

Abstract

Many species live in family groups where juveniles receive parental care. The families of some large migrating species often stay together through one or more migration events. How the social status of families, pairs and single animals influences their migration timing and space-use is not yet well understood. Here we focus on the family size dynamics of greater white-fronted geese *Anser a. albifrons* on their wintering grounds. We gathered 17 years of observation data on foraging flocks of wintering geese in the Netherlands and northern Germany, and tracked 13 complete families with GPS transmitters. Taking into account effects carried over from the summer, we explored how the distance of the wintering site from the breeding grounds, number of juveniles in a family, number of individuals in a flock and the age-ratio of flocks develop over time. We related the probability of a family splitting to the number and frequency of flight events. Sixty days after the first autumn arrivals, families with more juveniles winter farther west, where flocks are smaller. The number of juveniles in a family, flock size, age-ratio, and the number of families in flocks is correlated with the number of days since first arrival. Families that undertake more flights in winter are more likely to split. Our data suggest that many juvenile white-fronted geese separate from their parents during the winter, and that this species is differentially migratory by age and social class in both autumn and spring. These findings are important for further investigation of the influence of climate and habitat change on large migrants that subsist in families long after hatching, and their conservation and management.

Keywords *Anser albifrons*, family size, differential migration, foraging flocks, family separation

Introduction

Most species' young receive direct or indirect parental care, which improves their own survival and provides inclusive fitness gains to their relatives (Hamilton 1964). Such care is usually in the form of food, shelter and protection (Clutton-Brock 1991). The duration of care varies strongly between and within species (Clutton-Brock 1991). Large migratory species often stay in family groups throughout the first or later migration events (see Warren et al. 1993, Kruckenberg 2005). This has direct survival and fitness benefits for both young and parents in terms of shared vigilance and higher social status within larger aggregations (Black and Owen 1989, Roberts 1996).

Many large waterbirds, such as the geese *Anserini*, live in groups composed of families throughout much of the year. Flocking behaviour is most apparent in winter, when goose families gather to form often enormous feeding flocks (Elder and Elder 1949). Maintaining family bonds within flocks confers benefits as larger social units are dominant over smaller ones, and dominance rank increases with the number of members in the unit (e.g. in Canada geese *Branta canadensis*; Hanson 1953, and barnacle geese *B. leucopsis*; Loonen et al. 1999). The size advantage allows larger families to occupy optimal foraging positions in flocks at lesser cost and win access to better resources (Black et al. 1992; Black and Owen 1989). In addition, parents of some

species benefit in summer from the presence of nest-attending sub-adults (Fox and Stroud 1988).

Over the course of a year, goose family bonds are affected by a number of factors. The success of a pair hatching and fledging young is often determined by a combination of weather conditions and levels of summer predation on the breeding grounds (Dhondt 1987, Summers and Underhill 1987, Bêty et al. 2004). The impact of summer predation linked to the abundance of lemmings and voles *Arvicolinae* has historically been significant in some species, as to be detectable at the population level in winter (Summers and Underhill 1987, Nolet et al. 2013). Autumn migration takes a further toll in long-distance migrants, especially on juvenile birds (Owen and Black 1989, Francis et al. 1992). In spring, juvenile geese often become independent of parents (Prevett and MacInnes 1980, Johnson and Raveling 1988, Black and Owen 1989), but some juveniles may remain associated with parents through the spring migration and on the breeding grounds, where they help to fend off predators and competitors (Ely 1979). Some even remain associated with their parents the following winter (Kruckenberg 2005). The mechanistic causes underlying family separation might be of either accidental nature (Prevett and MacInnes 1980), or the result of adults chasing off juveniles prior to spring migration (Black and Owen 1989, Poisbleau et al. 2008).

