Family size dynamics in wintering geese

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Introduction

Living in groups entails both costs and benefits for individuals. Group members benefit from more social interactions, and from the increased sensory and physical capabilities of the group (Krause and Ruxton 2002). It has been shown that geese in larger flocks spend less time on the lookout for predators and have more time to feed (Roberts 1996). Among the costs of group living is the increased competition for limited resources in larger groups (Krause and Ruxton 2002). Living in families offers all the benefits of groups, while costs are shared with relatives. Animals may lose some direct fitness in family groups, but this is offset by the inclusive fitness gained from related group members (Hamilton 1964, Rodman 1981). Thus animal societies composed of one or more families are common across taxa, from eusocial insects (Crozier and Pamilo 1996) to large herbivores (Archie et al. 2006) and cooperative carnivores (Van Horn et al. 2004).

Waterbirds such as geese *Anserini* live in groups composed of families. This is most apparent in winter, when families gather to form flocks (Elder and Elder 1949). Maintaining family bonds within flocks confers benefits since families are dominant over pairs and individuals, and family dominance rank increases with the number of members, for example in Canada geese *Branta canadensis* (Hanson 1953), snow geese *Anser caerulscens* (Gregoire and Ankney 1990), and barnacle geese *B. leucopsis* (Loonen et al. 1999). This allows larger families to occupy optimal foraging positions in flocks at lesser cost, and win access to better resources (Black et al. 1992). Both parents and offspring benefit from family bonds maintained across seasons, as juveniles gain access to more uninterrupted feeding in winter, and parents gain dominance rank (Black and Owen 1989). Parents of some species benefit in summer from the presence of nest-attending sub-adults (Fox and Stroud 1988), for example, barnacle geese that are associated with their young through a winter, for example, are more likely to return with a brood the next year (Black and Owen 1989).

The development of family bonds within a winter is, however, not fully understood, and appears to be variable. Small species, such as Ross' geese *A. rossii* show weak family bonds in winter, perhaps because these confer no dominance benefit against much larger snow geese with which they form mixed flocks (Jónsson and Afton 2008). Similarly, cackling geese *B. hutchinsii* show weak pair and family associations in winter likely because they graze in large, dense flocks with high levels of disturbance. As cackling geese move to areas with less disturbance prior to spring migration, pair bonds strengthen (Johnson and Raveling 1988). In contrast, larger taxa such as giant Canada geese *B. canadensis maxima* and Greenland white-fronted geese *A. albifrons flavirostris* show strong, extended family bonds (Warren et al. 1993). In general, small, grazing species tend to dissolve families in winter (Johnson and Raveling 1988), while large species that need to teach juveniles to locate and handle high quality foods tend to maintain them (Warren et al. 1993, Kruckenberg 2005).

The question of what space-use and movement decisions families make on the wintering grounds has not been well explored, especially in the context of the number of accompanying juveniles. Some effect is expected, since juvenile dark-bellied brent geese *Branta b. bernicla* undertaking the autumn migration with parents affect their flight speed (Green and Alerstam 2000). Like other birds, geese can be differentially migratory with different population classes occupying different wintering areas (Cristol et al. 1999). For example, the white and blue morphs of snow geese show longitudinal separation during migration (Cooke et al. 1975). Further, more juveniles of Pacific black brent geese *B. b. nigricans* winter closer to the breeding grounds (Schamber et al. 2007). However, how accompanying juveniles influence where families winter is not well understood.

Though the maintenance of family bonds in geese is beneficial, separation of juveniles from parents is the norm among most animals. Juvenile geese leave the family as spring approaches (Prevett and MacInnes 1980, Johnson and Raveling 1988, Black and Owen 1989). In the smaller *Branta* geese, parents become increasingly aggressive towards young and intentionally chase them off (Black and Owen 1989, Poisbleau et al. 2008). This is also reported in larger greylag geese *A. anser* (Scheiber et al. 2013). However, family splits in winter are not well studied. In wintering snow geese, family separation is held to be caused by a lack of coordination between members during chaotic take-offs in large flocks, and is thus seen as accidental (Prevett and MacInnes 1980). Separated birds attempt to locate their families, and similar behaviour is observed in Canada geese (Elder and Elder 1949). Investigating the role of flight events in family size dynamics requires accurate, fine-scale knowledge of individual positions, and obtaining such data for whole families of highly mobile species has historically presented challenges.

