Abstract

Many species live in family groups where juveniles receive parental care. The families of some large migrating species often stay together through one or more migration events. How the social status of families, pairs and single animals influences their migration timing and space-use is not yet well understood. Here we focus on the family size dynamics of greater white-fronted geese *Anser a. albifrons* on their wintering grounds. We gathered 17 years of observation data on foraging flocks of wintering geese in the Netherlands and northern Germany, and tracked 13 complete families with GPS transmitters. Taking into account effects carried over from the summer, we explored how the distance of the wintering site from the breeding grounds, number of juveniles in a family, number of individuals in a flock and the age-ratio of flocks develop over time. We related the probability of a family splitting to the number and frequency of flight events. Sixty days after the first autumn arrivals, families with more juveniles winter farther west, where flocks are smaller. The number of juveniles in a family, flock size, age-ratio, and the number of families in flocks is correlated with the number of days since first arrival. Families that undertake more flights in winter are more likely to split. Our data suggest that many juvenile white-fronted geese separate from their parents during the winter, and that this species is differentially migratory by age and social class in both autumn and spring. These findings are important for further investigation of the influence of climate and habitat change on large migrants that subsist in families long after hatching, and their conservation and management.

Introduction

Most species' young receive direct or indirect parental care, which improves their own survival and provides inclusive fitness gains to their relatives (Hamilton 1964). Such care is usually in the form of food, shelter and protection (Clutton-Brock 1991). The duration of care varies strongly between and within species (Clutton-Brock 1991). Large migratory species often stay in family groups throughout the first or later migration events (see Warren et al. 1993, Kruckenberg 2005). This has direct survival and fitness benefits for both young and parents in terms of shared vigilance and higher social status within larger aggregations (Black and Owen 1989, Roberts 1996).

Many large waterbirds, such as the geese *Anserini*, live in groups composed of families throughout much of the year. Flocking behaviour is most apparent in winter, when goose families gather to form often enormous feeding flocks (Elder and Elder 1949). Maintaining family bonds within flocks confers benefits as larger social units are dominant over smaller ones, and dominance rank increases with the number of members in the unit (e.g. in Canada geese *Branta canadensis;* Hanson 1953, and barnacle geese *B. leucopsis*; Loonen et al. 1999). The size advantage allows larger families to occupy optimal foraging positions in flocks at lesser cost and win access to better resources (Black et al. 1992; Black and Owen 1989). In addition, parents of some

42   species benefit in summer from the presence of nest-attending sub-adults (Fox and

43   Stroud 1988).

44   Over the course of a year, goose family bonds are affected by a number of factors. The

45   success of a pair hatching and fledging young is often determined by a combination of

46   weather conditions and levels of summer predation on the breeding grounds (Dhondt

47   1987, Summers and Underhill 1987, Bêty et al. 2004). The impact of summer predation

48   linked to the abundance of lemmings and voles *Arvicolinae* has historically been

49   significant in some species, as to be detectable at the population level in winter

50   (Summers and Underhill 1987, Nolet et al. 2013). Autumn migration takes a further toll

51   in long-distance migrants, especially on juvenile birds (Owen and Black 1989, Francis et

52   al. 1992). In spring, juvenile geese often become independent of parents (Prevett and

53   MacInnes 1980, Johnson and Raveling 1988, Black and Owen 1989), but some juveniles

54   may remain associated with parents through the spring migration and on the breeding

55   grounds, where they help to fend off predators and competitors (Ely 1979). Some even

56   remain associated with their parents the following winter (Kruckenberg 2005). The

57   mechanistic causes underlying family separation might be of either accidental nature

58   (Prevett and MacInnes 1980), or the result of adults chasing off juveniles prior to spring

59   migration (Black and Owen 1989, Poisbleau et al. 2008).

60   The development of family bonds in winter appears to be variable between species and

61   populations. In general, smaller species that are observed in mixed flocks tend to

62   dissolve families in winter (Johnson and Raveling 1988, Jónsson and Afton 2008),

63   whereas larger species tend to maintain families for longer (Warren et al. 1993,

64   Kruckenberg 2005). Moreover, migration speed and spatial distribution may differ

65   between population classes, such as pairs with and without offspring (Cooke et al. 1975,

66   Cristol et al. 1999, Green & Alerstam 2000, Schamber et al. 2007). Previous studies have

67   noted a change in goose distribution in winter in response to severe cold (Philippona

68   1966, Lok et al. 1992). Such distributional changes serve as a convenient starting point

69   for an examination of climatic factors affecting spatial patterns in goose flocks and

70   families, especially in light of drastic changes observed in the spatial and migration

71   ecology of similar species sharing the wintering site.

