Family size dynamics in wintering geese

Journal:	*Oikos*
Manuscript ID	Draft
Wiley - Manuscript type:	Research
Keywords:	Anser albifrons, Family size, Differential migration
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.

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).

101   To estimate the effect of autumn migration mortality, we determined family sizes on the

102   breeding grounds on Kolguyev Island, Russia (approx. 69°N, 49°E, Fig. 1B) in August

103   2016, approximately one month prior to the autumn migration. On Kolguyev Island, 116

104   records of successful and unsuccessful families were collected (Tab. 1).

105   ## Family tracking

106   We collected half-hourly positions of a total of 13 complete goose families (13 adult

107   pairs, 38 juveniles) fitted with GPS transmitters in the core wintering range within the

108   Netherlands, between November and January (2013, n = 3, 2014, n = 4: e-obs GmbH,

109   backpacks with Teflon harness, weight 45 g; 2016, n = 6: madebytheo, integrated into

110   neckband, weight 35 g). These selectively large families were tracked within the study

111   site (2 - 10°E, 50 - 54°N) during winter (before 1 April) for 34 – 135 days. A reference bird

112   was identified in each family as the parent with the greater number of GPS fixes within

113   the study period, which was the male in all cases except one. For all families, we

114   identified the day and position where splits were first detected as a decrease in the

115   number of family members within a 1000m radius of the reference bird (see Fig. 1A). We

116   then determined the daily split probability by a binomial fit on the classification of each

117   day as a success or failure (1 or 0) depending on whether a split occurred or not. We

118   defined 'flights' as displacements >1 km over the 30 minute sampling interval, and

119   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

207   Supplementary material Fig. A2). Family sizes of neckbanded geese (model *2.a* adapted)

208   decreased over time as well (χ^2 = 19.936, p = < 0.001, see Fig. 3); flock sizes of this

209   dataset were not available.

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

211   predation (χ^2 = 12.935, p < 0.001, see Supplementary material Fig. A2). However, this

212   increase was very low with on average 0.78 additional juveniles per family per unit

213   increase in the predation index. When excluding unsuccessful pairs from the neckband-

214   resighting data, the relation with summer predation became insignificant (χ^2 = 0.1321, p

215   = 0.716, see Supplementary material Fig. A2), indicating a qualitative rather than

216   quantitative effect of predation on nest success.

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

218   7250, p < 0.001) and the number of days since goose arrival in autumn (χ^2 = 158.3, p <

219   0.001, see Fig. 4A), but was unaffected by summer predation (χ^2 = 0, p = 0.98). Further,

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

221   11.253, p = 0.0008, see Fig. 5A). Also, the number of successful families in a flock was

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

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

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

Flock size in winter

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

227   93,629, p = < 0.001, see Fig. 5A), and grew slightly over the winter (χ^2 = 4,824, p < 0.001).

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

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

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

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

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

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

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

235   0.323), or of summer predation (χ^2 = 0.013, p = 0.908).

236

237

Family size prior to autumn migration

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

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

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

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

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

Probability of family splits

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

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

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

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

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

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

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

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

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

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

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

256   Fig 6B).

Discussion

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

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

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

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

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

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

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

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

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

267   disturbance events.

268   ## Spatial dynamics of family size

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

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

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

272   1996). This explanation is supported by the fact that family sizes did not vary spatially

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

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

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

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

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

278

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

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

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

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

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

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

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

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

Temporal dynamics of family size

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

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

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

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

292   1993, Kruckenberg 2005). The separation of juveniles from their parents should result in

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

308   (Prevett and MacInnes 1980).

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

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

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

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

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

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

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

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

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

318   tracked families were selected to be large.

Effects of winter climate conditions

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

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

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

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

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

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

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

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

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

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

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

331   days.

Relation to breeding sites

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

349   brood failure.

General conclusion

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

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

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

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

355   2010), as well as conservation effort. Climate, habitat change, and change of feeding

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

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

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

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

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

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

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

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

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

365   **References**

366   1.   Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. - Journal of

367   Statistical Software 67: 1–48.

368   2.   Bêty, J. et al. 2004. Individual variation in timing of migration: Causes and

369   reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). -

370   Behavioral Ecology and Sociobiology 57: 1–8.

371   3.   Black, J. M. and Owen, M. 1989. Parent-offspring relationships in wintering

372   barnacle geese. - Animal Behaviour 37: 187–198.

