z = -1.267$, $P = < 0.001$).

Discussion

We determined family sizes and age ratios of white-fronted geese in late summer on the breeding grounds and after autumn migration in their wintering areas. We evaluated these data regarding different scales of social organization of goose families and flocks to improve our understanding of 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, family sizes dropping significantly. On the wintering grounds then, families leverage their social dominance to occupy climatically milder sites further from the breeding grounds in winter, where goose flocks are also smaller. Over the winter, families become smaller, but large and more sedentary families are less likely to split or lose members to predation or hunting. Family split events were shown to relate to flight intensity, thus likely being accidental due to disturbance events. The age ratio of flocks increased significantly through the winter, with a marked increase in the proportion of independent juveniles as well as the proportion of family-associated birds just before spring migration.

Autumn migration and family size

Our result that families were significantly larger on the breeding sites at 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; Menu et al. 2005). These studies concluded that autumn migration-related mortality in Arctic goose populations is mainly due to strong density-driven competition for resources prior to and during autumn migration, which leads to juveniles being under-fueled for the journey and thus unsuccessful. Autumn migration in our population of white-fronted geese has one important stopover site for fuelling close to the breeding grounds, but is then characterized by non-stop, quick flight to the wintering grounds (Kölzsch et al. 2016), avoiding hunters. Such flight might be problematic for juveniles if not properly fueled.

Juvenile summertime survival of Arctic-breeding birds including geese has earlier been strongly linked to the cyclical abundance of and concomitant levels of predation on Arctic rodents *Arvicolinae* in the 'Alternative Prey Hypothesis' (Summers and Underhill 1987). However, Kolguyev Island lacks lemmings and their associated cycle (Kondratyev and Zaynagutdinova 2008; Kruckenberg et al. 2008), so that young geese form the regular, main prey of most predators there (Pokrovsky et al. 2015). This is shown to result in strong family size decreases between hatching (early July; mean ≈ 3) and fledging (end July; mean ≈ 2; see Kondratyev and Zaynagutdinova 2008). We report nearly the same mean family size pre-migration (mid-August; mean = 2.38) as at fledging, suggesting both that we sampled in a year with typical predation levels, and that most juveniles in August were sufficiently grown to avoid all but the largest predators (such as Arctic Fox *Vulpes lagopus,* Rough-legged Buzzard *Buteo lagopus* and Glaucous Gull *Larus hyperboreus*). Finally, adult geese are effective at countering predation attempts on their young (Thompson and Raveling 1987), allowing the conclusion that reductions in family size likely occurred during 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 time 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 may present 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 around January), young geese also become independent rather than only being taken out from the population. This is in line with the finding that juvenile mortality is unrelated to hunting in the Pink-footed Goose *A. brachyrhynchus* which also winters in parts of the study area (Madsen et al. 2002).

334   Juvenile independence from parents should result in a consequently steady reduction in the proportion of family-
335   associated birds in flocks over the winter, but our findings showed the opposite. We suggest two possible
336   explanations. First, it is likely that most pairs do not dissociate from all their young over a single winter (Ely 1979;
337   Warren et al. 1993; Kruckenberg 2005). Second, families with juveniles may begin spring migration later than pairs
338   without young, mirroring their differential autumn migration arrival, which is later than that of single and paired
339   geese (Jongejans et al. 2015). This proposed differential migration is further supported by the strong temporal
340   increases in proportions of juveniles in foraging flocks. We hypothesise that in spring, single and paired geese
341   without young leave the wintering grounds for Arctic breeding sites first, followed by families with young and
342   finally independent juveniles. While this is contrary to previous work on the spring migration of pink-footed geese
343   (Madsen 2001), it is interestingly similar to the migration of some juvenile snow geese, which, having separated from
344   their parents, appear to arrive somewhat later to the breeding grounds than adults (Prevett and MacInnes 1980).

