# Methods: Data

## Study species

Greater White-fronted geese (*Anser albifrons*) are similar in size but somewhat smaller than the common Greylag goose (*Anser anser*). They are named for the distinctive patch of white feathers at the base of the bill and beginning of the forehead. Adults are also identified by the black tiger-stripe markings on the chest. First winter birds lack the white front, the black chest stripes, and the neck grooving common to adults of many *Anser* species.

Madsen and Cracknell (1999) have compiled some of the most comprehensive information on the movement ecology of this species in their book on *Goose Populations of the Western Palearctic*. Whitefronts have a circumpolar distribution, and breed in the tundra between the 10°C and 4°C July isotherns. The Palearctic populations winter across Europe and Asia, with one of the largest combined ranges among the geese. The Eurasian breeding range is now exclusively within Russia (Alphéraky 1904), and stretches from the Kanin Peninsula (45°E) to the Kolyma river (155°E) in the Russian far-east. The Western Palearctic population which winters in Europe breeds between the Kanin Peninsula the Khatanga river (104°E). This population is further divided into five main wintering groups based on the flyways they use. Geese reaching western Europe and Britain from Russia take the Baltic - North Sea flyway. Madsen summarises some decades of leg-ring and neckband recoveries to state that the breeding grounds of North Sea wintering whitefronts lie between the Kanin Peninsula and the River Yenisei (98°E). The species shows high site fidelity during winter (Wilson et al. 1991), but populations from the different flyways have been found to mix.

Adults form life-long pair bonds, and migrate, feed and roost together. Family bonds between parents and juveniles, and between siblings, are strong and long-lasting in the Greenland subspecies. Families regroup successfully after capture and subsequent individual release in both wintering (Miller and Dzubin 1965) and breeding areas [*pers.obs*] Juveniles follow parents on their first autumn migration, and are almost always seen with them or with siblings during their first winter. Around 40% of these geese are still with their parents in the second winter, 30% in the third, and 20% in the fourth. (Warren et al. 1993). Alloparental care, or nest attendance and anti-predator defence on the breeding grounds is a likely benefit and has been sporadically reported in the Greenland (Stroud 1982) and Pacific subspecies (Ely 1979). Larger goose families are also more dominant within wintering flocks than smaller ones or pairs, and

when in dispersed family groups, accrue the benefits of flocking while sharing the costs with related individuals.

## Study site

We focused on a generous spatial extent between 0° and 10°E, and between 50°N and 54°N, in order to capture the species' wintering grounds along the North Sea coast, while excluding both the well known Slimbridge Whitefronts (Boyd 1965), as well as the Baltic Sea wintering population. This area includes the very north of France, Belgium, the Netherlands, Luxembourg, and the German states of Saarland, Rhineland-Palatinate, North Rhine-Westphalia, Lower Saxony, Bremen, Hamburg, and parts of Schleswig-Holstein. The region is part of the Northern European Plain, and has no major relief features, while drainage is plentiful via a number of large rivers which include the Rhine, Meuse, IJssel, Ems, and Elbe. The landscape is human dominated, with urban centres surrounded by agricultural land. Farmland is of two broad types: grains and below-ground crops largely for human consumption, and pasture for livestock. Freshly planted winter crops and harvest remains serve as dense, high energy food sources for up to 2.5 million individuals of five main species of migratory geese (Koffijberg et al. 2017, Fox and Abraham (2017)). The presence of wind turbines may once have made parts of the landscape unavailable for migrating geese, but this avoidance has largely disappeared as geese have become habituated to them (Madsen and Boertmann 2008). The North Sea population of Whitefronts wintering in this region has stabilised at around 1.4 million from historic lows in the 1960s, following several years of conservation-enabled and crop-feeding boosted exponential growth (Fox et al. 2010, Fox and Madsen (2017)). Whitefronts also make up a larger proportion of wintering *Anser* geese than they used to in some parts of the study area (Mooij 1982), and while forming largely homogeneous flocks sometimes thousands strong, are also to be seen in mixed flocks with other species.