373   4.   Black, J. M. et al. 1992. Foraging dynamics in goose flocks: The cost of living on

374   the edge. - Animal Behaviour 44: 41–50.

375   5.   Clutton-Brock, T. H. 1991. The evolution of parental care. - Princeton University

376   Press.

377   6.   Cooke, F. et al. 1975. Gene flow between breeding populations of Lesser Snow

378   Geese. - The Auk 92: 493–510.

379   7.   Crozier, R. H. and Pamilo, P. 1996. Evolution of Social Insect Colonies. - Oxford

380   University Press, Oxford, UK.

381   8.   Dhondt, A. A. 1987. Cycles of lemmings and Brent geese *Branta b. bernicla*: A

382   comment on the hypothesis of Roselaar and Summers. - Bird Study 34: 151–154.

383   9.   Elder, W. H. and Elder, N. L. 1949. Role of the family in the formation of goose

384   flocks. - Wilson Bull 61: 133–140.

385   10.   Ely, C. R. 1979. Breeding biology of the white-fronted goose (*Anser albifrons*

386   *frontalis*) on the Yukon-Kuskokwim delta, Alaska.

387   11.   Fox, A. D. and Stroud, D. A. 1988. The breeding biology of the Greenland White-

388   fronted Goose (*Anser albifrons flavirostris*). - Kommissionen for Videnskabelige

389   Undersøgelser i Grønland.

390   12.   Fox, A. D. and Madsen, J. 2017. Threatened species to super-abundance: The

391   unexpected international implications of successful goose conservation. - Ambio 46:

392   179–187.

393   13.   Fox, A. et al. 2005. Effects of agricultural change on abundance, fitness

394   components and distribution of two Arctic-nesting goose populations. - Global Change

395   Biology 11: 881–893.

396   14.   Francis, C. M. et al. 1992. Long-term changes in survival rates of lesser snow

397   geese. - Ecology 73: 1346–1362.

398   15.   Green, M. and Alerstam, T. 2000. Flight speeds and climb rates of brent geese:

399   Mass-dependent differences between spring and autumn migration. - Journal of Avian

400   Biology 31: 215–225.

401   16.   Hamilton, W. 1964. The genetical evolution of social behaviour. I. - Journal of

402   Theoretical Biology 7: 1–16.

403   17.   Hanson, H. C. 1953. Inter-family dominance in Canada geese. - The Auk 70: 11–

404   16.

405   18.   Johnson, J. C. and Raveling, D. G. 1988. Weak family associations in Cackling

406   Geese during winter: Effects of body size and food resources on goose social

407   organization. - Waterfowl in Winter: 71–89.

408   19.   Jongejans, E. et al. 2015. Naar een effectief en internationaal verantwoord

409   beheer van de in Nederland overwinterende populatie Kolganzen. - SOVON

410   Vogelonderzoek Nederland.

411   20.   Jónsson, J. E. and Afton, A. D. 2008. Lesser Snow geese and Ross's geese form

412   mixed flocks during winter but differ in family maintenance and social status. - The

413   Wilson Journal of Ornithology 120: 725–731.

414   21.   Klaassen, M. 1996. Metabolic constraints on long-distance migration in birds. -

415   Journal of Experimental Biology 199: 57–64.

416   22.   Koffijberg, K. 2006. Herkenning en ruipatronen van eerstejaars kolganzen in de

417   winter. - Limosa 79: 163.

418   23.   Kruckenberg, H. 2005. Wann werden "die Kleinen" endlich erwachsen?

419   Untersuchungen zum Familienzusammenhalt farbmarkierter Blessgänse *Anser albifrons*

420   *albifrons*. - Vogelwelt 126: 253.