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

352   **Spatial dynamics of family size**

353   Our results show that flock sizes were smaller further from the breeding grounds, which can be explained by the
354   metabolic constraints that determine maximum flight distance and duration of migration (Klaassen 1996). GPS tracks
355   of geese from Kolguev Island in the autumns of 2014 – 2016 showed that many geese used short stopovers in Poland
356   or Northern Germany before entering our study area (*unpublished data,* see also Kölzsch et al. 2016). Thus, flight
357   restrictions might already have been active earlier, especially for geese travelling with young. This is supported by
358   the fact that large goose families had moved further away from the breeding sites (i.e. further into the study site) only
359   in the winter season (90-180 days after arrival), after having refueled in more westerly sites.

360   Once all geese had arrived and foraging sites became saturated, food seems to have been more limited and was
361   eventually also limited by snow cover. It seems that large, socially dominant families then moved further to occupy
362   climatically milder sites which are more favourable (Vangilder and Smith 1985, Schamber et al. 2007). This supports
363   both our *second hypothesis* and the earlier suggestion of differential use of wintering sites according to social status
364   (Jongejans et al. 2015) and is in line with current knowledge of goose foraging preferences (Fox and Madsen 2017).
365   Geese tolerate snow depths of about 15 cm before relocating to areas with better access to forage (Philippona 1966).
366   Such conditions have become rare in the study area over the past decade, and usually do not occur before winter. This
367   might explain why spatial differences in family size are only observed in winter and not autumn. Limited habitat
368   availability in the western Netherlands and Belgium, combined with high hunting pressure in France and the high
369   energetic costs of long flights, seems to lead to geese aggregating in large flocks on the remaining accessible
370   grassland sites on cold, snowy days.

371   Finally, our results indicate that larger families were associated with smaller flocks, confirming our *third hypothesis*.
372   This finding in combination with the spatial pattern of large families wintering further from the breeding grounds
373   might allow the conclusion that larger flocks have a lower proportion of juveniles overall (Jongejans et al. 2015).
374   However, large flocks had a higher proportion of independent juveniles and a correspondingly lower proportion of
375   geese associated in families, suggesting that as juveniles separate from their parents they gather with other juveniles
376   and pairs of adults in flocks to gain group-living benefits (Prevett and MacInnes 1980). However, contrary to
377   expectations that both the above proportions would be well predicted by distance to the breeding grounds, no such
378   trends were found. This could be linked to population movements in late winter and early spring, when geese seem to
379   spread out across the study area to prepare for the spring migration (Kölzsch et al. 2016).

380

381   **Conclusions**

382 Overall, we show that social structure, and especially family cohesion, has strong effects on the spatial and temporal
383 dynamics of our white-fronted geese in their wintering grounds and likely on migration and summer dynamics
384 through carry-over effects. Social status (family size) drives migration timing of adults as well as winter site
385 selection. Though our population of white-fronted geese seems stable, a recent drop in recruitment is becoming
386 notable (Jongejans et al. 2015(Jongejans et al. 2015)). This, in combination with the trends reported in our study,
387 could lead to changes in spatial-temporal population patterns, e.g. an earlier arrival of adult geese to the wintering
388 sites. Furthermore and in contrast to earlier studies (Kruckenberg 2005), our data suggest that large numbers of
389 white-fronted goose juveniles reach independence each winter, likely due to high levels of disturbance. As this can
390 lead to more juveniles staying longer in the wintering grounds, it might also lead to higher mortality of juveniles
391 during spring migration (*unpublished data* AK) and eventually further decrease of recruitment into the breeding
392 population. Recent levels of climate and habitat change and increased levels of derogation shooting or hunting
393 (Jongejans et al. 2015) can deteriorate conditions for white-fronted geese in the different areas they use through the
394 year. It remains to be seen how geese will adapt, but conservation and management actions need to closely monitor
395 population development (Stroud et al. 2017; Lefebvre et al. 2017) and should take into account social structure driven
396 population dynamics as we present here.

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Conflict of interest

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

Ethical approval

404 Approval for catching and tagging goose families was obtained from the Animal Welfare Committee of the Royal
405 Netherlands Academy of Arts and Sciences (DEC NIOO13.14).