## Flock counts

We gained access to four datasets relating to the study species from our region of interest. The first was a set of flock attributes: flock size, age ratio (percentage of first winter birds), the numbers of families of each size, and other associated information (time, habitat type, observer identity). These data were collected by volunteers ($n = 75$) across western and central Europe ($n = 8764$). We refer to the number of juveniles associated with an adult as 'family size' throughout. The values are thus whole numbers with a biologically determined upper limit. These data only counted successful families, ie, the minimum family size was one (juvenile), and lacked information on the social (paired or not) and breeding status (unsuccessful or immature) of the remainder of the geese in the flock.

Flocks are often larger than can be sampled in their entirety in the field. In 6% of cases,

the flock size was missing, and this was reconstructed as either the related (and in 31% of cases, identical) number of geese sampled, or, if that value was also missing ($n = 28$), as the sum of the number of adults and juveniles. In cases where the percentage of first winter birds was missing ($n = 50$), it was calculated from the number of juveniles and the flock size.

We filtered these data temporally; though the data contained observations since 1957, the number of records before the breeding year 2000 was low ($\sim 7\%$), and we retained only records made between autumn 2000 and spring 2017 ($n = 7,416$). In order to facilitate downstream analyses, we checked whether each record had a complete date (year, month, day), and in cases where the day was missing ($n = 32$), we assigned it to the 15th. In all cases hereon, 'year' refers to the goose breeding year, which begins in June.

Nearly all ($> 99\%$) records had associated site names, with flocks recorded at 1567 unique sites. This data was geocoded using the Google Maps Geocoding API accessed by the function geocode from the package ggmap (Kahle and Wickham 2013) using one of 123 unique look-up names associated with the site names. Exclusion of sites without geocoded coordinates, or from outside the study area left 7149 records of flocks, in 1884 of which family sizes and frequencies were also known. All 1884 flocks for which data on families were available lay between 4°E and 8°E. Family level data were then extracted from each flock to get variables for each family ($n$ families = 51,037).

Each record was assigned one of the zones, "East Frisia", "IJsselmeer", "Rhinelands", and "Southwest", based on the province in the Netherlands, or the district in Germany, in which it was made. Zones cover areas in or around the names given. The Rhinelands zone had almost as many records as the other zones combined, and this could have biased any trend in the data. We sought to avoid this by retaining only half the original number of records, with random selection.

## Observations of marked geese

A large number of geese of different species have been fitted with numbered neckbands, which allows for field identification. Observations of such geese are reported and displayed on the website geese.org. These records include the code on the neckband, the codes of associated geese, the number of juveniles, and the position. We obtained these records in order to add to our analyses. We removed the following types of records: those in which a goose was seen with neither juveniles nor a social partner, one of the two records in which two birds of a pair had been reported separately when seen together, those in which the bird was less than two years old at the time of observation, and those which lay outside the spatial temporal range described above. 10,635 records remained, reported from 8,416 unique coordinate pairs.

These data differed from the flock level counts in three important respects. First, the records lacked information on the size of the flock in which each goose was seen, and

on other flock attributes such as habitat type. Second, the data contained records of pairs observed with no young, since the focus was on ringed individuals, rather than families. Finally, the data contained records from sites further afield than the flock count data, indeed, the spatial extent of our study was chosen based on that of the records obtained in this dataset.

## Flight activity

Goose populations on the wintering grounds are related to the timing of both autumn and spring migration, increasing after the start of the former, and decreasing towards the end of the latter. This makes it important to know when the migrations have begun or ended. To determine these dates we accessed goose flight activity data from *Trektellen* [`trektellen.org`] sites across the Netherlands. These data were filtered to exclude sites that lay close to goose night roosts so as to avoid noise in the data from daily, rather than migratory, movements. Data were further filtered to exclude flights that did not match the direction of migration appropriate to the season. From these data, we calculated the first date in each autumn (ending December) and the last date in each spring (ending July) on which goose flight activity, in the form of number of geese flying per hour of observation time, was at or above the 90th percentile of within- breeding year season specific activity. We took these dates to represent the beginning of goose arrival from the autumn migration, and the end of goose departure on the spring migration, respectively. By our method, goose arrival over the years was between September 26 and October 30, and the end of spring migration was between March 03 and April 01. We added these dates to the flock, family, and individual level data, matching them by breeding year, and then calculated the number of days between each observation and the two extremes of goose migration.