421   24.   Kruckenberg, H. et al. 2008. White-fronted goose flyway population status. -

422   Angew. Feldbiol 2: 77.

423   25.   Lok, M. et al. 1992. Numbers and distribution of wild geese in the netherlands,

424   1984-89, with special reference to weather conditions. - Wildfowl 43: 107–116.

425   26.   Loonen, M. J. J. E. et al. 1999. The benefit of large broods in barnacle geese: A

426   study using natural and experimental manipulations. - Journal of Animal Ecology 68:

427   753–768.

428   27.   Madsen, J. 2001. Spring migration strategies in Pink-footed Geese *Anser*

429   *brachyrhynchus* and consequences for spring fattering and fecundity. - Ardea 89: 43–55.

430   28.   Madsen, J. 2010. Age bias in the bag of pink-footed geese *anser brachyrhynchus*:

431   Influence of flocking behaviour on vulnerability. - European Journal of Wildlife Research

432   56: 577–582.

433   29.   Madsen, J. et al. 1999. Goose populations of the Western Palearctic. - National

434   Environmental Research Institute, Denmark; Wetlands International, Wageningen, The

435   Netherlands.

436   30.   Nolet, B. A. et al. 2013. Faltering lemming cycles reduce productivity and

437   population size of a migratory Arctic goose species. - Journal of Animal Ecology 82: 804–

438   813.

439   31.   Owen, M. and Black, J. M. 1989. Factors affecting the survival of barnacle geese

440   on migration from the breeding grounds. - Journal of Animal Ecology 58: 603–617.

441   32.   Philippona, J. 1966. Geese in cold winter weather. - Wildfowl 17: 3.

442   33.   Poisbleau, M. et al. 2008. Dominance relationships in dark-bellied brent geese

443   *Branta bernicla bernicla* at spring staging areas. - Ardea 96: 135–139.

444   34.   Prevett, J. P. and MacInnes, C. D. 1980. Family and Other Social Groups in Snow

445   Geese. - Wildlife Monographs: 3–46.

446   35.   R Core Team 2017. R: A language and environment for statistical computing. - R

447   Foundation for Statistical Computing.

448   36.   Roberts, G. 1996. Why individual vigilance declines as group size increases. -

449   Animal behaviour 51: 1077–1086.

450   37.   Schamber, J. L. et al. 2007. Latitudinal variation in population structure of

451   wintering Pacific Black Brant. - Journal of Field Ornithology 78: 74–82.

452   38.   Scheiber, I. B. et al. 2013. The Social Life of Greylag Geese. - Cambridge University

453   Press.

454   39.   Stroud, D. A. et al. 2017. Key actions towards the sustainable management of

455   european geese. - Ambio 46: 328–338.

456   40.   Summers, R. and Underhill, L. 1987. Factors related to breeding production of

457   Brent geese *Branta b. bernicla* and waders (*Charadrii*) on the Taimyr Peninsula. - Bird

458   Study 34: 161–171.

459   41.   Van Turnhout, C. et al. 2009. Veranderingen in timing van zichtbare najaarstrek

460   over Nederland: Een pleidooi voor hernieuwde standaardisatie van trektellingen. -

461   Limosa 82: 68.

462   42.   Vangilder, L. D. and Smith, L. M. 1985. Differential distribution of wintering brant

463   by necklace type. - The Auk 102: 645–647.

464   43.   Warren, S. M. et al. 1993. Extended parent-offspring relationships in Greenland

465   White-fronted geese (*Anser albifrons flavirostris*). - The Auk 110: 145–148.

466   44.   Wood, S. N. 2013. Generalized additive models: An introduction with R. -

