Family size dynamics in wintering geese

Introduction

Families are important components of animal groups, and among migratory waterfowl, are thought to underlie the formation of flocks (Elder and Elder 1949).The maintenance of family bonds is advantageous since families are dominant over pairs and singles (Poisbleau et al. 2006, Badzinski (2003)). Family dominance rank increases with the number of juveniles, and larger families can win access to better resources (Loonen et al. 1999, Gregoire and Ankney (1990)). The need to teach juveniles to locate, select, and handle high quality foods may contribute to the continuation of such bonds over multiple breeding years (Warren et al. 1993). Within breeding years, however, the development of family size is not fully understood, and appears to be variable, with the retention of members favoured among larger taxa (Jónsson and Afton 2008, Warren et al. (1993)). Extended family bonds increase the fitness of both parents and young, with the presence of adults allowing offspring 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), boosting parental production (Black and Owen 1989).

The likelihood of breeding success is also higher in birds that winter closer to their summer grounds (Schamber 2001). In Pacific black brent geese *Branta bernicla nigricans*, more juveniles winter closer to the breeding grounds (Schamber et al. 2007), possibly because they are part of larger, more dominant families that can displace subordinate social units - unsuccessful pairs and singles - to more distant sites (Vangilder and Smith 1985), but the influence of family size on wintering site selection is not well studied. Any explanation of spatial and temporal variation in waterfowl family size in winter must take into account that the breeding success of Arctic birds is also strongly influenced by the abundance of rodents, primarily lemmings *Lemmus spp.* and *Dicrostonyx spp.* (Summers 1986), and is predicted to be highest in years when lemming density is low and that of predators is high (Dhondt 1987). The effect of summer predation on the proportion of first winter juveniles has been described in 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 goose species wintering in continental western Europe (Fox and Madsen 2017). Long term observations of this species offer an interesting opportunity to investigate the dynamics of Arctic goose families over space and time. Accounts from the wintering grounds suggest that the Baltic-North Sea flyway population of whitefronts (Philippona 1972) is differentially migratory, with more successful families wintering farther away from the breeding grounds than smaller ones. Further, these families are observed in smaller flocks, but flocks are also reportedly smaller in the west. Family bonds also reportedly weaken over a single winter, in contrast to the multi-year bonds of the Greenland subspecies *flavirostris* (Warren et al. 1993). These issues have received some attention (Jongejans et al. 2015), and set up a number of interactions to explore. Here, we test the variation of family size in wintering geese

along gradients of longitude, flock size, summer predation, and time since arrival, in order to better understand the population of the species.

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). The topography is largely flat and well drained (Poulsen and East 2017). High intensity agriculture serves as a dense food source for up to 2.5 million individuals of five main species of migratory geese (Koffijberg et al. 2017, Fox and Abraham (2017)). Whitefronts 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 four classes of data collected during winter (ending March 31): long term flocks counts (n = 7,149, *SOVON*) and family frequencies (n = 51,037), observation records of individually marked geese (n = 10,635, *geese.org*), records of goose flight activity (n = 6,266, *trektellen.org*), and high frequency tracks from thirteen families fitted with position logger/transmitters (n = 64, *MPIO*). These data had been filtered to exclude records of single individuals, and of double entries for pairs in which both marked birds were logged separately when seen together. We also 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 mass arrival of geese in autumn, and to end with the end of their mass departure in spring. Following methods in Jongejans et al. (2015), Blomqvist et al. (2002) and Nolet et al. (2013), we estimated a pooled mean index of summer predation for the breeding grounds (Madsen and Cracknell 1999) 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 (Kruckenberg et al. 2008).

We selected longitude, flock size, summer predation index, and number of days since autumn arrival as the main predictors required to test hypothesised effects on the number of juveniles (hereafter, family size), the flock size, and the proportion of first winter young in flocks. We used generalised linear mixed models (GLMMs) or generalised additive models (GAMs) from the *lme4* (Bates et al. 2015) and *mgcv* (Wood 2013) packages in R (R Core Team 2017) as appropriate to model these effects. We used the Ω_0^2 metric (Xu 2003) to compare the residual variance of full GLMMs against the residual variance of their fixed intercept only null equivalents, and the inbuilt R^2 value from the *mgcv* package for GAMs to assess the goodness of fit of our models. We assessed the importance of each predictor using Type II Wald χ^2 tests. Tables below show model structure and output.

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($p = 0.308$, $\chi^2 = 1.04$).

References

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.

Blomqvist, S. et al. 2002. Indirect effects of lemming cycles on sandpiper dynamics: 50 years of counts from southern Sweden. - Oecologia 133: 146–158.

Conover, M. R. 2012. Delayed nesting by female canada geese (branta canadensis): Benefits and costs. - The Auk 129: 140–146.

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.

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 super-abundance: The unexpected international implications of successful goose conservation. - Ambio 46: 179–187.

Fox, A. D. and Abraham, K. F. 2017. Why geese benefit from the transition from natural vegetation to agriculture. - Ambio 46: 188–197.

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–

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.

127.

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.

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.

Koffijberg, K. et al. 2017. Responses of wintering geese to the designation of goose foraging areas in The Netherlands. - Ambio 46: 241–250.

Kruckenberg, H. et al. 2008. White-fronted goose flyway population status. - Angew. Feldbiol 2: 77.

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.

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.

Poulsen, T. M. and East, W. G. 2017. Europe. - Europe: Relief

R Core Team 2017. R: A language and environment for statistical computing. - R Foundation for Statis-

tical 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.

Summers, R. 1986. Breeding production of dark-bellied brent geese *Branta bernicla bernicla* in relation to lemming cycles. - Bird Study 33: 105–108.

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.

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.

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

Xu, R. 2003. Measuring explained variation in linear mixed effects models. - Statistics in Medicine 22: 3527–3541.