72   Greater white-fronted geese *Anser a. albifrons*, hereafter white-fronted geese, are

73   among the most abundant geese wintering in continental Western Europe and occupy a

74   wide wintering range (Madsen et al. 1999), thus offering an interesting opportunity to

75   investigate the wintertime dynamics of goose families. We draw on long-term field

76   observations and high frequency GPS tracks of whole families of white-fronted geese

77   from their wintering grounds in the Netherlands and northern Germany to test the

78   following observational hypotheses: *1.* Families with more juveniles winter closer to the

79   breeding grounds, *2.* Larger families winter in smaller flocks, *3.* Families decrease in size

80   over the winter and *4.* Family separation is triggered by flight related disturbances.

Methods

Age ratios and family size

We and others observed flocks of feeding geese in winter and determined age-ratios by counting the number of adult and juvenile birds in each flock. In white-fronted geese, both age classes are easy to identify by plumage throughout winter and early spring (Koffijberg 2006). In a sub-sample of flocks, the number of juveniles per pair was assessed (here defined as one family), making use of characteristic behaviour and social interactions. Most counts were carried out at a large number of sites within the core wintering range (Fig. 1A) from October to January (81%), gradually declining in February (11%) and March (7%). April and September had many fewer counts, as most geese still had not arrived, or had already departed in this period. 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 (Tab. 1).

Additionally, we took pair status and the number of young from reported sightings of neck-banded individuals, submitted by observers to the www.geese.org portal. In contrast with age-ratio counts, these include records of pairs without accompanying juveniles (defined as unsuccessful families). Observations of marked geese did not include details on habitat type, flock size and observer. Data from 10,635 marked individuals, observed at 8,416 sites, were obtained after filtering for data from single geese without pair status or data on offspring (Tab. 1).

To estimate the effect of autumn migration mortality, we determined family sizes on the breeding grounds on Kolguyev Island, Russia (approx. 69°N, 49°E, Fig. 1B) in August 2016, approximately one month prior to the autumn migration. On Kolguyev Island, 116 records of successful and unsuccessful families were collected (Tab. 1).

Family tracking

We collected half-hourly positions of a total of 13 complete goose families (13 adult pairs, 38 juveniles) fitted with GPS transmitters in the core wintering range within the Netherlands, between November and January (2013, n = 3, 2014, n = 4: e-obs GmbH, backpacks with Teflon harness, weight 45 g; 2016, n = 6: madebytheo, integrated into neckband, weight 35 g). These selectively large families were tracked within the study site (2 - 10°E, 50 - 54°N) during winter (before 1 April) for 34 – 135 days. A reference bird was identified in each family as the parent with the greater number of GPS fixes within the study period, which was the male in all cases except one. For all families, we identified the day and position where splits were first detected as a decrease in the number of family members within a 1000m radius of the reference bird (see Fig. 1A). We then determined the daily split probability by a binomial fit on the classification of each day as a success or failure (1 or 0) depending on whether a split occurred or not. We defined 'flights' as displacements >1 km over the 30 minute sampling interval, and counted their number and daily frequency.

Context data

To relate our observations to the timing of migration we extracted peaks of daily counts (n = 6,266) of visible migration in the Netherlands (*www.trektellen.nl*; Van Turnhout et al. 2009) to determine yearly arrival dates in autumn and departure dates in spring. Data were pooled for 84 spring and 180 autumn counting sites . We excluded counts from sites close to night roosts, and records which did not match the direction of migration appropriate to the season; both in order to avoid bias by local movements.

Following previous work (Jongejans et al. 2015) we estimated an index of summer predation for the breeding grounds of this population from rodent abundance data (*www.arcticbirds.net*). We calculated a pooled mean of 0 - 2 (low - high) lemming indices for all available sites in the region, taking care to always include a value of 0 to reflect the absence of lemming cycles in the core breeding area on Kolguyev Island. The predation index takes into account the cyclical change in lemming abundance, with higher values when lemming abundance has decreased from the previous year, reflecting the increased predation pressure on Arctic birds due to abundant predators switching to alternative prey (see Dhondt 1987).