467   Chapman; Hall/CRC.

468   Supplementary material. Appendix 1.
469
470

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.
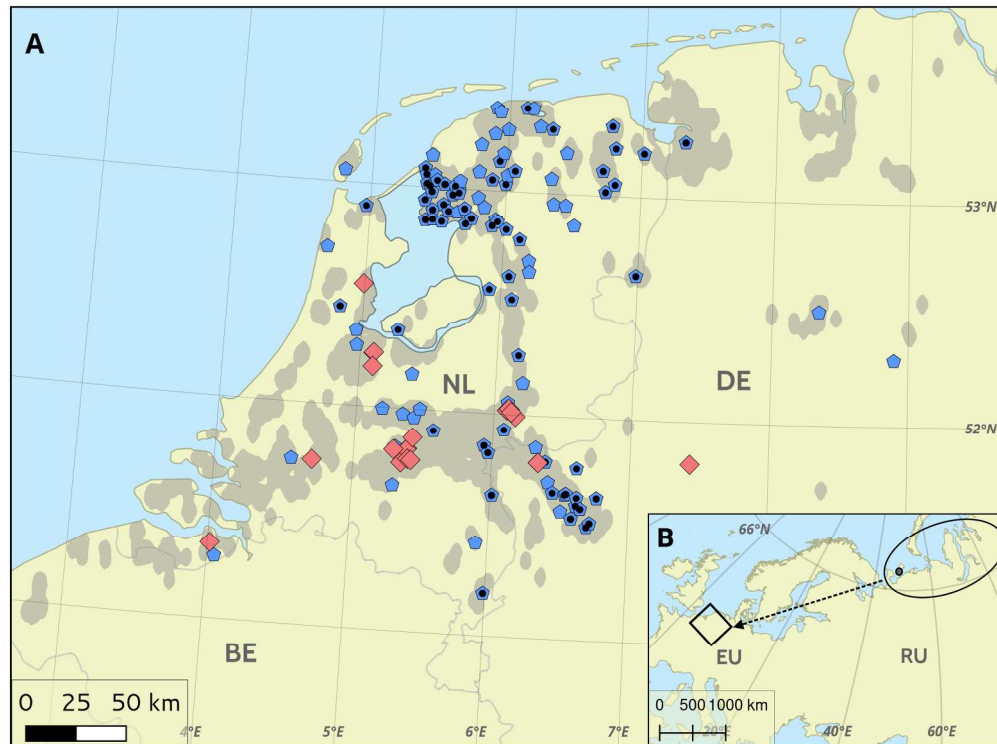
Fig. 1: A. Wintering grounds of greater white-fronted geese Anser a. albifrons in the Netherlands and northern Germany. 123 sites (blue pentagons) where the age-ratio of 7,149 flocks was determined, a subset of 65 sites (black dots) where 51,037 successful families were recorded in 1,884 flocks. Shaded area bounds 10,635 observations of neck-banded geese. 21 split events (red diamonds) were observed in 13 GPS tracked families. Observations correspond well with major rivers and waterbodies, marked in blue. Data were collected from 2000 - 2017.
B. Breeding grounds (ellipse) in Russia with Kolguyev Island (dot) and general flyway (arrow) to wintering area (rectangle).
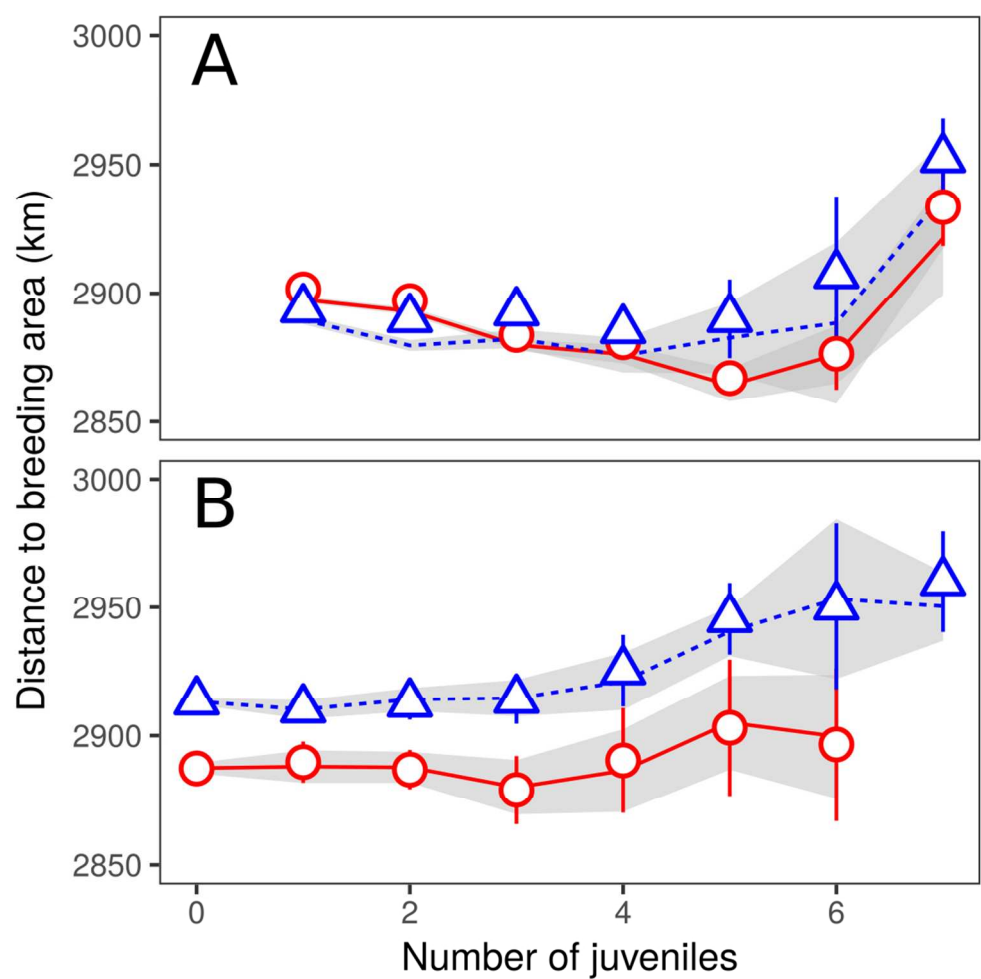
