

# Family size dynamics in wintering geese

## Introduction

Families are important components of animal groups. In the most extreme case, eusocial insect colonies are composed entirely of related individuals (Crozier and Pamilo 1996). Preference for kin holds in more complex vertebrates as well. For example, African savannah elephants *Loxodonta africana* living in unstable matriarchal fission-fusion societies prefer to remain part of a smaller 'core' group of their direct female relatives when larger groups split (Archie et al. 2006). Inclusive fitness through kin selection is posited as the basis for cooperation within groups (Hamilton 1964). However, spotted hyaena *Crocuta crocuta* clans which cooperate in risky behaviours such as hunting and conflict may also contain matrilineal units with low inter-relatedness (Van Horn et al. 2004).

Among waterfowl such as Canada geese *Branta canadensis*, family groups underlie the formation of migratory flocks (Elder and Elder 1949), and family membership confers benefits. For example, in tundra swans *Cygnus columbianus* and barnacle geese *B. leucopsis*, the maintenance of family bonds in wintering flocks is advantageous since families are dominant over pairs and singles (Badzinski 2003, Poisbleau et al. (2006)). Family dominance rank increases with the number of juveniles in snow Anser *caerulescens* and barnacle geese (Gregoire and Ankney 1990, Loonen et al. (1999)), and larger families of barnacle geese can occupy optimal foraging positions within flocks at lesser cost, thereby winning access to better resources (Black et al. 1992). The development of family bonds over the winter is not fully understood, and appears to be variable. Larger taxa such as giant Canada geese *B. canadensis maxima* appear to maintain family bonds longer (Warren et al. 1993), while smaller Ross' A. *rossii* and cackling geese *B. hutchinsii* show only weak family associations in winter (Johnson and Raveling 1988, Jónsson and Afton (2008)).

Geese can show high fidelity to wintering sites and food type (Wilson et al. 1991), and the need for geese to teach juveniles to locate and handle high quality foods may contribute to the continuation of parent-offspring bonds over multiple breeding years (Warren et al. 1993). When maintained, extended family bonds increase the fitness of both parents and young, with the presence of adults allowing barnacle geese more uninterrupted feeding in winter (Black and Owen 1989). Parents benefit in summer from the presence of nest-attending subadults from earlier broods who help in herding young, and in agonistic interactions, both against conspecifics (Conover

2012) and predators (Fox and Stroud 1988). This increases the chance of parents associated with their young in winter returning with young the following year (Black and Owen 1989).

Studies of family size at winter sites must take into account that waterfowl, like many birds, are often differentially migratory, with population classes selecting different wintering sites (Cristol et al. 1999). Segregation on the basis of sex along latitude is well studied in ducks (Leopold 1919, Nichols and Haramis (1980), Carbone and Owen (1995)). Among the geese, Pacific black brent geese *Branta bernicla nigricans* with a greater likelihood of breeding success were found wintering closer to their summer grounds (Schamber 2001). Further, more juveniles of the species winter closer to the breeding grounds (Schamber et al. 2007), as do more dominant social units (Vangilder and Smith 1985). Brent geese migrate in families, and the presence of juveniles is expected to affect the flight of adults (Green and Alerstam 2000). Within this context, it is not clear how the number of juveniles accompanying a pair on autumn migration influences where they will winter.

Any variation in goose family size must include the effect of the summer abundance of rodents, primarily the lemmings *Lemmus sibiricus* and *Dicrostonyx torquatus*, on the breeding success of Arctic birds (Angelstam et al. 1984). Geese are predicted to be least successful in years when lemming density is low and that of predators is high (Dhondt 1987). This lowering effect of summer predation on the proportion of first winter juveniles has been described in both waders *Charadrii* and dark-bellied brent geese *Branta bernicla bernicla* wintering in Scandinavia (Summers and Underhill 1987, Blomqvist et al. (2002)) and the Netherlands (Nolet et al. 2013). However, the mechanism by which predation pressure at the family level translates into population level effects is not well understood.

Among geese, family fission is simultaneously disadvantageous and reportedly the norm. This makes its ultimate evolutionary and proximate behavioural causes particularly interesting to study. At the proximate level, snow goose families are hypothesised to split on the wintering grounds when abrupt threat-induced flights prevent pre-flight coordination between members. Separated birds either remain airborne or systematically search nearby flocks until a family member is seen (Prevett and MacInnes 1980), and similar behaviour is observed in Canada geese (Elder and Elder 1949). Splits are likelier in larger flocks, which present greater challenges to maintaining family contact (Prevett and MacInnes 1980).