To test whether spatial patterns in this population could be explained by environmental effects, we gathered daily data from 51 sites (Koninklijk Nederlands Meteorologisch Instituut, Netherlands; Deutscher Wdetterdienst, Germany) for minimum temperature, total precipitation, and mean wind-speed. Sites were on average 20km (range: 4 - 83km) from the positions at which flocks were observed.

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 (family size counts and ring-sighting data; Tab. 1, Supplementary Material Tab. A1). Further, we tested whether (*2.a.*) the number of juveniles in a family and (*2.b.*) the total number of successful families was explained by flock size, the number of days since the arrival of geese in autumn or the level of summer predation (using family size counts; Tab. 1). To test for an effect of climate on the number of successful families in flocks, we added daily minimum temperature, daily total precipitation, and daily mean wind-speed as variables in model *2.b*. Further, we tested whether (*2.c*) the number of juveniles in families was different in the breeding grounds one month prior, and up to two months after autumn migration in 2016 (using family size counts in the wintering region and on Kolguyev Island, and ring-sighting data).

To place these results in a wider context, we examined (*3.*) how flock size (from age-ratio counts) was related to distance from the breeding grounds, the number of days since arrival, summer predation, climatic variables, 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 (using age-ratio counts; see Supplementary material Tab. A1).

Further, we examined whether (*5.*) the daily split probability was predicted by the number of days since arrival, the number of flights on that day, the cumulative number of flights since the beginning of the tracking period until that day, the distance travelled

163   that day, the cumulative distance travelled since the beginning of tracking until that day,

164   and the family size on that day (using GPS tracking data; Supplementary Material Tab.

165   A1).

166   All analyses were performed in the *R* environment (R Core Team 2017) (see

167   Supplementary Material Tab. A1). We used Poisson *lme4* (Bates et al. 2015) linear and

168   generalised linear mixed models (LMMs & GLMMs) to test *1* and *2.a*, a simple Poisson-

169   error generalised linear model to test *2.c* and a binomial-error GLMM for *5*. In *2.b*, *3*, and

170   *4*, we used *mgcv* (Wood 2013) Poisson (*2.b*) and binomial (*4*) generalised additive mixed

171   models (GAMMs) to include smooth functions of the flock size (in *2.b*) and the number

172   of days since winter (in *4*) as predictors. We included the breeding year, the observer

173   identity, the goose identity if known, and the habitat type as independent random

174   effects. Effects included in models were dependent on their availability in the datasets

175   used (see Supplementary Material Tab. A1).

176   ## Results

177   ### Age ratios and family sizes

178   The mean flock size was 712 birds (range: 2 - 20,000), with a mean proportion of first-

179   winter birds of 0.18 (range: 0 - 0.87). Flocks in which families were counted (family size

180   counts) held on average 540 birds (range: 3 - 11,000), with an average of 27 families

181   (range: 1 - 333) accompanied by a mean of 1.78 juveniles (range: 1 - 10).

182 On average, the family status of marked geese (ring-sighting data) was recorded 626

183 times each year (range: 62 - 1143), and these were accompanied by 0.59 juveniles

184 (range: 0 - 11) (see Appendix 1, Supplementary material Figs. A1.1, A1.2). The 116

185 observed families on Kolguyev Island in 2016 had a mean of 2.26 juveniles (range: 0 – 6).

186 ## Context data

187 Autumn migrants arrived between 26 September to 30 October, and flocks departed

188 between 3 March to 1 April, resulting in a wintering period for geese of on average 165

189 days (range: 124 – 183). Lemming abundance from the breeding grounds transformed

190 into a predation index ranged between 1.17 and 1.9, with very low variance between

191 years (σ^2 = 0.048).

192 ## Juveniles and wintering site choice

193 We found no influence of the number of juveniles in a family on how far from the

194 breeding grounds a family wintered in the first sixty days after arrival, neither in age-

195 ratio data (χ^2 = 3.27, p = 0.071), nor in ring-sighting data (χ^2 = 2.18, p = 0.134, Fig. 2).