The development of family bonds in winter appears to be variable between species and populations. In general, smaller species that are observed in mixed flocks tend to dissolve families in winter (Johnson and Raveling 1988, Jónsson and Afton 2008), whereas larger species tend to maintain families for longer (Warren et al. 1993,

Kruckenberg 2005). Moreover, migration speed and spatial distribution may differ between population classes, such as pairs with and without offspring (Cooke et al. 1975, Cristol et al. 1999, Green & Alerstam 2000, Schamber et al. 2007). Previous studies have noted a change in goose distribution in winter in response to severe cold (Philippona 1966, Lok et al. 1992). Such distributional changes serve as a convenient starting point for an examination of climatic factors affecting spatial patterns in goose flocks and families, especially in light of drastic changes observed in the spatial and migration ecology of similar species sharing the wintering site.

Greater white-fronted geese *Anser a. albifrons*, hereafter white-fronted geese, are among the most abundant geese wintering in continental Western Europe and occupy a wide wintering range (Madsen et al. 1999), thus offering an interesting opportunity to investigate the wintertime dynamics of goose families. We draw on long-term field observations and high frequency GPS tracks of whole families of white-fronted geese from their wintering grounds in the Netherlands and northern Germany to test the following observational hypotheses: 1. Families with more juveniles winter closer to the breeding grounds, 2. Larger families winter in smaller flocks, 3. Families decrease in size over the winter and 4. Family separation is triggered by flight related disturbances.

Methods

Age ratios and family size

We and others observed flocks of feeding geese in winter and determined age-ratios by counting the number of adult and juvenile birds in each flock. In white-fronted geese, both age classes are easy to identify by plumage throughout winter and early spring (Koffijberg 2006). In a sub-sample of flocks, the number of juveniles per pair was assessed (here defined as one family), making use of characteristic behaviour and social interactions. Most counts were carried out at a large number of sites within the core wintering range (Fig. 1A) from October to January (81%), gradually declining in February (11%) and March (7%). April and September had many fewer counts, as most geese still had not arrived, or had already departed in this period. We obtained 7,149 flock counts from 75 observers at 123 geocoded sites. Of these, 1,884 flocks counted by 17 observers at 65 sites held 51,037 successful families (Tab. 1).

Additionally, we took pair status and the number of young from reported sightings of neck-banded individuals, submitted by observers to the www.geese.org portal. In contrast with age-ratio counts, these include records of pairs without accompanying juveniles (defined as unsuccessful families). Observations of marked geese did not include details on habitat type, flock size and observer. Data from 10,635 marked individuals, observed at 8,416 sites, were obtained after filtering for data from single geese without pair status or data on offspring (Tab. 1).

To estimate the effect of autumn migration mortality, 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 records of successful and unsuccessful families were collected (Tab. 1).

Family tracking

We collected half-hourly positions of a total of 13 complete goose families (13 adult pairs, 38 juveniles) fitted with GPS transmitters in the core wintering range within the Netherlands, between November and January (2013, n = 3, 2014, n = 4: e-obs GmbH, backpacks with Teflon harness, weight 45 g; 2016, n = 6: madebytheo, integrated into neckband, weight 35 g). These selectively large families were tracked within the study site (2 - 10°E, 50 - 54°N) during winter (before 1 April) for 34 - 135 days. A reference bird was identified in each family as the parent with the greater number of GPS fixes within the study period, which was the male in all cases except one. For all families, we identified the day and position where splits were first detected as a decrease in the number of family members within a 1000m radius of the reference bird (see Fig. 1A). We then 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. We defined 'flights' as displacements >1 km over the 30 minute sampling interval, and counted their number and daily frequency.

Context data

To relate our observations to the timing of migration we extracted peaks of daily counts ($n = 6,266$) of visible migration in the Netherlands (www.trektellen.nl; Van Turnhout et al. 2009) to determine yearly arrival dates in autumn and departure dates in spring. Data were pooled for 84 spring and 180 autumn counting sites. We excluded counts from sites close to night roosts, and records which did not match the direction of migration appropriate to the season; both in order to avoid bias by local movements.