**Fig. 1:** Wintering grounds of greater white-fronted geese *Anser a. albifrons* in the Netherlands and north-west Germany with sites (dots,  $n = 64$ ) where successful families ( $n = 51,037$ ) within flocks ( $n = 1,884$ ) were recorded. Diamonds mark fission ( $n = 19$ ) in GPS tracked families ( $n = 13$ ). Shaded area bounds observations ( $n = 10,635$ ) of marked geese. Inset shows breeding grounds (ellipse) and wintering grounds (rectangle). Data were collected from 2000 - 2016.

Investigating the role of flight events in family size dynamics would require accurate, fine-scale knowledge of individual positions. Obtaining such data for highly mobile species has historically presented challenges.

Greater white-fronted geese *Anser albifrons albifrons*, hereafter whitefronts, are the most populous true geese wintering in continental western Europe (Fox and Madsen 2017), and offer an interesting opportunity to investigate the dynamics of Arctic goose families over space and time. Accounts from the wintering grounds suggest that in the Baltic-North Sea flyway population of whitefronts (Philippona 1972), successful families winter farther west than smaller ones. Further, these families are observed in smaller flocks, but a decreasing size of flocks from east to west confounds this. Family bonds reportedly weaken over a single winter, in contrast to the multi-year bonds of the Greenland subspecies *flavirostris* (Warren et al. 1993).

We draw on field observations and high frequency GPS tracks of whole families of whitefronts from their wintering grounds in the Netherlands and northern Germany (Mooij 1991), where they have been censused for some decades. The migration route, starting in the Russian Nenets, Yamal and Krasnoyarsk regions (Madsen and Cracknell 1999, Kruckenberg et al. 2008), spans a larger longitudinal than latitudinal gradient, the effect of which has not been extensively studied in migratory waterfowl. We exploit these peculiarities to test the expectations that: 1. Larger families winter to the west,

further from the breeding grounds 2. Larger families winter in smaller flocks, 3. Families decrease in size over the winter. Further, we attempt to test whether family fission is related to flight events.

## Methods

We used a combination of historical and contemporary white-front winter distributions (Mooij 1991, Madsen and Cracknell 1999, Fox et al. 2010) from north-western continental Europe to define our study area (0°E - 10°E, 50°N - 54°N). Whitefronts here have stabilised at around 1.4 million individuals from historic lows in the 1960s, following several years of conservation-enabled exponential growth (Fox et al. 2010, Fox and Madsen 2017).

Within this area, we collected the following classes of data from between the period autumn 2000 - spring 2017: (A) Flock counts in which observers censused flocks of whitefronts, (B) Family counts in which observers counted the sizes of successful families with at least one first winter juvenile (hereafter, juvenile) within a subset of the flocks above, (C) Observations of individually marked geese, including unsuccessful birds seen in a pair, and (D) Positions of goose families fitted with GPS loggers (e-obs GmbH, Grünwald, Germany, & madebytheo, Amsterdam, Netherlands), including flight events. These data were filtered to exclude records outside the spatial and temporal limits of our study. Records of single

marked geese without juveniles were also excluded.

We also collected records of goose flight activity from Trek-tellen (*trektellen.org*) sites across the Netherlands. We excluded flight activity records from sites close to night roosts, and records which did not match the direction of migration appropriate to the season. We used these data to find the beginning and end of the goose winter, which we took to begin with the first mass arrival of geese in autumn, and to end with the last mass departure in spring.

Following Jongejans et al. (2015), Blomqvist et al. (2002) and Nolet et al. (2013), we estimated an index of summer predation for the breeding grounds of this population from rodent abundance data available online (*arcticbirds.net*). We calculated a pooled mean of 0 - 2 (low - high) lemming indices from sites in the region, taking care to include a value of 0 in each year to reflect absence of a lemming cycle in the core breeding area on Kolguyev. The index reflects higher values in years when lemming abundance had decreased significantly from the previous year.

We first tested whether (A) the number of juveniles, hereafter family size, explained the distance from the breeding grounds at which families were recorded. Within flocks, we tested whether (B.1) family sizes, and (B.2) the total number of families were explained by the number of birds in the flock, hereafter flock size, the number of days since the arrival of geese in autumn, and the level of summer predation. Finally, we tested predictors of the probability of family fission. We examined whether (B.3) the daily split probability each day was predicted by the days since arrival, the number of flights, the cumulative number of flights, the distance travelled, the cumulative distance travelled, and the family size. For a subset of the tracked families bearing flight recording loggers, we examined (B.4) the half-hourly split probability in relation to the time since the last flight and the distance travelled in the previous half hour.