## Summer breeding success

The number of juveniles in families observed on the wintering grounds is a function of the breeding success of geese in the Arctic. This in turn is thought to be linked to the abundance of Arctic rodents, primarily lemmings (*Lemmus sp.* and *Dicrostonyx sp.*). This shows a cyclical pattern with a 3 – 4 year period, with a 'lemming peak' year followed immediately by a 'crash' year, with abundance rising until the next peak. The factors underlying that are thought to be largely intrinsic, but may also be related to the form of precipitation and its effect on the availability of vegetation to lemmings (Hansen et al. 2013).

Summers and Underhill (1987) hypothesised that goose breeding success is high in 'lemming peak' years, since Arctic predators switch from their preferred lemming prey to goose eggs and young when lemmings are scarce. Dhondt (1987) amended this alternate prey hypothesis (AHP) to reflect that predator populations are linked to, but also lag behind, lemming abundance. Goose breeding success is thus predicted to be

lowest in the years immediately following lemming peaks, when a dearth of lemmings and a surfeit of predators combine to produce predation pressure on goose young that's higher than the mean. This logic has been found to explain winter estimates of breeding success of both geese and waders wintering in Scandinavia (Blomqvist et al. 2002), and of Dark-bellied Brent geese (*Branta b. bernicla*) wintering along the North Sea coast (Nolet et al. 2013).

Within this context, we sought to calculate an index for the summer predation pressure on our population, following the method presented earlier in Blomqvist et al. (2002), Nolet et al. (2013), and Koffijberg (2010). The breeding grounds of our population lie above the Arctic Circle (66.5°N), and between the Kanin Peninsula (45°E) and the River Yenisei (85°E) (Madsen and Cracknell 1999) in the Nenets and Yamal regions of Russia. We could not asses rodent abundance for this area from the literature, which focuses largely on lemming abundance from the Taimyr Peninsula (98°E) (Kokorev and Kuksov 2002, used in Blomqvist et al. (2002), and in Nolet et al. (2013)). While it is suggested that lemming cycles in some regions of Scandinavia (Angerbjörn et al. 2001), and in the high Arctic of Svalbard (Hansen et al. 2013) may be synchronised by climatic fluctuations, we did not expect lemming cycles in the Nenets and Yamal regions to be synchronised with those of Taimyr, and preferred to use our own index.

We obtained rodent abundance indices for the relevant region from the website *Arctic Birds* [www.arcticbirds.net], an initiative of the International Breeding Conditions Survey on Arctic Birds. Nolet et al. (2013) previously used the same approach to to fill in gaps in the dataset they used. Sites on *Arctic Birds* are marked on a map and binned into four classes: "Unclear", "Low or absent", "Average", and "High". The same sites are not present in each year. We graded these sites on a 0 – 3 scale, with 0 for "Unclear, and 3 for"High". The distinction between sites graded 0 and 1 was itself unclear. Both 0 and 1 were used in different years to mark the island of Kolguyev, which is well known to have no lemming cycle. We took 0 to indicate a near or full absence of lemmings rather than an unsurveyed site, and also included an entry of 0 for Kolguyev in each year. Around 30% of the North Sea population of Whitefronts breeds on Kolguyev, where it forms the major prey base for the island's predators (Kondratyev and Zaynagutdinova 2008), making this an important addition to the data.

We averaged the lemming index across the sites in each year, and then for each year $t$, we calculated a predation index ($P_t$).

$$P_t = \frac{L_{t-1} - L_t + 3}{2} \tag{1}$$

## Tracked families

The only families for which trends in size and position could be studied with some certainty were those which had been fitted with GPS receiving position

logger/transmitters during the winters of 2013 ($n = 3$), 2014 ($n = 4$), and 2016 ($n = 6$). Position loggers in 2013 and 2014 were backpacks (e–obs GmbH), and in 2016 were numbered neckband loggers supplied by Theo Gerrits (madebytheo). These loggers were set to record a baseline of one position every 30 minutes, though the actual fix frequency depended on the mode in which the remotely programmable device was then operating. Data from these loggers were uploaded remotely to the animal tracking database Movebank, from where they were retrieved prior to analysis.