Following previous work (Jongejans et al. 2015) we estimated an index of summer predation for the breeding grounds of this population from rodent abundance data (www.arcticbirds.net). We calculated a pooled mean of 0 - 2 (low - high) lemming indices for all available sites in the region, taking care to always include a value of 0 to reflect the absence of lemming cycles in the core breeding area on Kolguyev Island. The predation index takes into account the cyclical change in lemming abundance, with higher values when lemming abundance has decreased from the previous year, reflecting the increased predation pressure on Arctic birds due to abundant predators switching to alternative prey (see Dhondt 1987).

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

Analyses

We first tested whether (1.) the number of juveniles, which determines family size, was correlated with the distance from the breeding grounds at which families were observed (family size counts and ring-sighting data; Tab. 1, Supplementary Material Tab. A1).

Further, we tested whether (2.a.) the number of juveniles in a family and (2.b.) the total number of successful families was explained by flock size, the number of days since the arrival of geese in autumn or the level of summer predation (using family size counts; Tab. 1). To test for an effect of climate on the number of successful families in flocks, we added daily minimum temperature, daily total precipitation, and daily mean wind-speed as variables in model 2.b. Further, we tested whether (2.c) the number of juveniles in families was different in the breeding grounds one month prior, and up to two months after autumn migration in 2016 (using family size counts in the wintering region and on Kolguyev Island, and ring-sighting data).

To place these results in a wider context, we examined (3.) how flock size (from age-ratio counts) was related to distance from the breeding grounds, the number of days since arrival, summer predation, climatic variables, and examined whether (4.) the proportion of juveniles in flocks was explained by the flock size, distance from the breeding grounds, number of days since arrival, and summer predation (using age-ratio counts; see Supplementary material Tab. A1).

Further, we examined whether (5.) the daily split probability was predicted by the number of days since arrival, the number of flights on that day, the cumulative number of flights since the beginning of the tracking period until that day, the distance travelled

that day, the cumulative distance travelled since the beginning of tracking until that day, and the family size on that day (using GPS tracking data; Supplementary Material Tab. A1).

All analyses were performed in the R environment (R Core Team 2017) (see Supplementary Material Tab. A1). We used Poisson *lme4* (Bates et al. 2015) linear and generalised linear mixed models (LMMs & GLMMs) to test 1 and 2.a, a simple Poisson-error generalised linear model to test 2.c and a binomial-error GLMM for 5. In 2.b, 3, and 4, we used *mgcv* (Wood 2013) Poisson (2.b) and binomial (4) generalised additive mixed models (GAMMs) to include smooth functions of the flock size (in 2.b) and the number of days since winter (in 4) as predictors. We included the breeding year, the observer identity, the goose identity if known, and the habitat type as independent random effects. Effects included in models were dependent on their availability in the datasets used (see Supplementary Material Tab. A1).

Results

Age ratios and family sizes

The mean flock size was 712 birds (range: 2 - 20,000), with a mean proportion of first-winter birds of 0.18 (range: 0 - 0.87). Flocks in which families were counted (family size counts) held on average 540 birds (range: 3 - 11,000), with an average of 27 families (range: 1 - 333) accompanied by a mean of 1.78 juveniles (range: 1 - 10).

On average, the family status of marked geese (ring-sighting data) was recorded 626 times each year (range: 62 - 1143), and these were accompanied by 0.59 juveniles (range: 0 - 11) (see Appendix 1, Supplementary material Figs. A1.1, A1.2). The 116 observed families on Kolguyev Island in 2016 had a mean of 2.26 juveniles (range: 0 - 6).

Context data

Autumn migrants arrived between 26 September to 30 October, and flocks departed between 3 March to 1 April, resulting in a wintering period for geese of on average 165 days (range: 124 - 183). Lemming abundance from the breeding grounds transformed into a predation index ranged between 1.17 and 1.9, with very low variance between years ($\sigma^2 = 0.048$).