To add context, we searched for (C) an effect on flock size of distance from the breeding grounds, the number of days since arrival, and summer predation, and examined whether (D) 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. All analyses were performed in the R environment (R Core Team 2017).

We used generalised linear mixed models (GLMMs) as implemented by the *lme4* package (Bates et al. 2015) in cases A, B.1, B.3, B.4 and C, where we expected linear relationships. In cases B.2 and D, we sought to include smooth functions of covariates as predictors, and used generalised additive mixed models (GAMMs) as implemented by the *gam4* and *mgcv* packages when specifying nested and *iid* random effects, respectively (Wood 2013, Wood and Scheipl 2016). We specified the following *iid* random effects when using datasets A and B: breeding year (hereafter, year), observer identity and habitat type. Models using dataset C and D included goose or family identity and breeding year as random effects. We assessed

the importance of each predictor using Type II Wald  $\chi^2$  tests.

## Results

We gathered data on flock sizes, sizes of families in flocks, observations of marked geese, the positions of GPS tracked families of geese, and supplementary information on the flight activity of geese in the wintering areas, and on the abundance of Arctic rodents on their breeding grounds. After filtering the data (mapped in figure 1), we obtained 7,149 flock counts from 75 observers at 123 geocoded sites. Of these, 1,884 flocks counted by 17 observers at 64 sites yielded 51,037 successful families. A further 10,635 marked geese were observed at 8,416 sites. We could not obtain data on the habitat type, flock size, and observer identity for these records.

Half-hourly positions from 64 individual geese (13 adult pairs, 38 juveniles) in 13 families were recorded in the winters of 2013 ( $n = 3$ ), 2014 ( $n = 4$ ), and 2016 ( $n = 6$ ). 2016 families carried accelerometer coupled position loggers which recorded 0.5 Hz flight bursts. On average, families were tracked for 78 days ( $SE = 8.44$ ), travelling 11 km per day ( $SE = 0.6$ ). At the daily scale, we defined flights as movements of above 1000 metres. Families flew a mean of twice ( $SE = 0.05$ ) per day, and 98 times ( $SE = 2.6$ ) over the tracking period. For 2016 families, we identified true flight activity, which occurred 5 times ( $SE = 0.11$ ) times a day, and 468 times ( $SE = 63$ ) over the tracking period. 21 family fission events occurred and were not restricted to juveniles.

Goose flight activity records from 84 spring and 180 autumn sites (overlap = 72) yielded 6,266 days of data. Geese began to arrive between September 26 and October 30, and the last geese left between March 03 and April 01, resulting in a mean goose winter of 165 days. Lemming abundance from the breeding grounds transformed into a predation index ranged between 1.17 and 1.9, with very low variance ( $\sigma^2 = 0.048$ ).

We found no influence of family size on how far from the breeding grounds a family wintered in the first sixty days after arrival (datasets B and C, model A,  $\chi^2_B = 1.135$ ,  $p_B = 0.286$ ,  $\chi^2_C = 2.007$ ,  $p_C = 0.157$ ). Later in the winter, larger families from dataset B wintered farther west ( $\chi^2 = 4.194$ ,  $p = 0.041$ ), while dataset C did not reveal any influence of family size on wintering site ( $\chi^2 = 0.27$ ,  $p = 0.6033$ , see Fig. 2). In all cases, geese were found farther west later in the winter ( $\chi^2 = 116.5641$ ,  $p < 2 \times 10^{-16}$ ).

Family size (dataset B, model B.1) was insensitive to flock size ( $\chi^2 = 0.270$ ,  $p = 0.6033$ ) and summer predation ( $\chi^2 = 0.337$ ,  $p = 0.562$ ), but decreased through the winter ( $\chi^2 = 74.166$ ,  $p < 2 \times 10^{-16}$ ). Family sizes of marked geese (dataset C) decreased over time ( $\chi^2 = 19.936$ ,  $p = 8.01 \times 10^{-6}$ ), but showed an increase with the level of summer predation ( $\chi^2 = 12.935$ ,  $p = 3.2 \times 10^{-4}$ ). We tested whether the exclusion of unsuccessful pairs from family counts in flocks biased the data by similarly excluding such records from observations of

marked geese. We confirmed this bias in sampling method by failing to find any effect of summer predation after excluding unsuccessful pairs from data *C* ( $\chi^2 = 0.1321$ ,  $p = 0.716$ ).