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407   **Tables**

408

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	Resightings of neck-banded individuals	10,635	8,416	2.7º - 9.7ºE, 50.9º - 53.9ºN
E	GPS tracking of complete 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				

409   **Tab. 1** Summary of field observations and satellite telemetry

Model	Type	Dataset	Response	Fixed effects	Random effects	Records used
Main hypotheses						
1	Kruskall-Wallis + Nemenyi post-hoc	A, C, D	Family size	Dataset	–	2,641 (A: 110; C: 2,266; D: 265)
2	Poisson GLMM	C, D	Distance to breeding grounds	1, 3, 4	7, 8^C, 9^C, 10^D	C: 46,476; D: 10,609
3	Poisson GLMM	C, D	Family size	2, 3	7, 8^C, 9^C, 10^D	C: 46,476; D: 10,609
4	Binomial GLMM	E	Daily split probability	3, 12, 13, 14	11	1,009
Context trends						
5	Poisson GLMM	B	Flock size	3, 4, 5	7, 8, 9	6,533
6	Binomial GLMM	B	Flock age ratio	2, 3, 4, 5	7, 8, 9	7,085
7	Binomial GLMM	B	Proportion of independent juveniles $$1 - \frac{\sum_{x=1}^{x=n} \text{family size}_i}{\text{total number of juveniles}}$$	2, 3, 4, 5	7, 8, 9	1,661
8	Binomial GLMM	B	Proportion of geese in families $$1 - \frac{\sum_{x=1}^{x=n} \text{family size}_i + 2n}{\text{flock size}}$$	2, 3, 4, 5	7, 8, 9	1,661

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 wind speed, 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; C: Dataset C, D: Dataset D