196 Later in winter, age-ratio data indicated that larger families winter somewhat farther

197 west (χ^2 = 6.026, p = 0.014), while ring-sighting data did not reveal any difference (χ^2 =

198 0.023, p = 0.879). Even when selecting only the successful families in the ring-sighting

199 data, no effect could be found (χ^2 = 0.892, p = 0.345). This difference is likely due to

200 lower sample size and fewer observed random effects in the ring-sighting data. The

201   proportion of successful pairs, assessed by ring-sighting data, was not related to the

202   distance of their wintering site from the breeding grounds (χ^2 = 1.071, p = 0.301).

Family size in winter

204   The number of juveniles in a family (successful families counted in flocks, model *2.a*)

205   decreased through the winter (χ^2 = 74.166, p < 0.001, see Fig. 3), but was insensitive to

206   flock size (χ^2 = 0.270, p = 0.6033) and summer predation (χ^2 = 0.337, p = 0.562, see Fig.

207   A2). Family sizes of neckbanded geese (model *2.a* adapted) decreased over time as well

208   (χ^2 = 19.936, p = < 0.001, see Fig. 3); flock sizes of this dataset were not available.

209   Surprisingly, family sizes of neckbanded geese increased with the level of summer

210   predation (χ^2 = 12.935, p < 0.001, see Fig. A2). However, this increase was very low with

211   on average 0.78 additional juveniles per family per unit increase in the predation index.

212   When excluding unsuccessful pairs from the neckband-resighting data, the relation with

213   summer predation became insignificant (χ^2 = 0.1321, p = 0.716, see Fig. A2), indicating a

214   qualitative rather than quantitative effect of predation on nest success.

215   The number of successful families in flocks (model *2.b*) increased with flock size (χ^2 =

216   7250, p < 0.001) and the number of days since goose arrival in autumn (χ^2 = 158.3, p <

217   0.001, see Fig. 4A), but was unaffected by summer predation (χ^2 = 0, p = 0.98). Further,

218   there were more successful families in flocks farther from the breeding grounds (χ^2 =

219   11.253, p = 0.0008, see Fig. 5A). Also, the number of successful families in a flock was

220   higher when daily minimum temperatures were higher (χ^2 = 7.318, p = 0.007), and

221   decreased weakly with rising daily precipitation (χ^2 = 3.931, p = 0.047). Wind speed was

222   not an important predictor (χ^2 = 2.644, p = 0.104).

Flock size in winter

224   Flocks (model 3) were significantly smaller farther from the breeding grounds (χ^2 =

225   93,629, p = < 0.001, see Fig. 5A), and grew slightly over the winter (χ^2 = 4,824, p < 0.001).

226   Flock size was affected by each of the climatic predictors, decreasing with worsening

227   weather: increasing precipitation (χ^2 = 3193, p < 0.001) and increasing daily wind speed (

228   χ^2 = 25,906, p < 0.001). However, flock sizes increased with decreasing daily minimum

229   temperatures (χ^2 = 365, p < 0.001).

230   Within flocks, juvenile proportions increased through the winter (χ^2 = 18.82, p = 0.001,

231   see Fig. A4b), and decreased with increasing flock size (χ^2 = 5.921, p = 0.015, see Fig.

232   A4c), but did not show any effect of distance from the breeding grounds (χ^2 = 0.979, p =

233   0.323), or of summer predation (χ^2 = 0.013, p = 0.908).

Family size prior to autumn migration

237   Families of geese observed approximately one month prior to the onset of migration in

238   the breeding area on Kolguyev Island had significantly more juveniles than successful

239   families (family size count) in flocks (GLM, z = -4.285, p < 0.001) and families of marked

geese (ring-sighting data) (GLM, z = -14.511, p < 0.001) recorded in the first two months

following the population's arrival on the wintering grounds (model *2.c*).

Probability of family splits

Families fitted with GPS transmitters travelled on average 11 km each day (range: 0 -

306). On average, they travelled a distance > 1km twice per day (range: 0 - 10) and in

total 98 times (range: 63 - 367) over the tracking period. 21 family split events were

recorded in the 13 families and were not restricted to juveniles.