The daily probability of families fissioning was significantly lower later in the winter ( $\chi^2 = 8.314$ ,  $p = 0.004$ ), and lower in larger families ( $\chi^2 = 11.41$ ,  $p = 7.32 \times 10^{-4}$ ). 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 more flights in total ( $\chi^2 = 143.23$ ,  $p < 2 \times 10^{-16}$ ), but decreased in families that moved more overall ( $\chi^2 = 182.63$ ,  $p < 2 \times 10^{-16}$ ). At a finer scale, split probability increased with time since the previous flight ( $\chi^2 = 6.07$ ,  $p = 0.014$ ), but was not related to the distance travelled in the previous half hour ( $\chi^2 = 0.389$ ,  $p = 0.533$ ).

Flocks were significantly smaller farther from the breeding grounds ( $\chi^2 = 66599$ ,  $p < 2 \times 10^{-16}$ ), and grew slightly over the winter ( $\chi^2 = 4975$ ,  $p < 2 \times 10^{-16}$ ). Larger flocks also had more families ( $\chi^2 = 7777$ ,  $p < 2 \times 10^{-16}$ ). Within flocks, juvenile proportions increased through the winter ( $\chi^2 = 19.43$ ,  $p = 0.001$ ), and decreased with increasing flock size ( $\chi^2 = 5.921$ ,  $p = 0.015$ ), but did not show any effect of distance from the breeding grounds ( $\chi^2 = 1.015$ ,  $p = 0.314$ ), or of summer predation ( $\chi^2 = 0.021$ ,  $p = 0.883$ ). We tested whether this result was due to the use of unverified lemming abundance data by substituting the predation index calculated by Nolet et al. (2013) from published (Kokorev and Kuksov 2002) and novel trapping data, but again found no effect ( $\chi^2 = 1.835$ ,  $p = 0.175$ ).

## Discussion

We studied how the size of whitefront families is related to where, when and with how many flockmates they are seen in the wintering grounds. The size of successful families was not a determinant of where they were seen in the first two months after the arrival of the population in autumn, but in the remaining period, larger families were found farther to the west (Fig. 2). This is at odds with the pattern in black brent geese, in which more dominant social units winter at sites closer to the breeding areas (Vangilder and Smith 1985). It further suggests that the point of arrival of geese on the wintering grounds is controlled by extrinsic factors such as weather or flock heading, and that an assortment period is required before they settle on long-term wintering areas, to which they can be quite faithful (Wilson et al. 1991).

A decrease in family sizes over time was seen in all our datasets, indicating a swift reduction in the strength of bonds (Fig. 3a). A contrasting trend of multi-year bonds is known from the Greenland subspecies *flavirostris*, and has been recorded in the Pacific subspecies *frontalis* (Ely 1979, Warren et al. 1993), but we were not able to quantify these from our data. Family fission probability showed a positive relationship with time since the end of the previous flight and the

cumulative number of flights over the winter. A negative relationship was found for the number of days since arrival and the cumulative distance flown, despite a moderate negative correlation (-0.472) between the two predictors. Larger families were also less likely to split. This supports the hypothesis that family fission is a result of the frequency of flight activity (for example in Prevett and MacInnes 1980), rather than the actual distance flown.

The size of successful families was unaffected by the level of summer predation. By contrast, marked geese had larger families in years with high summer predation. This difference in trends could be based in the inclusion of unsuccessful families among marked geese. The increase in family size with predation levels could be explained if goose pairs suffer total clutch loss during high predation years, resulting in the survival of families that are naturally larger. This might result if geese more effective at repelling predators also have higher fecundity. Larger emperor geese *A. canagica* and whitefronts are better than smaller species at defending clutches (Thompson and Raveling 1987), and larger black brent and lesser snow geese have higher fecundity than smaller ones (Davies et al. 1988, Sedinger et al. 1995), lending this idea some support. Migration mortality might also be a significant factor in the decoupling of family size and summer predation. We found that in 2016, families of geese observed ca. one month pre-migration on Kolguyev were significantly larger than successful ( $z = -4.285$ ,  $p = 1.83 \times 10^{-50}$ ) and all ( $z = -14.511$ ,  $p < 2 \times 10^{-160}$ ) families recorded in the first two months following their arrival on the wintering grounds.