410   **Tab. 2** Summary of models used for data analyses

411

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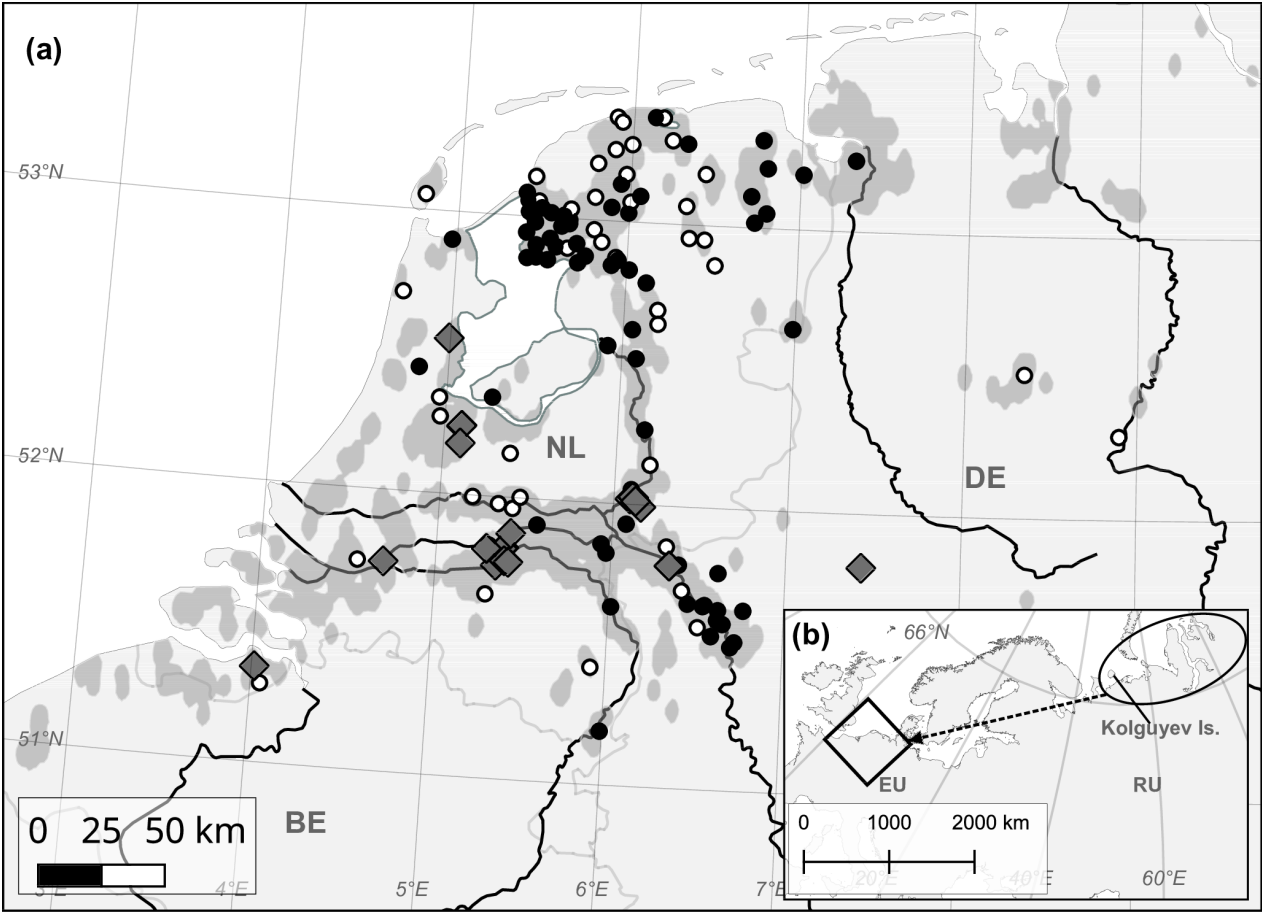
414 **Fig. 1** (a) Wintering grounds of white-fronted geese in the Netherlands and northern Germany, showing 123 sites