Juveniles and wintering site choice

We found no influence of the number of juveniles in a family on how far from the breeding grounds a family wintered in the first sixty days after arrival, neither in age-ratio data ($\chi^2 = 3.27$, $p = 0.071$), nor in ring-sighting data ($\chi^2 = 2.18$, $p = 0.134$, Fig. 2). Later in winter, age-ratio data indicated that larger families winter somewhat farther west ($\chi^2 = 6.026$, $p = 0.014$), while ring-sighting data did not reveal any difference ($\chi^2 = 0.023$, $p = 0.879$). Even when selecting only the successful families in the ring-sighting data, no effect could be found ($\chi^2 = 0.892$, $p = 0.345$). This difference is likely due to lower sample size and fewer observed random effects in the ring-sighting data. The

proportion of successful pairs, assessed by ring-sighting data, was not related to the distance of their wintering site from the breeding grounds ($\chi^2 = 1.071$, $p = 0.301$).

Family size in winter

The number of juveniles in a family (successful families counted in flocks, model 2.a) decreased through the winter ($\chi^2 = 74.166$, $p < 0.001$, see Fig. 3), but was insensitive to flock size ($\chi^2 = 0.270$, $p = 0.6033$) and summer predation ($\chi^2 = 0.337$, $p = 0.562$, see Supplementary material Fig. A2). Family sizes of neckbanded geese (model 2.a adapted) decreased over time as well ($\chi^2 = 19.936$, $p < 0.001$, see Fig. 3); flock sizes of this dataset were not available.

Surprisingly, family sizes of neckbanded geese increased with the level of summer predation ($\chi^2 = 12.935$, $p < 0.001$, see Supplementary material Fig. A2). However, this increase was very low with on average 0.78 additional juveniles per family per unit increase in the predation index. When excluding unsuccessful pairs from the neckband-resighting data, the relation with summer predation became insignificant ($\chi^2 = 0.1321$, $p = 0.716$, see Supplementary material Fig. A2), indicating a qualitative rather than quantitative effect of predation on nest success.

The number of successful families in flocks (model 2.b) increased with flock size ($\chi^2 = 7250$, $p < 0.001$) and the number of days since goose arrival in autumn ($\chi^2 = 158.3$, $p < 0.001$, see Fig. 4A), but was unaffected by summer predation ($\chi^2 = 0$, $p = 0.98$). Further, there were more successful families in flocks farther from the breeding grounds ($\chi^2 = 11.253$, $p = 0.0008$, see Fig. 5A). Also, the number of successful families in a flock was

higher when daily minimum temperatures were higher ($\chi^2 = 7.318$, $p = 0.007$), and decreased weakly with rising daily precipitation ($\chi^2 = 3.931$, $p = 0.047$). Wind speed was not an important predictor ($\chi^2 = 2.644$, $p = 0.104$).

Flock size in winter

Flocks (model 3) were significantly smaller farther from the breeding grounds ($\chi^2 = 93,629$, $p < 0.001$, see Fig. 5A), and grew slightly over the winter ($\chi^2 = 4,824$, $p < 0.001$). Flock size was affected by each of the climatic predictors, decreasing with worsening weather: increasing precipitation ($\chi^2 = 3193$, $p < 0.001$) and increasing daily wind speed ($\chi^2 = 25,906$, $p < 0.001$). However, flock sizes increased with decreasing daily minimum temperatures ($\chi^2 = 365$, $p < 0.001$).

Within flocks, juvenile proportions increased through the winter ($\chi^2 = 18.82$, $p = 0.001$, see Fig. A4b), and decreased with increasing flock size ($\chi^2 = 5.921$, $p = 0.015$, see Fig. A4c), but did not show any effect of distance from the breeding grounds ($\chi^2 = 0.979$, $p = 0.323$), or of summer predation ($\chi^2 = 0.013$, $p = 0.908$).