Flock size decreased with distance from the breeding grounds, as would be expected from a simple distance - energy expenditure relationship. Larger flocks contained more families, conforming to early ideas of how migratory goose flocks form (Elder and Elder 1949). The proportion of first winter birds in flocks decreased with flock size. Combined with smaller flocks and larger families in the west, this lends support to the hypothesis that more successful families winter in smaller flocks. Such flocks would have higher relatedness, allowing competition costs to be balanced by the benefits of association with kin (Hamilton 1964). Juvenile proportion also increased as winter progressed, further supporting the position that family bonds weaken over time. We suggest the population is age-differentially migratory, with adults likely leaving before immature juveniles to reap the breeding benefits of early arrival in the Arctic.

The proportion of juveniles was unaffected by the level of summer predation. The proximate explanation is that there is very little variance in predation index between years. Ultimately, this may reflect that whitefronts nest across a large enough geographic range that predation pressure is largely constant over time. Further, it is suggested that as lemming cycles falter with climate change, there has been a homogenisation of predation levels across the Arctic (Nolet et al. 2013). This is in line with findings in Jongejans et al. (2015), which suggest that since the 1990s, breeding success in North Sea

whitefronts has been decoupled from lemming abundance, even as the Pannonian population continues to respond.

Some issues remain which we have not been able to explore with the current data. How families choose their wintering sites waits on families of varying sizes being fitted with GPS loggers on the breeding grounds and tracked along the autumn migration. We suggest that pairs with juveniles select sites with lower probabilities of snow, which are farther west in coastal areas. Since snow cover is insubstantial until mid-winter, this could also explain the two months families take to select wintering sites. Another dynamic that merits study is noted by Jónsson and Afton (2008) wherein the maintenance of family bonds is contingent on the species' dominance rank in a mixed-species flock. We expect that in such flocks the family sizes of the smaller species will be predicted by the probability of a family winning contests against the median social unit of the heterospecific. Finally, the proximate mechanisms underlying family fission remain of particular interest. Both parents and offspring stand to gain from continued association over a number of years. Indeed, conditions favour large, extended families. We suggest that splits are akin to abrupt regime shifts that are well studied in very different systems (for example Kéfi et al. 2014), and could be similarly predicted given data from a sufficient number of families.

## References

- Angelstam, P. et al. 1984. Role of predation in short-term population fluctuations of some birds and mammals in fennoscandia. - *Oecologia* 62: 199–208.
- Archie, E. A. et al. 2006. The ties that bind: Genetic relatedness predicts the fission and fusion of social groups in wild african elephants. - *Proceedings of the Royal Society of London B: Biological Sciences* 273: 513–522.
- Badzinski, S. S. 2003. Dominance relations and agonistic behaviour of tundra swans (*cygnus columbianus columbianus*) during fall and spring migration. - *Canadian Journal of Zoology* 81: 727–733.
- Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. - *Journal of Statistical Software* 67: 1–48.
- Black, J. M. and Owen, M. 1989. Parent-offspring relationships in wintering barnacle geese. - *Animal behaviour* 37: 187–198.
- Black, J. M. et al. 1992. Foraging dynamics in goose flocks: The cost of living on the edge. - *Animal Behaviour* 44: 41–50.
- Blomqvist, S. et al. 2002. Indirect effects of lemming cycles on sandpiper dynamics: 50 years of counts from southern Sweden. - *Oecologia* 133: 146–158.
- Carbone, C. and Owen, M. 1995. Differential migration of the sexes of pochard *aythya ferina*: Results from a european survey. - *Wildfowl* 46: 99–108.
- Conover, M. R. 2012. Delayed nesting by female canada geese (*branta canadensis*): Benefits and costs. - *The Auk* 129: 140–146.
- Cristol, D. A. et al. 1999. Differential migration revisited. - In: *Current ornithology*. Springer, ppp. 33–88.
- Crozier, R. H. and Pamilo, P. 1996. Evolution of socialinsect colonies. - Oxford University Press, Oxford, UK.
- Davies, J. C. et al. 1988. Body-size variation and fitness components in lesser snow geese (*chen caerulescens caerulescens*). - *The Auk*: 639–648.
- 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.
- Elder, W. H. and Elder, N. L. 1949. Role of the family in the formation of goose flocks. - *Wilson Bull* 61: 133–140.
- Ely, C. R. 1979. Breeding biology of the white-fronted goose (*Anser albifrons frontalis*) on the Yukon-Kuskokwim delta, Alaska.
- 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*.
- Fox, A. D. and Madsen, J. 2017. Threatened species to superabundance: The unexpected international implications of successful goose conservation. - *Ambio* 46: 179–187.
- Fox, A. D. et al. 2010. Current estimates of goose population sizes in western Europe, a gap analysis and assessment of trends. - *Ornis svecica* 20: 115–127.
- 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.
- Gregoire, P. E. and Ankney, C. D. 1990. Agonistic behavior and dominance relationships among lesser snow geese during winter and spring migration. - *The Auk*: 550–560.
- Hamilton, W. 1964. The genetical evolution of social behaviour. i. - *Journal of Theoretical Biology* 7: 1–16.
- 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.
- Jongejans, E. et al. 2015. Naar een effectief en internationaal verantwoord beheer van de in nederland overwinterende populatie kolganzen.
- 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.
- Kéfi, S. et al. 2014. Early warning signals of ecological transi-