415 (filled and open circles) where the age ratio of 7,149 flocks was determined (dataset B), and the subset of 65 sites
416 (filled black circles) where 51,037 successful families were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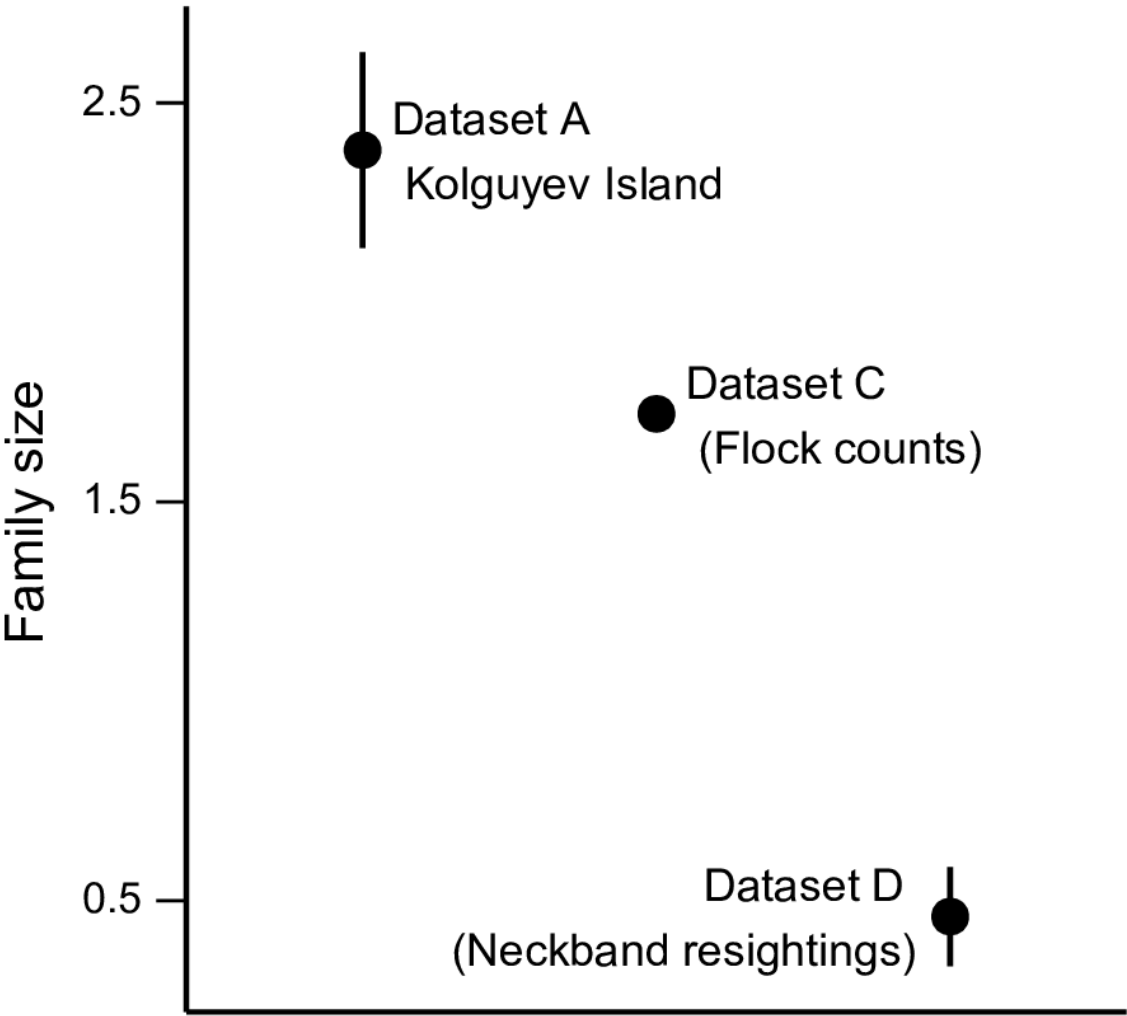420 from Madsen et al. 1999)

