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 matrilines 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 explore 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)).

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 transmitters. 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 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 reflected 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, 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 *gamm4* and *mgcv* packages when specifying nested and *iid* random effects, respectively (Wood and Scheipl 2016, Wood (2013)). 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* included goose identity, and goose identity nested within breeding year as random effects, since geese could be observed multiple times within and between years. We assessed the importance of each predictor using Type II Wald χ^2 tests.

Results

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. 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 ($n = 6$). A mean of 6,628 positions per individual were recorded over 138 days on average, during which 19 fission events occurred, which 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 during the first sixty days after arrival (datasets B and C, model A, $\chi^2_B = 1.135$, $p_B = 0.286$, $\chi^2_C = 2.179$, $p_C = 0.139$). Over the remainder, 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 ($\chi^2 = 0.023$, $p = 0.879$).

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 ($\chi^2 = 12.935$, $p = 3.2 \times 10^{-4}$). The effect of summer predation on family size could be masked by a sampling method which counted only successful families, as in dataset B, for instance if higher levels of predation caused some goose pairs to fail to fledge any young at all. We confirmed this bias in sampling method by failing to find any effect of summer predation after excluding unsuccessful pairs from data C ($\chi^2 = 0.1321$, $p = 0.716$).

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 summer predation ($\chi^2 = 0.021$, $p = 0.883$). We tested whether this unexpected 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 these data also did not exlain observed variation ($\chi^2 = 1.835$, $p = 0.175$).

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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
n 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*
n 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 $\chi 2$ values. Asteriks indicate significant effects.

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