Family size prior to autumn migration

Families of geese observed approximately one month prior to the onset of migration in the breeding area on Kolguyev Island had significantly more juveniles than successful families (family size count) in flocks (GLM, $z = -4.285$, $p < 0.001$) and families of marked

geese (ring-sighting data) (GLM, $z = -14.511$, $p < 0.001$) recorded in the first two months following the population's arrival on the wintering grounds (model 2.c).

Probability of family splits

Families fitted with GPS transmitters travelled on average 11 km each day (range: 0 - 306). On average, they travelled a distance > 1 km twice per day (range: 0 - 10) and in total 98 times (range: 63 - 367) over the tracking period. 21 family split events were recorded in the 13 families and were not restricted to juveniles.

The daily split probability of families (model 5) was significantly lower later in the winter ($\chi^2 = 8.314$, $p = 0.004$, Fig 6A), and lower in larger families ($\chi^2 = 11.41$, $p < 0.001$, Fig 6C).

There was no effect of the daily number of flights ($\chi^2 = 0.018$, $p = 0.893$), nor the daily distance moved ($\chi^2 = 2.99$, $p = 0.083$). Split probability was higher in families that made cumulatively more flights in the period between the beginning of tracking and the split ($\chi^2 = 143.23$, $p < 0.001$, Fig 6D), and increased in families that moved a longer cumulative distance in the period between the start of tracking and the split ($\chi^2 = 182.63$, $p < 0.001$, Fig 6B).

Discussion

We have quantified the spatial-temporal distribution and size dynamics of white-fronted goose families in wintering flocks in the context of winter climate, predation risk in summer, and mortality during autumn migration. In support of our hypothesis, we found

that large families wintered farther from the breeding grounds, but only during the second half of winter. Larger families did not select for smaller flocks, but flocks were generally smaller in the west. As expected, family size did decrease over the winter, but our results indicate that families were less likely to separate later in winter and with increasing family size. We found some evidence for the suggestion that families that flew more often were more likely to separate, split events thus likely being accidental during disturbance events.

Spatial dynamics of family size

Our baseline result that flock sizes are smaller in the west of the wintering region, i.e. further from the breeding sites, can be explained by metabolic constraints that determine maximum flight distances and duration even during migration (Klaassen 1996). This explanation is supported by the fact that family sizes did not vary spatially during the first winter months. However, once all geese have arrived and wintering sites begin filling up. As food becomes more limited, it seems that large, socially dominant families (Vangilder and Smith 1985, Schamber et al. 2007) move further to occupy climatically milder sites. This supports the earlier suggestion of differential use of wintering sites (Jongejans et al. 2015) according to social status.

Contrary to expectations, larger families were generally not associated with smaller flocks. Rather, it was a coincidence that larger families as well as small flocks were found further from the breeding sites. Furthermore, spatial differences in family wintering

areas might have led to the finding that larger flocks appeared to have a lower proportion of juveniles (Jongejans et al. 2015). Large goose families selecting for optimal sites seem to be one driver of the variation in juvenile proportion between wintering sites (Schamber et al. 2007). However, independent juveniles observed in wintering flocks (Hanson 1953, Loonen et al. 1999) may dampen this variation.

Temporal dynamics of family size

The finding that family size decreased through the winter points towards a steady reduction in the number of juveniles associated with families, and to high variation in the age at which young geese leave their parents. Some young geese may be found associated with the parents even in their second or third winter (Ely 1979, Warren et al. 1993, Kruckenberg 2005). The separation of juveniles from their parents should result in a reduction of the number of successful families in flocks over the winter. However, we could not find such a pattern, rather the opposite. This might be partly explained by the suggestion that most pairs do not become dissociated from all their young during winter, i.e., that split events are accidental rather than triggered by the parents (Prevett and MacInnes 1980). Furthermore, families with juveniles might have departed later for spring migration than pairs without young, mirroring their differential autumn migration arrival which is later than other adult geese (Jongejans et al. 2015).