Logger data were filtered to fit within the spatial extents of the study area, and data collected after March 31 each spring were excluded from the analysis. A major component of these data were 'flight bursts', high fix frequency (0.5 or 1 Hz) records triggered by takeoff as measured by on-board accelerometers. These bursts were removed, and only data with the baseline sampling interval retained. Fixes where the logger position error was estimated to be above 20m were also removed. To fully account for irregularities in sampling interval introduced by the logger not functioning as ideal, the remaining data were averaged over every half hour so as to obtain a regular timeseries of data. This allowed for a meaningful matching of positions within families at the same timestamp.

The adult in the family with the greater number of logged positions was set to be the 'reference'. In doing so, we hoped to obtain a longer sequence of reference-to-individual distances, which might also result in capturing more family dynamics. The distance between the reference and all other individuals in the family was calculated using the Vincenty ellipsoid method for geographic coordinates (Vincenty 1975) implemented by the `geosphere` package in `R` (Hijmans 2016). These distances were used to determine the number of family members within a 250m radius of the reference, and the family size per day was obtained as the maximum number of members within that radius during a day. Due to an accretion of errors at the level of the logger and in rounding and averaging the data, the sizes of some families as calculated above fluctuated drastically over time. We then considered the family size on each day to be maximum of the family sizes on all days between that one and the final day. We did not differentiate cases in which the adult pair of the family split from other types of family size decrease, which in our data included juvenile independence, juvenile death, and logger malfunction.

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# References

Alphéraky, S. 1904. The geese ofEuropeand asia. – Translated version, London in press.

Angerbjörn, A. et al. 2001. Geographical and temporal patterns of lemming popula-

tion dynamics in fennoscandia. – Ecography 24: 298–308.

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

Boyd, H. 1965. Breeding success of white-fronted geese from the nenets national area. – Wildfowl in press.

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.

Ely, C. R. 1979. Breeding biology of the white-fronted goose (anser albifrons frontalis) on the yukon-kuskokwim delta, alaska.

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. and Madsen, J. 2017. Threatened species to super-abundance: 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.

Hansen, B. B. et al. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the high arctic. – Science 339: 313–315.

Hijmans, R. J. 2016. Geosphere: Spherical trigonometry.

Kahle, D. and Wickham, H. 2013. Ggmap: Spatial visualization with ggplot2. – The R Journal 5: 144–161.

Koffijberg, K. 2010. Breeding success amongst greater whitefronted geese in 2009/10–a progress report. – Goose Bull. Nov 2010: 32–34.

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

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.

Kondratyev, A. and Zaynagutdinova, E. 2008. Greater white-fronted geese (*Anser albifrons*) and bean geese (a. fabalis) on kolguev island–abundance, habitat distribution, and breeding biology. – Vogelwelt 129: 326–333.

Madsen, J. and Cracknell, G. 1999. Goose populations of the western palearctic. in press.

Madsen, J. and Boertmann, D. 2008. Animal behavioral adaptation to changing landscapes: Spring-staging geese habituate to wind farms. – Landscape ecology 23: 1007–

1011.

Miller, H. and Dzubin, A. 1965. Regrouping of family members of the White-Fronted goose (*Anser albifrons*) after individual release. – Bird-Banding 36: 184–191.

Mooij, J. 1982. The " niederrhein"(Lower rhine) area (north rhine westphalia, federal republic of germany), a goose wintering area of increasing importance in the dutch-german border region. – Aquila 89: 285–297.

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.

Stroud, D. A. 1982. Observations on the incubation and post-hatching behaviour of the greenland white-fronted goose. – Wildfowl 33: 63–72.

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.

Vincenty, T. 1975. Direct and inverse solutions of geodesics on the ellipsoid with application of nested equations. – Survey review 23: 88–93.

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.