422 **Fig. 2** Mean family size in the core breeding grounds on Kolguyev Island in August 2016 (dataset A), one month
423 prior to migration, and in the core wintering range in the Netherlands and Northern Germany from two different
424 datasets (counting data = dataset C, marked birds = dataset D), observed within the first 60 days of goose autumn
425 arrivals in 2016. Note that values for both dataset C (without zero family sizes) and dataset D (with zero family sizes)
426 can be compared with the Kolguev Island family size, as the latter is basically the same value if including or
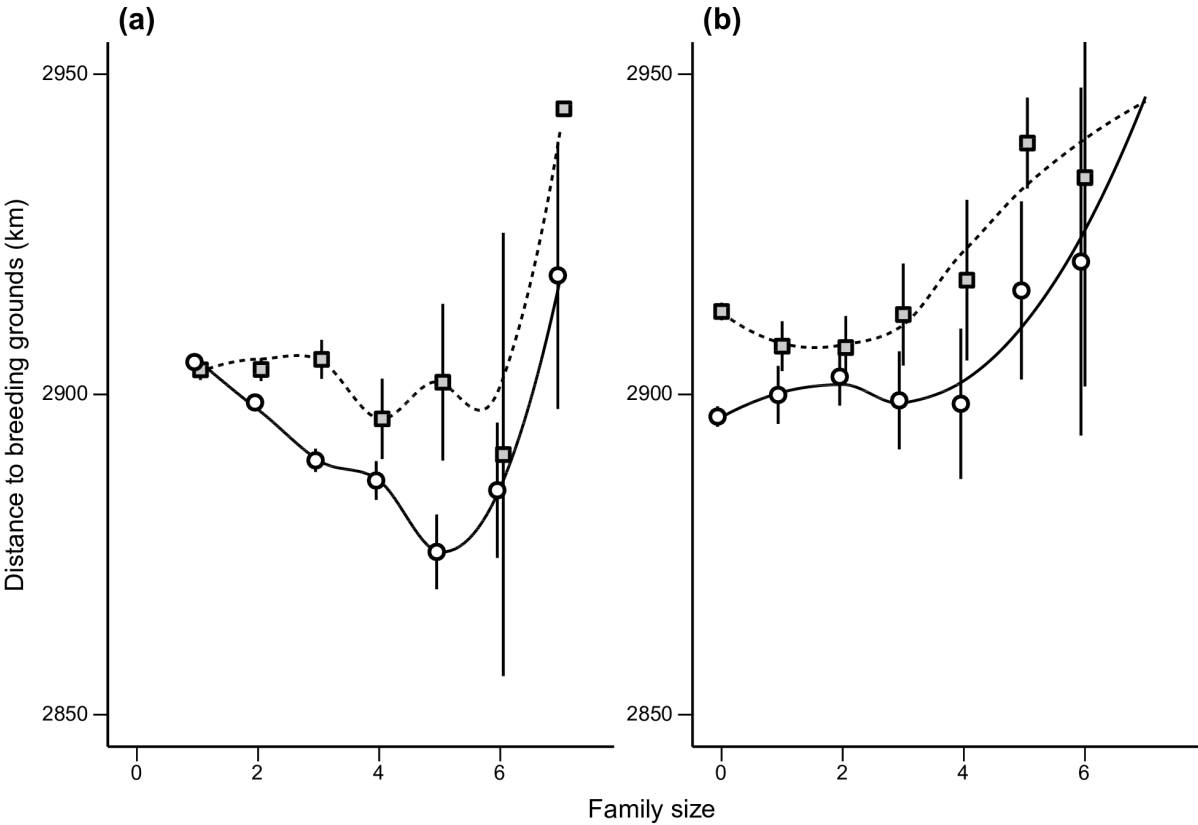427 excluding size zero families

