

Family size dynamics in wintering geese

Introduction

Families are important components of animal groups, and animals preferentially group with related individuals. In the most extreme case, eusocial insect colonies are composed 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 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 sub-adults from earlier broods who help in herding young, and in agonistic interactions, both against conspecifics (Conover 2012) and predators (Fox and Stroud 1988). For instance, barnacle geese associated with their young in winter were more likely to return 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 explanation of variation in goose family size in winter must include the effect of the summer abundance of rodents, primarily lemmings *Lemmus spp.* and *Dicrostonyx spp.*, on the breeding success of Arctic birds (Summers 1986). 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.

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 flocks are also reportedly smaller to the west. Family bonds reportedly weaken over a single winter, in contrast to the multi-year bonds of the Greenland subspecies *flavirostris* (Warren et al. 1993). Further, the population is also suspected to be differentially migratory in autumn with respect to breeding success, and in spring with respect to age, with breeding birds arriving later, and adults intending to breed leaving earlier (Jongejans et al. 2015).

To investigate these phenomena, we draw on field observations 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, 4. Flocks are smaller further from the breeding grounds, and 5. The proportion of juveniles in flocks increases over the winter.

Methods

We used a combination of historical and contemporary whitefront 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)).

Move numbers to results. Within this area, we collected the following classes of data: *A*. Flock counts ($n = 7,149$), in which observers ($n = 75$) censused flocks of whitefronts, *B*. Family counts ($n = 51,037$), 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 ($n = 1,884$), *C*. Observations of individually marked geese ($n = 10,635$), and *D*. Half-hourly positions of goose families fitted with GPS transmitters over three winters. 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 Trektellen (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 calculate the number of days between each observation and 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. We expected this method to exclude activity from early arrivals and stragglers, and to avoid noise from non-migratory movements.

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

We tested our hypotheses in a sequence reflecting the chain of causality. We first tested (*A*) whether 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. We then tested for (*C*) an effect on flock size of distance from the breeding grounds, the number of days since arrival, and summer predation. Finally, we tested 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* 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 *mgcv* package (Wood 2013). We specified the following *iid* mixed effects: breeding year, observer identity and habitat type. We evaluated the goodness of fit of the models using the Ω_0^2 (Xu 2003) metric to compare the residual variance of full models against the residual variance of their fixed intercept only null

equivalents. We assessed the importance of each predictor using Type II Wald χ^2 tests.

Results

The size of successful families recorded in flocks was found to be unexpectedly insensitive to most predictors. The number of juveniles accompanying pairs increased slightly with longitudinal position, ie, from west to east, but not significantly ($p = 0.874$, $\chi^2 = 0.025$), but did, however, decrease significantly as expected through the winter ($p < 2 \times 10^{-16}$, $\chi^2 = 87.2641$). Individual observations showed a different trend; while not significant, there was a slight decrease in size from west to east ($p = 0.244$, $\chi^2 = 1.36$), and the number of juveniles seen with individuals also decreased over the winter ($p = 1.17 \times 10^{-5}$, $\chi^2 = 19.21$).

As hypothesised, flocks were smaller in the west, and also tended to be larger the more days since the first autumn arrivals had passed ($p < 2 \times 10^{-16}$, $\chi^2 = 10340$). Consistent with the earliest ideas on how geese form flocks (Elder and Elder 1949), the number of families in flocks increased very rapidly with their size ($p < 2 \times 10^{-16}$, $\chi^2 = 8196$), but the size of successful families in flocks decreased slightly as flocks grew ($p = 0.257$, $\chi^2 = 1.28$). Further, the proportion of first winter juveniles in flocks was not affected significantly by their longitudinal position ($p = 0.442$, $\chi^2 = 1.03$). However, it increased significantly through the winter as expected ($p = 0.00174$, $\chi^2 = 9.82$). Larger flocks also had a lower proportion of juveniles than expected ($p = 0.015$, $\chi^2 = 5.89$).

The effects of summer predation were not consistent across the levels of the population. The size of successful families in flocks increased, though not significantly, with the level of summer predation ($p = 0.377$, $\chi^2 = 0.78$), while the number of juveniles seen with marked geese was significantly decreased with high summer predation ($p = 6.45 \times 10^{-6}$, $\chi^2 = 20.35$). The apparent difference in trends might be explained by the fact that only successful families were counted in flocks. The effect of summer predation on family size could be masked by such a sampling method, especially if higher levels of predation caused goose pairs to fail to fledge any young at all. On testing this idea by excluding observations of unsuccessful pairs from our analysis, we found a similar trend as that of the family data from flocks, though it was still not a significant one ($p = 0.896$, $\chi^2 = 0.016$). At a higher level, the number of successful families in flocks showed a marked decrease with the level of summer predation ($p = 7.13 \times 10^{-16}$, $\chi^2 = 65.09$). This did not translate into a lower juvenile proportion ($p = 0.931$, $\chi^2 = 0.058$), or decreased flock sizes ($p = 0.308$, $\chi^2 = 1.04$).

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| Response | Data source | Fixed effects | Random effects | Model |
|-------------------|-------------------------|---------------|----------------|-------|
| Family size | Family counts | 1, 2, 3, 4 | 5, 6, 7 | GLMM |
| Family size | Individual observations | 1, 3, 4 | 5, 8 | GLMM |
| <i>n</i> families | Family counts | 1, 2, 3, 4 | 5, 6, 7 | GAM |
| Flock size | Flock counts | 1, 3, 4 | 5, 6, 7 | GLMM |
| Juvenile prop. | Flock counts | 1, 2, 3, 4 | 5, 6, 7 | GAM |

Table 1: Model structures; effect codes: 1 Longitude, 2 Flock size, 3 Days since arrivals, 4 Summer predation index, 5 Breeding year, 6 Habitat type, 7 Observer identity, 8 Goose identity.

| Reponse | Predictor | | | |
|-------------------------------|-----------|------------|--------------------|------------------|
| | Longitude | Flock size | Days since arrival | Summer predation |
| Family size, flocks | 0.0249 | 1.2836 | 87.2641* | 0.7805 |
| Family size, successful pairs | 0.0127 | - | 5.4859* | 0.0162 |
| Family size, all pairs | 1.3561 | - | 19.2147* | 20.3484* |
| <i>n</i> families | 0.416 | 8196* | - | 65.098* |
| Flock size | 10340* | - | 4476* | 1.039 |
| Juvenile proportion | 1.029 | 5.888* | 9.816* | 0.058 |

Table 2: Model output and predictor χ^2 values. Asteriks indicate significant effects.

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