Observational studies of goose family sizes must account for summer conditions on the breeding grounds. Rodent abundance cycles - primarily of lemmings *Lemmus spp.* and *Dicrostonyx spp.* - have previously been thought to have a significant impact on the breeding success of Arctic birds, geese included (Summers 1986). Lemmings have 3 - 4 year cycles of abundance, with 'peak' years of high density followed by 'crash' years of scarcity. Arctic predators preferentially target lemmings and shift to bird eggs and young as alternative prey when lemmings are scarce (Angelstam et al. 1984). This effect is most pronounced when a lemming peak is followed by a crash: predation pressure on geese increases as predators multiply in the peak year and then target birds in the crash year (Dhondt 1987). This causes marked decreases in the proportion of first winter juveniles in both waders *Charadrii* and geese wintering in Europe (Summers and Underhill 1987). 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 white-fronted geese, are among the most abundant geese wintering in continental western Europe (Madsen et al. 1999), and offer an interesting opportunity to investigate the wintertime dynamics of goose families. Accounts suggest that in the Baltic-North Sea flyway population of white-fronted geese (Philippona 1972), larger families winter farther west than smaller ones. Further, these families are observed in smaller flocks, but this may be an artefact of smaller flocks observed farther west. Family bonds reportedly weaken within winters, contrary to the trend expected for large geese that families stay together through the winter, and sometimes beyond (Warren et al. 1993, Kruckenberg 2005). 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 (Mooij 1991, Madsen et al. 1999, Fox et al. 2010) to test the hypotheses 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.* Family size in winter is dependent on summer predation pressure, and *5.* Family separation is predicted by the number and frequency of flights, and the time since take-off.

Methods

Observation and position data

We collected the following classes of data from western Europe: (*A*) Flock counts in which observers censused flocks of white-fronted geese and counted the numbers of adults and juveniles, (*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, and (*C*) Observations of geese marked with numbered plastic neckbands in pairs or with juveniles, including records of pairs with no juveniles. These data were filtered to exclude records outside the spatial (2 - 10°E, 50 - 54°N) and temporal

(autumn 2000 - spring 2017, breeding years 2000 - 2016) limits of our study. After filtering census data (*A, B, C*) (mapped in Fig.1), 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. A further 10,635 marked geese were observed at 8,416 sites. Observations of marked geese did not include details on habitat type, flock size and observer.

We also collected (*D*) positions of 13 goose families (13 adult pairs, 38 juveniles) fitted with GPS loggers (2013, n = 3, 2014, n = 4: e-obs GmBH, & 2016, n = 6: madebytheo). In addition, 2016 loggers collected 0.5 Hz position data from take-off events. Families fitted with GPS loggers were were tracked within the wintering area for 78 days on average (range: 34 - 135). For all families, we identified days on which splits occurred. Before analysing the daily probability of splitting, we defined 'flights' as displacement events over 1km every day, and counted their number and daily frequency. For 2016 families, we identified the half-hour when they split, and used the available take-off data to find the time since the last take-off at each half-hour.

Supplementary data

To relate observation data to migration timing, we collected daily records (n = 6,266) of flock flight intensity from from 84 spring and 180 autumn Trektellen sites (overlap = 72) (see *trektellen.org*, Van Turnhout et al. (2009)) in 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 each goose winter across the study period. We took the goose winter to begin with the first mass arrival of geese in autumn, and to end with the last mass departure in spring.

Following previous studies (Jongejans et al. 2015) we estimated an index of summer predation for the breeding grounds of this population from rodent abundance data (*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 Island. The index takes into account the change in lemming abundance, with higher values when lemming abundance had decreased from the previous year reflecting the increased predation pressure on Arctic birds from abundant predators switching to alternative prey.