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 fits 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
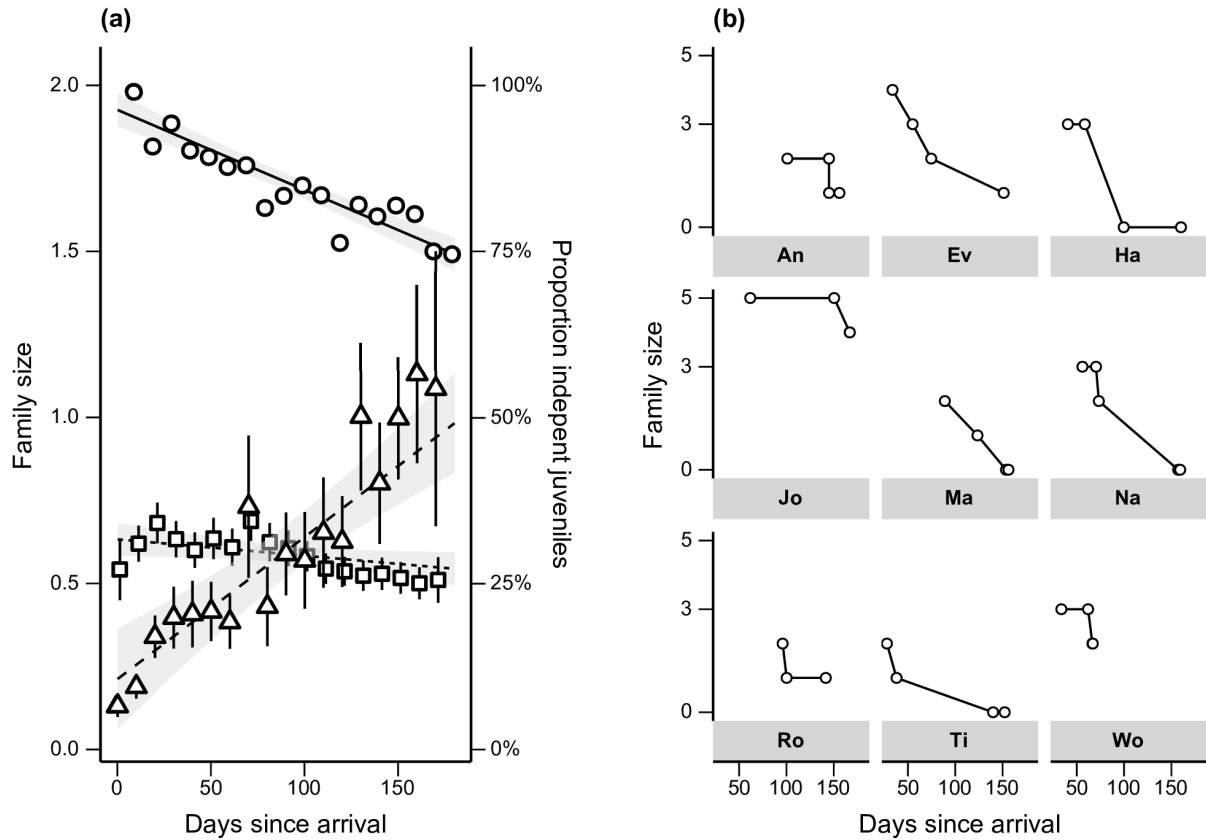
Fig. 4 (a) Mean family size in 10 day intervals since goose autumn arrival (symbols) in flock counts (dataset C, circles), neckband-resightings (dataset D, squares) and GLMM fits (lines) for model 3. Triangles and the dot-dash line represent the mean proportion of first winter juveniles observed in flock counts (dataset C), which are not associated with parents and the GLMM fit for model 7. Vertical lineranges and shaded grey areas represent 95% confidence intervals at each point. (b) Family size development over winter (circles) in 9 of 13 GPS tracked families (family identity in header bar). The first circle in each sub-plot indicates family size immediately after the start of tagging, while the last circle represents family size at the end of the tracking period (either 1April or when the family crossed the 8°E longitude line). Symbols overlap when events are temporally proximate
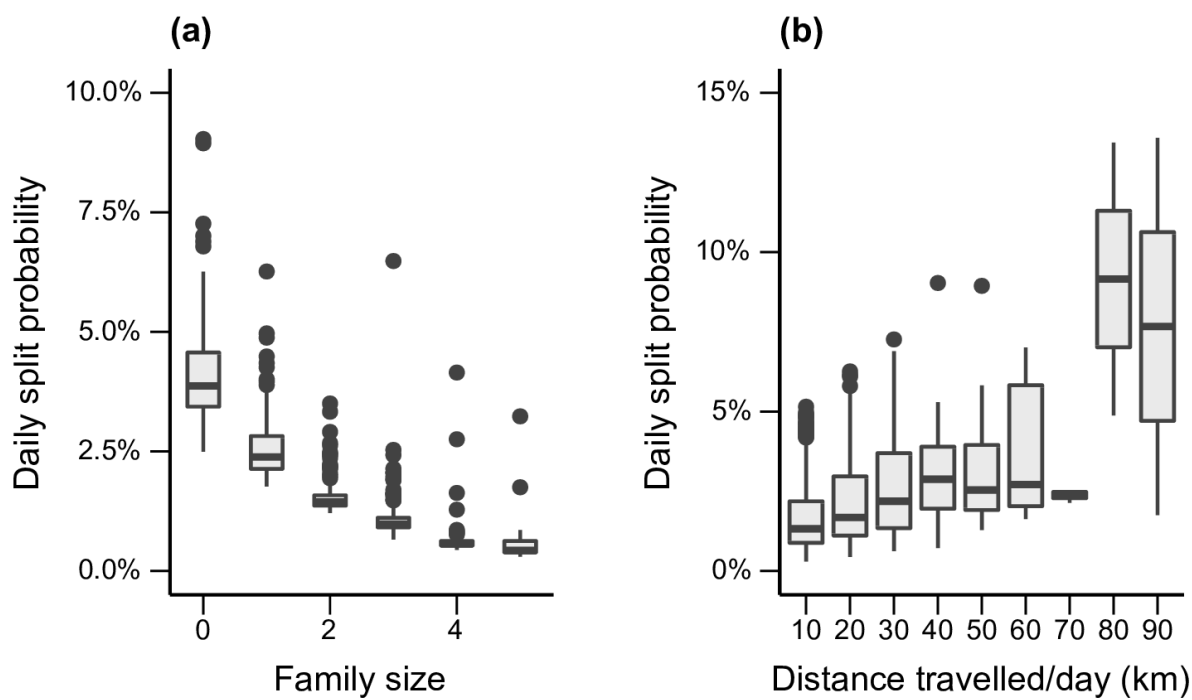
443　　**Fig. 5** Boxplots of daily predicted split probability of GPS tracked families in relation to (a) family size, and (b) daily
444　　distance travelled