- tions: Methods for spatial patterns. - PloS one 9: e92097.
- Kokorev, Y. and Kuksov, V. 2002. Population dynamics of lemmings, *Lemmus sibirica* and *Dicrostonyx torquatus*, and Arctic fox *Alopex lagopus* on the Taimyr peninsula, Siberia, 1960–2001. - *Ornis Svecica* 12: 139–143.
- Kruckenbergh, H. et al. 2008. White-fronted goose flyway population status. - *Angew. Feldbiol* 2: 77.
- Leopold, A. 1919. Differential sex migration of mallards in new mexico. - *The Condor* 21: 182–183.
- 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.
- Madsen, J. and Cracknell, G. 1999. Goose populations of the Western Palearctic. in press.
- Mooij, J. H. 1991. Numbers and distribution of grey geese (genus *Anser*) in the Federal Republic of Germany, with special reference to the lower Rhine region. - *Ardea* 79: 125–134.
- Nichols, J. D. and Haramis, G. M. 1980. Sex-specific differences in winter distribution patterns of canvasbacks. - *Condor*: 406–416.
- 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.
- Philippona, J. 1972. Die Blessgans: Zug und Überwinterung in europa und südwestasien. - Ziemsen.
- Poisbleau, M. et al. 2006. Social dominance correlates and family status in wintering dark-bellied brent geese, *Branta bernicla bernicla*. - *Animal Behaviour* 71: 1351–1358.
- Prevett, J. P. and MacInnes, C. D. 1980. Family and other social groups in snow geese. - *Wildlife Monographs*: 3–46.
- R Core Team 2017. R: A language and environment for statistical computing. - R Foundation for Statistical Computing.
- Schamber, J. L. 2001. Cross-seasonal effects on reproductive performance of pacific black brant.
- Schamber, J. L. et al. 2007. Latitudinal variation in population structure of wintering pacific black brant. - *Journal of Field Ornithology* 78: 74–82.
- Sedinger, J. S. et al. 1995. Environmental influence on life-history traits: Growth, survival, and fecundity in black brant (*branta bernicla*). - *Ecology* 76: 2404–2414.
- 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.
- Thompson, S. C. and Raveling, D. G. 1987. Incubation behavior of emperor geese compared with other geese: Interactions of predation, body size, and energetics. - *The Auk* 104: 707–716.
- Van Horn, R. C. et al. 2004. Behavioural structuring of relatedness in the spotted hyena (*crocuta crocuta*) suggests direct fitness benefits of clan-level cooperation. - *Molecular Ecology* 13: 449–458.
- Vangilder, L. D. and Smith, L. M. 1985. Differential distribution of wintering brant by necklace type. - *The Auk* 102: 645–647.
- Warren, S. M. et al. 1993. Extended parent-offspring relationships in Greenland White-fronted geese (*Anser albifrons flavirostris*). - *The Auk* 110: 145–148.
- Wilson, H. et al. 1991. Winter site fidelity in Greenland White-fronted geese (*Anser albifrons flavirostris*), implications for conservation and management. - *Ardea* 79: 287–294.
- Wood, S. N. 2013. Generalized additive models: An introduction with R. - Chapman; Hall/CRC.
- Wood, S. and Scheipl, F. 2016. Gamm4: Generalized additive mixed models using 'mgcv' and 'lme4'.