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 For this, we used datasets *B* and *C*. Within flocks, we tested whether (*2.a.*) family sizes, and (*2.b.*) 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

Dataset	Type	Records	Sites	Spatial extent (°)	Temporal extent
A	Flock counts	7,149	123	4.0 - 8.8 E, 51.1 - 53.4 N	2000 - 2017
B	Family counts	51,037	65	4.8 - 7.3 E, 51.1 - 53.4 N	2000 - 2017
C	Marked geese	10,635	8,416	2.7 - 9.7 E, 50.9 - 53.9 N	2000 - 2017
D	Family GPS tracks	13[a]; 32,630[b]	32,630	3.9 - 7.9 E, 51.3 - 54.3 N	2013[c], 2014[d], 2016[e]

a: Number of families, b: Number of half hourly positions, c: 3 families, d: 4 families, e: 5 families

Tab. 1: Spatial and temporal range of datasets used.

geese in autumn, and the level of summer predation. To add context, we searched for (*3.*) an effect on flock size of distance from the breeding grounds, the number of days since arrival, and summer predation, 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.

Further, we examined whether (*5.a.*) the split probability (no-split or split, binomial distribution) each day was predicted by the days since arrival, the number of flights that day, the cumulative number of flights until that day, the distance travelled that day, the cumulative distance travelled until that day, and the family size on that day. For the 2016 families we identified take-offs as 0.5 Hz records with a ground speed above 2 m/s, and tested (*5.b.*) the half-hourly split probability in relation to the time since the last take-off and the distance travelled in the previous half hour.

All analyses were performed in the *R* environment (R Core Team 2017). We used *lme4* (Bates et al. 2015) generalised linear mixed models (GLMMs) to test *1, 2.a, 3, 5.a* and *5.b*, where we expected linear relationships. In cases *2.b* and *4*, we used *mgcv* (Wood 2013) generalised additive mixed models (GAMMs) to include smooth functions of the flocksize (*2.b*) and the number of days since winter (*4, 5.b*) as predictors. We included some covariates as random effects, and models were dependent on the datasets used for the effects tested in each (see Table 1). We assessed the importance of each predictor using Type II Wald χ^2 tests, and effect sizes using Cohen's $f\hat{}2$ (see Appendix 1).

Results

Data filtering

Flock count data from 16 breeding years and subsequent winters yielded a mean 420 flock counts per year (range: 67 (2001) - 672 (2005)). Except one record in August 2016, Aprils (n = 24) and Septembers (n = 76) had the fewest records, with most observations from October - January (81%, n = 5,785). Observations declined over February (11%) and March (6.8%). The mean flock size was 712 (range: 2 - 20,000), with a mean proportion of first-winter birds of 0.18 (range: 0 - 0.87). Flocks in which families were held on average 540 birds (range: 3 - 11,000), in which the mean number of juveniles in families was 1.78 (range: 1 - 10). On average, 626 marked

geese (range: 62 - 1143) were observed each year, accompanied by 0.59 juveniles (range: 0 - 11)

Families fitted with GPS loggers travelled 11 km per day (range: 0 - 306). At the daily scale, we defined flights as movements of above 1000 metres. Families flew a mean of twice (range: 0 - 10) per day, and 98 times (range: 63 - 367) over the tracking period. In 2016 families take-offs occurred on average 5 times (range: 1 - 15) times a day, and 470 times (range: 328 - 659) over the tracking period. 21 family splits occurred and were not restricted to juveniles. 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 between years (σ^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 (dataset *B*: successful families in flocks, and *C*: families of marked geese, model *1*, χ^2 B = 1.135, p B = 0.286, χ^2 C = 2.007, p C = 0.157, see Fig.2). Later in the winter, larger families from dataset *B* (successful families in flocks) wintered farther west (χ^2 = 4.194, p = 0.041), while dataset *C* (families of marked geese) did not reveal any influence of juvenile number on wintering site (χ^2 = 0.27, p = 0.6033). In all cases, geese were found farther west with increasing number of days since arrival (χ^2 = 116.5641, p < 0.001, see Fig.2).

Family size in winter

The number of juveniles in a family (dataset *B*: successful families in flocks, model *2.a*) decreased through the winter (χ^2 = 74.166, p < 0.001, see Fig.3), but was insensitive to flock size (χ^2 = 0.270, p = 0.6033) and summer predation (χ^2 = 0.337, p = 0.562, see Fig.4). Family sizes of marked geese (dataset *C*: families of marked geese, model *2.a* adapted) decreased over time (χ^2 = 19.936, p = < 0.001, see Fig.3), but showed an increase with the level of summer predation (χ^2 = 12.935, p < 0.001, see Fig.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 ($\chi^2 = 0.1321$, $p = 0.716$, see Fig.4). The number of successful families in flocks increased with flock size ($\chi^2 = 7162$, $p < 0.001$, see Fig.5), and the number of days since goose arrival in autumn ($\chi^2 = 171.3$, $p < 0.001$, see Fig.6), 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 ($\chi^2 = 12.73$, $p = 0.0004$, see Fig.7).