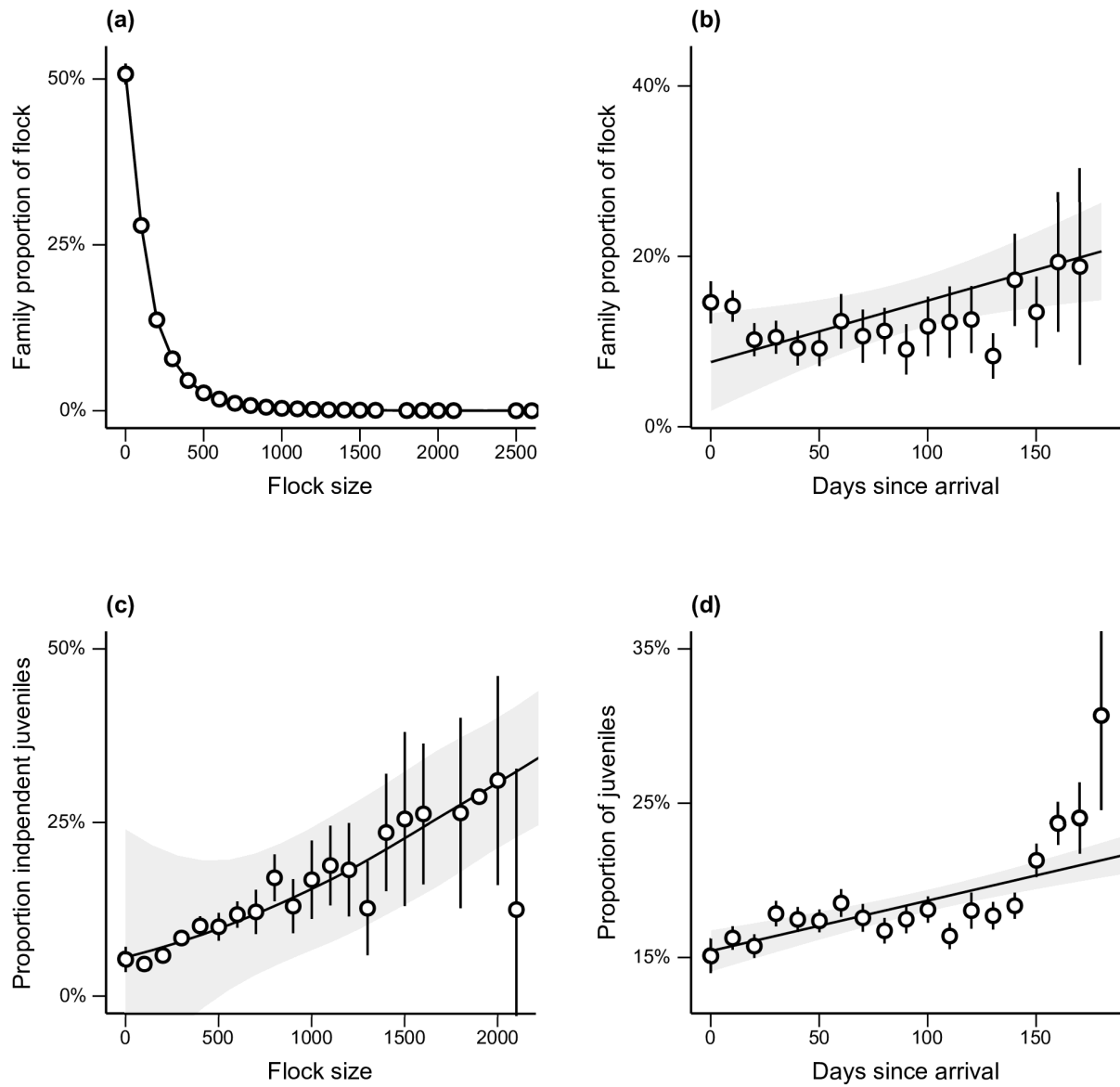446 **Fig. 6** Mean values (symbols) and GLMM fits (lines) for (a) the proportion of flocks composed of family-associated
447 geese at different flock sizes, and (b) the proportion of family-associated birds in a flock as a function of the days
448 since autumn arrivals, (c) the proportion of flock juveniles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