The daily split probability of families (model *5*) was significantly lower later in the winter

(χ^2 = 8.314, p = 0.004, Fig 6A), and lower in larger families (χ^2 = 11.41, p < 0.001, Fig 6C).

There was no effect of the daily number of flights (χ^2 = 0.018, p = 0.893), nor the daily

distance moved (χ^2 = 2.99, p = 0.083). Split probability was higher in families that made

cumulatively more flights in the period between the beginning of tracking and the split

(χ^2 = 143.23, p < 0.001, Fig 6D), and increased in families that moved a longer cumulative

distance in the period between the start of tracking and the split (χ^2 = 182.63, p < 0.001,

Fig 6B).

Discussion

We have quantified the spatial-temporal distribution and size dynamics of white-fronted

goose families in wintering flocks in the context of winter climate, predation risk in

summer, and mortality during autumn migration. In support of our hypothesis, we found

259   that large families wintered farther from the breeding grounds, but only during the

260   second half of winter. Larger families did not select for smaller flocks, but flocks were

261   generally smaller in the west. As expected, family size did decrease over the winter, but

262   our results indicate that families were less likely to separate later in winter and with

263   increasing family size. We found some evidence for the suggestion that families that flew

264   more often were more likely to separate, split events thus likely being accidental during

265   disturbance events.

266 ## Spatial dynamics of family size

267   Our baseline result that flock sizes are smaller in the west of the wintering region, i.e.

268   further from the breeding sites, can be explained by metabolic constraints that

269   determine maximum flight distances and duration even during migration (Klaassen

270   1996). This explanation is supported by the fact that family sizes did not vary spatially

271   during the first winter months. However, once all geese have arrived and wintering sites

272   begin filling up. As food becomes more limited, it seems that large, socially dominant

273   families (Vangilder and Smith 1985, Schamber et al. 2007) move further to occupy

274   climatically milder sites. This supports the earlier suggestion of differential use of

275   wintering sites (Jongejans et al. 2015) according to social status.

276

277   Contrary to expectations, larger families were generally not associated with smaller

278   flocks. Rather, it was a coincidence that larger families as well as small flocks were found

279   further from the breeding sites. Furthermore, spatial differences in family wintering

280   areas might have led to the finding that larger flocks appeared to have a lower

281   proportion of juveniles (Jongejans et al. 2015). Large goose families selecting for optimal

282   sites seem to be one driver of the variation in juvenile proportion between wintering

283   sites (Schamber et al. 2007). However, independent juveniles observed in wintering

284   flocks (Hanson 1953, Loonen et al. 1999) may dampen this variation.

285   ## Temporal dynamics of family size

286   The finding that family size decreased through the winter points towards a steady

287   reduction in the number of juveniles associated with families, and to high variation in

288   the age at which young geese leave their parents. Some young geese may be found

289   associated with the parents even in their second or third winter (Ely 1979, Warren et al.

290   1993, Kruckenberg 2005). The separation of juveniles from their parents should result in

291   a reduction of the number of successful families in flocks over the winter. However, we

292   could not find such a pattern, rather the opposite. This might be partly explained by the

293   suggestion that most pairs do not become dissociated from all their young during winter,

294   i.e., that split events are accidental rather than triggered by the parents (Prevett and

295   MacInnes 1980). Furthermore, families with juveniles might have departed later for

296   spring migration than pairs without young, mirroring their differential autumn migration

297   arrival which is later than other adult geese (Jongejans et al. 2015).

298   This proposed differential migration timing is further supported by the strong, non-linear

299   temporal increases of proportions of juveniles in foraging flocks. The general hypothesis

300   may be put forward that it is adults without young that first leave the wintering grounds

301 for northerly breeding and moulting sites on spring migration, followed by families with

302 young, with indpendent juveniles bringing up the rear. Our finding runs contrary to

303 previous studies on the spring migration of pink-footed *A. brachyrhynchus* and snow

304 geese (Madsen 2001; Bêty et al. 2004). Interestingly though, juvenile snow geese

305 generally also apparently follow a migration schedule that is different from the adults

306 (Prevett and MacInnes 1980).

307 Data from the 13 GPS tracked goose families support the suggestion that dissociations of

308 juveniles from their families are accidental during winter (Prevett and MacInnes 1980).