Flock size in winter

Flocks were significantly smaller farther from the breeding grounds ($\chi^2 = 66599$, $p = < 0.001$, see Fig.8), and grew slightly over the winter ($\chi^2 = 4975$, $p < 0.001$). Within flocks, juvenile proportions increased through the winter ($\chi^2 = 19.43$, $p = 0.001$, see Fig.9), 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 ($\chi^2 = 0.021$, $p = 0.883$).

Probability of family splits

The daily probability of families separating (see Fig.10) was significantly lower later in the winter ($\chi^2 = 8.314$, $p = 0.004$), and lower in larger families ($\chi^2 = 11.41$, $p < 0.001$). 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 over the period leading up to the split ($\chi^2 = 143.23$, $p < 0.001$), but decreased in families that moved a shorter cumulative distance over the days leading up to splits ($\chi^2 = 182.63$, $p < 0.001$). At the half-hour scale, split probability increased with time since the previous take-off ($\chi^2 = 6.07$, $p = 0.014$), but was not related to the distance travelled in the previous half hour ($\chi^2 = 0.389$, $p = 0.533$).

Discussion

We studied how the size of white-fronted goose families is related to where, when and with how many flockmates they are seen in the wintering grounds. We found support for the effect of the size of successful families on how far they migrate from the breeding grounds, but only later in winter. Further, the number of successful families in flocks was higher in the west. We also confirmed that family size decreases over the winter, but found that it is insensitive to flock size, and shows mixed responses to summer predation. Families are less likely to split later in winter, and with increasing family size. We found only indirect evidence that flights are responsible for family splits in winter. We showed that flocks are smaller farther from the breeding grounds, and found that they increase in size over the winter. Additionally, larger flocks have more successful families. The proportion of first year birds in flocks is lower in larger flocks, but increases as winter progresses.

Social status has been found in previous studies to influence geese's selection of wintering sites, with dominant social units displacing subordinate ones from optimal wintering locations (Vangilder and Smith 1985, Schamber et al. 2007). Our finding that larger families winter to the west of the study area is similar to one found by Jongejans et al. (2015). It fits the idea that dominant social units occupy optimal wintering sites if the spatial distribution of white-fronted goose families reflects habitat suitability. Geese can exploit most of the highly productive landscape, and have become tolerant of human disturbance and previously deterrent structures such as wind turbines (Madsen and Boertmann 2008, Fox and Madsen 2017). Any habitat selection is thus likely to be against conditions that impede foraging, such as snow and ice cover coupled with strong winds (Philippona 1966). Geese tolerate snow depths of ca. 15cm, conditions in excess of which are not noted in the Netherlands before midwinter (Philippona 1966), and have become rare within the study period. Western areas near the North Sea coast may be expected to benefit from its moderating effect on temperature, with fewer instances of conditions that geese would prefer to avoid. This could explain why adults with juveniles would choose to winter there after midwinter. The movement of geese to the south later in winter has been reported before, with peak counts of white-fronted geese in the Netherlands in November (Hornman et al. 2015), but only in January in Belgium (Devos and Kuijken 2010).

Juvenile independence has been reported across goose taxa (eg. Prevett and MacInnes 1980, Johnson and Raveling 1988, Black and Owen 1989) as being concurrent with the arrival of spring. Previous studies have shown that spring copulation in the breeding pair triggers juvenile departure (Fischer 1965, Prevett and MacInnes 1980). We find support for the hypothesis that the number of juveniles with adults decreases through the winter. The dissociation of juveniles from parents should result in some families losing their only offspring, thus reducing the number of successful families counted in flocks over time. Our finding that the number of families seen in flocks increases with time contradicts this expectation. An explanation would be that social status predicts variation in spring migration timing, as it does the autumn arrival (Jongejans et al. 2015). However, previous studies have not found such an effect (Madsen 2001, Bêty et al. 2004).