This proposed differential migration timing is further supported by the strong, non-linear temporal increases of proportions of juveniles in foraging flocks. The general hypothesis may be put forward that it is adults without young that first leave the wintering grounds

for northerly breeding and moulting sites on spring migration, followed by families with young, with independent juveniles bringing up the rear. Our finding runs contrary to previous studies on the spring migration of pink-footed *A. brachyrhynchus* and snow geese (Madsen 2001; Bêty et al. 2004). Interestingly though, juvenile snow geese generally also apparently follow a migration schedule that is different from the adults (Prevett and MacInnes 1980).

Data from the 13 GPS tracked goose families support the suggestion that dissociations of juveniles from their families are accidental during winter (Prevett and MacInnes 1980). In most cases, juveniles split off one at a time, and not all at once. The daily probability of families losing young increased with cumulative flight time. However, our finding that split probability was reduced towards the end of winter contradicts our results from counting data, and previous findings that most juveniles were more likely to become independent towards spring (Prevett and MacInnes 1980, Johnson and Raveling 1988, Black and Owen 1989, Scheiber et al. 2013). A likely explanation might be found in relation to the previous result that larger families were less likely to split, as our 13 tracked families were selected to be large.

Effects of winter climate conditions

The negative responses of number of successful families in flocks and flock size to cold and wet weather are in line with current knowledge of goose foraging preferences (Fox and Madsen 2017). Geese have been found to tolerate snow depths of about 15 cm before relocating to areas with better access to forage (Philippona 1966). Such

conditions have become rare over the past decade and usually do not occur in the Netherlands before midwinter. This is in accordance with spatial differences in family size only being observed in late winter. Large, dominant families thus seek to occupy the rather limited western, coastal sites with moderate temperatures. Limited habitat availability in the west of the Netherlands and Belgium, combined with high hunting pressure in France, and the high energetic costs of long flights seem to lead to geese aggregating in large flocks on the remaining accessible grassland sites on cold, snowy days.

Relation to breeding sites

Our result that families were significantly larger prior to migration than in the first two months on the wintering grounds is in line with previous findings of high juvenile autumn mortality (Owen and Black 1989; Francis et al. 1992). As in those studies, we assume that mortality in our population is also mainly due to higher parasitic loads and strong density-driven competition for resources prior to and during autumn migration. Previously, juvenile survival of Arctic-breeding birds, including geese, was understood to be driven by predation, which in turn was driven by the cyclical abundance of Arctic rodents (Summers and Underhill 1987). However, our study supports the idea that the breeding success of white-fronted geese on the Baltic-North Sea flyway is unrelated to summer predation in recent years (Jongejans et al. 2015). This may be possibly due to faltering lemming cycles (Nolet et al. 2013), or because an increasing proportion of the population breeds in areas like Kolguyev Island, that altogether lack Arctic rodents and

associated phenomena (Kruckenberg et al. 2008). On the other hand, our finding that the number of juveniles seen with marked geese increased during years of increased predation suggests a qualitative rather than quantitative response, to wit that in years of high predation, some geese succeed in raising large families, but many more suffer total brood failure.

General conclusion

Based on the spatial and temporal patterns of wintering goose families, we argue that management actions (Stroud et al. 2017) have to consider that the proportion of juvenile geese in foraging flocks is higher in some areas and times of the year. It is crucial to distinguish between adult survival and recruitment for population control (Madsen 2010), as well as conservation effort. Climate, habitat change, and change of feeding habits are suggested to have led to increased goose densities, range expansion and range shifts (Fox et al. 2005). As high densities lead to low recruitment in the Arctic breeding grounds (Owen and Black 1989, Francis et al. 1992), goose populations might become less flexible and highly vulnerable to rapidly changing conditions. Furthermore, our results show that higher levels of disturbance in the wintering sites and migration stopovers, e.g. as a result of increased management actions, would induce more goose family splits and additionally change population structure and survival rates. Such disruption of the mechanisms of cultural transmission of space use could cause levels of adaptability to changing environmental conditions to change in unpredictable ways.