309 In most cases, juveniles split off one at a time, an not all at once. The daily probability of

310 families losing young increased with cumulative flight time. However, our finding that

311 split probability was reduced towards the end of winter contradicts our results from

312 counting data, and previous findings that most juveniles were more likely to become

313 independent towards spring (Prevett and MacInnes 1980, Johnson and Raveling 1988,

314 Black and Owen 1989, Scheiber et al. 2013). A likely explanation might be found in

315 relation to the previous result that larger families were less likely to split, as our 13

316 tracked families were selected to be large.

317 ## Effects of winter climate conditions

318 The negative responses of number of successful families in flocks and flock size to cold

319 and wet weather are in line with current knowledge of goose foraging preferences (Fox

320 and Madsen 2017). Geese have been found to tolerate snow depths of about 15 cm

321 before relocating to areas with better access to forage (Philippona 1966). Such

322   conditions have become rare over the past decade and usually do not occur in the

323   Netherlands before midwinter. This is in accordance with spatial differences in family size

324   only being observed in late winter. Large, dominant families thus seek to occupy the

325   rather limitedwestern, coastal sites with moderate temperatures. Limited habitat

326   availability in the west of the Netherlands and Belgium, combined with high hunting

327   pressure in France, and the high energetic costs of long flights seem to lead to geese

328   aggregating in large flocks on the remaining accessible grassland sites on cold, snowy

329   days.

Relation to breeding sites

331   Our result that families were significantly larger prior to migration than in the first two

332   months on the wintering grounds is in line with previous findings of high juvenile

333   autumn mortality (Owen and Black 1989; Francis et al. 1992). As in those studies, we

334   assume that mortality in our population is also mainly due to higher parasitic loads and

335   strong density-driven competition for resources prior to and during autumn migration.

336   Previously, juvenile survival of Arctic-breeding birds, including geese, was understood to

337   be driven by predation, which in turn was driven by the cyclical abundance of Arctic

338   rodents (Summers and Underhill 1987). However, our study supports the idea that the

339   breeding success of white-fronted geese on the Baltic-North Sea flyway is unrelated to

340   summer predation in recent years (Jongejans et al. 2015). This may be possibly due to

341   faltering lemming cycles (Nolet et al. 2013), or because an increasing proportion of the

342   population breeds in areas like Kolguyev Island, that altogether lack Arctic rodents and

343 associated phenomena (Kruckenberg et al. 2008). On the other hand, our finding that

344 the number of juveniles seen with marked geese increased during years of increased

345 predation suggests a qualitative rather than quantitative response, to wit that in years of

346 high predation, some geese succeed in raising large families, but many more suffer total

347 brood failure.

General conclusion

349 Based on the spatial and temporal patterns of wintering goose families, we argue that

350 management actions (Stroud et al. 2017) have to consider that the proportion of

351 juvenile geese in foraging flocks is higher in some areas and times of the year. It is crucial

352 to distinguish between adult survival and recruitment for population control (Madsen

353 2010), as well as conservation effort. Climate, habitat change, and change of feeding

354 habits are suggested to have led to increased goose densities, range expansion and

355 range shifts (Fox et al. 2005). As high densities lead to low recruitment in the Arctic

356 breeding grounds (Owen and Black 1989, Francis et al. 1992), goose populations might

357 become less flexible and highly vulnerable to rapidly changing conditions. Furthermore,

358 our results show that higher levels of disturbance in the wintering sites and migration

359 stopovers, e.g. as a result of increased management actions, would induce more goose

360 family splits and additionally change population structure and survival rates. Such

361 disruption of the mechanisms of cultural transmission of space use could cause levels of

362 adaptability to changing environmental conditions to change in unpredictable ways.

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467
468

Type	Records	Sites	Spatial extent
Age-ratio counts	7,149	123	4.0° - 8.8°E, 51.1° - 53.4°N
Family sizes	51,037	65	4.8° - 7.3°E, 51.1° - 53.4°N
Ring-sighting data	10,635	8,416	2.7° - 9.7°E, 50.9° - 53.9°N
Familie sizes on Kolguyev	116	26	49°E, 69°N
GPS tracking of families	32,630[a], 13[b]	32,630	3.9° - 7.9°E, 51.3° - 54.3°N
a: Half-hourly family positions, b: Number of families tracked			

Table 1: Datasets of goose observations and tracking.