Our findings regarding the relation, or lack thereof, between family sizes and juvenile proportion and summer predation are at odds with previous studies which link breeding success in Arctic birds to the abundance of Arctic rodents (Angelstam et al. 1984, Summers 1986, Summers and Underhill 1987, Blomqvist et al. 2002 etc.). However, more recent studies indicate that since the 2000s, in Baltic-North Sea flyway white-fronted geese, breeding success no longer seems to be correlated with summer predation (Jongejans et al. 2015). The causes for this effect are not well known. It is suggested that more white-fronted geese now breed on Kolguyev Island where they experience a constant level of pre-

dation, since the island lacks lemmings and associated phenomena (Kruckenberg et al. 2008). Further, it has been suggested that an expanded white-fronted goose breeding range results in the entire population not being uniformly affected by predation, since lemming cycles are not expected to be synchronised across regions. This could allow white-fronted geese from low predation areas to have larger families than the mean, even as those facing increased predation do poorly (Jongejans et al. 2015). For example, the Pannonian wintering population of whitefronts that breeds farther east on the Taimyr Peninsula continues to show a breeding success correlated with the predation index, and by extension, lemming abundance cycles. A large breeding range also means that variation in predation pressure is lost due to year-wise averaging across the breeding range. Future models could correct for this by accounting for the summering site of each family observed in winter. Further, lemming cycles are in northern Russia appear to be faltering overall and this could also explain why cyclicity in goose breeding success is reduced (Nolet et al. 2013). Angerbjörn et al. (2001) found that the cyclicity of lemming populations in Fennoscandia has been previously disrupted and re-established in the later-19th and 20th centuries. This lends support to the idea that northern Russian lemming cyclicity might be undergoing similar temporary disruption, following which they could be restored.

The increase in marked geese's family size with the level of predation could suggest that facing high predation pressure, geese either fledge large families or fail entirely. This could be the case if geese more effective at repelling predators also have higher fecundity. Body size may be an important driver. Larger emperor geese *A. canagica* and white-fronted geese 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). We posit that 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 approx. one month pre-migration on Kolguyev had significantly more juveniles (mean = 2.25) than successful families (dataset *B*, mean = 1.78) (GLM, z = -4.285, p < 0.001) and all families of marked geese (dataset *C*, mean = 0.59) (GLM, z = -14.511, p < 0.001) recorded in the first two months following their arrival on the wintering grounds.

Bird migration is strictly constrained by metabolic factors. Energy reserves and water balance especially determine how far and how fast a bird can fly, and thus where it must stopover, and by extension, terminate migration (Klaassen 1996). Our finding that flocks are smaller to the west of the wintering area (approx. 3 - 4°E) fit well in this context, and it is to be expected that fewer geese would choose to winter farther west when climatically suitable and similarly agricultural sites can be found to the east. Our results that larger flocks had a lower proportion of first-year birds must be considered in the context of the previous outcome that larger families winter in the west, where flocks are smaller and have more successful families. This likely results in a higher juve-

nile proportion from small flocks, producing the trend we see. Consequently, one would expect a higher proportion of juveniles in westerly flocks, but we did not find that flock juvenile proportion varies over the study site. This is contrary to the expectation that goose families selecting for optimal sites drive variation in juvenile proportion over wintering areas (eg. Schamber et al. 2007). However, independent juveniles observed in wintering flocks (eg. Hanson 1953, Gregoire and Ankney 1990, Loonen et al. 1999) may dampen any variation.

The result that flock juvenile proportion rises non-linearly over the winter is in line with the previous finding that the number of successful families in flocks increases with time. However, this trend may be due in larger part to white-fronted geese being age-differentially migratory, with pairs without young leaving the breeding grounds earlier than families and juveniles. An effect of age on spring departure timing has been unsuccessfully sought for in similar species (pink-footed geese Madsen 2001, snow geese, Bêty et al. 2004). In snow geese, the continued influx of juveniles to the breeding grounds for some weeks after the arrival of the breeding population does suggest that independent juveniles follow a different migration schedule (Prevett and MacInnes 1980). The question of age-differential migration would ideally be resolved with age-ratios of flocks on spring migration. The population likely does not receive an influx of juveniles towards the end of winter, leading us to conclude that juveniles do indeed leave later than adults in spring.