References

1. Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. - Journal of Statistical Software 67: 1-48.
2. Bêty, J. et al. 2004. Individual variation in timing of migration: Causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). - Behavioral Ecology and Sociobiology 57: 1-8.
3. Black, J. M. and Owen, M. 1989. Parent-offspring relationships in wintering barnacle geese. - Animal Behaviour 37: 187-198.
4. Black, J. M. et al. 1992. Foraging dynamics in goose flocks: The cost of living on the edge. - Animal Behaviour 44: 41-50.
5. Clutton-Brock, T. H. 1991. The evolution of parental care. - Princeton University Press.
6. Cooke, F. et al. 1975. Gene flow between breeding populations of Lesser Snow Geese. - The Auk 92: 493-510.
7. Crozier, R. H. and Pamilo, P. 1996. Evolution of Social Insect Colonies. - Oxford University Press, Oxford, UK.
8. Dhondt, A. A. 1987. Cycles of lemmings and Brent geese *Branta b. bernicla*: A comment on the hypothesis of Roselaar and Summers. - Bird Study 34: 151-154.

9. Elder, W. H. and Elder, N. L. 1949. Role of the family in the formation of goose flocks. - Wilson Bull 61: 133-140.
10. Ely, C. R. 1979. Breeding biology of the white-fronted goose (*Anser albifrons frontalis*) on the Yukon-Kuskokwim delta, Alaska.
11. Fox, A. D. and Stroud, D. A. 1988. The breeding biology of the Greenland White-fronted Goose (*Anser albifrons flavirostris*). - Kommissionen for Videnskabelige Undersøgelser i Grønland.
12. Fox, A. D. and Madsen, J. 2017. Threatened species to super-abundance: The unexpected international implications of successful goose conservation. - Ambio 46: 179-187.
13. Fox, A. et al. 2005. Effects of agricultural change on abundance, fitness components and distribution of two Arctic-nesting goose populations. - Global Change Biology 11: 881-893.
14. Francis, C. M. et al. 1992. Long-term changes in survival rates of lesser snow geese. - Ecology 73: 1346-1362.
15. Green, M. and Alerstam, T. 2000. Flight speeds and climb rates of brent geese: Mass-dependent differences between spring and autumn migration. - Journal of Avian Biology 31: 215-225.
16. Hamilton, W. 1964. The genetical evolution of social behaviour. I. - Journal of Theoretical Biology 7: 1-16.

17. Hanson, H. C. 1953. Inter-family dominance in Canada geese. - The Auk 70: 11-16.
18. Johnson, J. C. and Raveling, D. G. 1988. Weak family associations in Cackling Geese during winter: Effects of body size and food resources on goose social organization. - Waterfowl in Winter: 71-89.
19. Jongejans, E. et al. 2015. Naar een effectief en internationaal verantwoord beheer van de in Nederland overwinterende populatie Kolganzen. - SOVON Vogelonderzoek Nederland.
20. Jónsson, J. E. and Afton, A. D. 2008. Lesser Snow geese and Ross's geese form mixed flocks during winter but differ in family maintenance and social status. - The Wilson Journal of Ornithology 120: 725-731.
21. Klaassen, M. 1996. Metabolic constraints on long-distance migration in birds. - Journal of Experimental Biology 199: 57-64.
22. Koffijberg, K. 2006. Herkenning en ruipatronen van eerstejaars kolganzen in de winter. - Limosa 79: 163.
23. Kruckenberg, H. 2005. Wann werden "die Kleinen" endlich erwachsen? Untersuchungen zum Familienzusammenhalt farbmarkierter Blessgänse *Anser albifrons albifrons*. - Vogelwelt 126: 253.
24. Kruckenberg, H. et al. 2008. White-fronted goose flyway population status. - Angew. Feldbiol 2: 77.