Finally, our findings that daily split probability decreases with the distance travelled, and is reduced later in winter are largely novel. They contradict the consensus that geese become independent towards spring (Prevett and MacInnes 1980, Johnson and Raveling 1988, Black and Owen 1989, Scheiber et al. 2013). We also did not differentiate between juvenile separation, juvenile death, and separation of breeding pair in our analysis, and this coupled with our low sample size of 13 families could have biased the results. Nonetheless, our results that the number of flights undertaken by a family were a good predictor of whether it would split are in accordance with the idea that flights are disruptive events that contribute to separation (Prevett and MacInnes 1980). As we have found, one would expect that in such scenarios larger families are easier to locate and cohere to. The positive relation between the probability of splitting at each half hour and the time since the last take-off is best ascribed to a very low sample size of 6 families in which only 8 splits were recorded.

The results we obtained add significantly to our knowledge of greater white-fronted geese. White-fronted goose families likely leverage their dominance to occupy optimal sites as winter progresses. Simultaneously, they undergo a steady reduction in the number of associated juveniles. Our findings show that young split off from families earlier than previously thought in this species in which families are thought to remain together throughout the winter, and sometimes longer than a year (Ely 1979, Warren et al. 1993, Kruckenberg 2005). Remaining on the wintering grounds later than other social classes, families and independent juveniles make

this population differentially migratory by both age and social status. Previous authors (Madsen 2001, Bêty et al. 2004) have sought such an effect, and we present it as a novel finding for geese. At the policy level, this provides support for the continued yearly cessation of wild goose hunting in January, especially since families and juveniles tend to cluster and are already over-represented in autumn hunting bags (Madsen 2010).

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Appendix 1

Model summaries

We provide a table summarising structures of models used in the analysis. This table includes Cohen's f^2 effect sizes that are based on the variance explained. Cohen's f^2 was calculated for each model thus:

$$f^2 = \frac{R^2}{1 - R^2} \tag{1}$$

where R^2 is the coefficient of determination. We calculated pseudo-R^2 for our models as the R^2 of a linear model taking the model response of a null generalised mixed model as the response, and the generalised mixed model fit as the predictor. These values corresponded closely with pseudo-R^2 provided by the *mgcv* package for generalised additive models and were considered reliable. Cohen's f^2 values of 0.02, 0.15, and 0.35 are respectively considered small, medium, and large.

Model	Type	Dataset	Response	Fixed effects	Random effects	Records used	Cohen's f^2
1	GLMM	B	5	1, 5	8, 9, 10	20,160[a]; 14,018[b]	3.22[a]; 4.74[b]
1	GLMM	C	5	1, 5	8, 11	3,289[a]; 7,320[b]	4.87[a]; 4.43[b]
2.a	GLMM	B	1	3, 5, 7	8, 9, 10	34,179	0.09
2.a	GLMM	C	1	5, 7	8, 11	10,426	7.72[c]; 0.62[d]
2.b	GAMM	A	2	3, 5, 7	8, 9, 10	837	9.36
3	GLMM	A	3	5, 6, 7	8, 9, 10	5,700	0.199
4	GAMM	A	4	5, 6, 7	8, 9, 10	5,659	0.52

Effects: *1: Number of juveniles per family, 2: Number of families, 3: Flock size,*
4: Proportion of juveniles, 5: Days since autumn arrival,
6: Distance to breeding grounds, 7: Predation index, 8: Breeding year,
9 Observer, 10: Habitat type, 11: Goose identity

a: ≤ 60 days after arrival, b: ≥ 60 days after arrival, c: All families, d: Only successful families

Tab. A1: Models and inputs based on observation data.

Model	Type	Response	Fixed effects	Random effects	Records used	Effect size
5.a	GLMM	1	2, 3, 4, 5, 6, 7	9	1,009[a]	0.08
5.b	GLMM	1	3, 8	9	21,271[b]	0.0004

Effects: *1: Split occurrence , 2: Family size, 3: Days since autumn arrival,*
4: Daily number of flights, 5: Cumulative number of previous flights,
6: Daily distance travelled, 7: Cumulative distance previously travelled,
8: Time since last take-off, 9: Family identity

a: Daily positions, b: Half-hourly positions

Tab. A2: Models and inputs based on GPS tracking data.