25. Lok, M. et al. 1992. Numbers and distribution of wild geese in the netherlands, 1984-89, with special reference to weather conditions. - Wildfowl 43: 107-116.
26. Loonen, M. J. J. E. et al. 1999. The benefit of large broods in barnacle geese: A study using natural and experimental manipulations. - Journal of Animal Ecology 68: 753-768.
27. Madsen, J. 2001. Spring migration strategies in Pink-footed Geese *Anser brachyrhynchus* and consequences for spring fattening and fecundity. - Ardea 89: 43-55.
28. Madsen, J. 2010. Age bias in the bag of pink-footed geese *anser brachyrhynchus*: Influence of flocking behaviour on vulnerability. - European Journal of Wildlife Research 56: 577-582.
29. Madsen, J. et al. 1999. Goose populations of the Western Palearctic. - National Environmental Research Institute, Denmark; Wetlands International, Wageningen, The Netherlands.
30. Nolet, B. A. et al. 2013. Faltering lemming cycles reduce productivity and population size of a migratory Arctic goose species. - Journal of Animal Ecology 82: 804-813.
31. Owen, M. and Black, J. M. 1989. Factors affecting the survival of barnacle geese on migration from the breeding grounds. - Journal of Animal Ecology 58: 603-617.
32. Philippona, J. 1966. Geese in cold winter weather. - Wildfowl 17: 3.

33. Poisbleau, M. et al. 2008. Dominance relationships in dark-bellied brent geese *Branta bernicla bernicla* at spring staging areas. - *Ardea* 96: 135–139.
34. Prevett, J. P. and MacInnes, C. D. 1980. Family and Other Social Groups in Snow Geese. - *Wildlife Monographs*: 3–46.
35. R Core Team 2017. R: A language and environment for statistical computing. - R Foundation for Statistical Computing.
36. Roberts, G. 1996. Why individual vigilance declines as group size increases. - *Animal behaviour* 51: 1077–1086.
37. Schamber, J. L. et al. 2007. Latitudinal variation in population structure of wintering Pacific Black Brant. - *Journal of Field Ornithology* 78: 74–82.
38. Scheiber, I. B. et al. 2013. The Social Life of Greylag Geese. - Cambridge University Press.
39. Stroud, D. A. et al. 2017. Key actions towards the sustainable management of european geese. - *Ambio* 46: 328–338.
40. Summers, R. and Underhill, L. 1987. Factors related to breeding production of Brent geese *Branta b. bernicla* and waders (*Charadrii*) on the Taimyr Peninsula. - *Bird Study* 34: 161–171.
41. Van Turnhout, C. et al. 2009. Veranderingen in timing van zichtbare najaarstrek over Nederland: Een pleidooi voor hernieuwde standaardisatie van trektellingen. - *Limosa* 82: 68.

462 42. Vangilder, L. D. and Smith, L. M. 1985. Differential distribution of wintering brant
463 by necklace type. - The Auk 102: 645-647.

464 43. Warren, S. M. et al. 1993. Extended parent-offspring relationships in Greenland
465 White-fronted geese (*Anser albifrons flavirostris*). - The Auk 110: 145-148.

466 44. Wood, S. N. 2013. Generalized additive models: An introduction with R. -
467 Chapman; Hall/CRC.

468 Supplementary material. Appendix 1.
469
470

Type	Records	Sites	Spatial extent
Age-ratio counts	7,149	123	4.0° - 8.8°E, 51.1° - 53.4°N
Family sizes	51,037	65	4.8° - 7.3°E, 51.1° - 53.4°N
Ring-sighting data	10,635	8,416	2.7° - 9.7°E, 50.9° - 53.9°N
Familie sizes on Kolguyev	116	26	49°E, 69°N
GPS tracking of families	32,630 ^a , 13 ^b	32,630	3.9° - 7.9°E, 51.3° - 54.3°N
a: Half-hourly family positions, b: Number of families tracked			

Table 1: Datasets of goose observations and tracking.