Fig. 2: LMM fits (lines), and mean distance of wintering sites from Kolguyev Island (symbols) per number of juveniles in a family, for family size counts (A) and ring-resightings (B).
Data and fit for records from < 60 days after arrival to the wintering grounds (red circles and solid lines), and data and fit for records > 60 days after arrival (blue triangles and dashed lines), and 95% confidence intervals for the data(vertical lines) and fits (shaded grey area are shown).
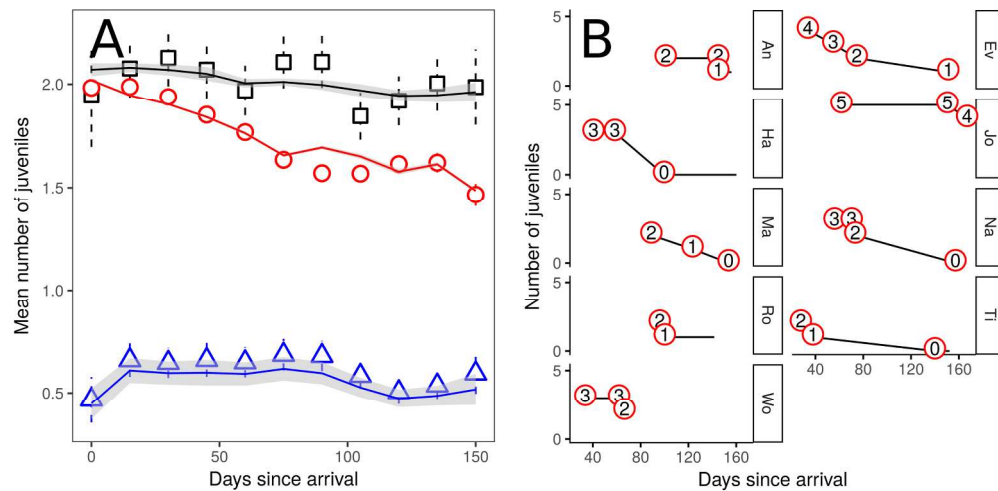
Fig. 3. A: GLMM fits (lines) and mean number of juveniles per family every 15 days since goose autumn arrival (shapes) for each dataset. Successful families in flocks (red circles and line), neckband-resightings including unsuccessful pairs (blue triangles and line), and neckband-resightings with only successful pairs (black squares and line).
B: Number of juveniles in each family (name in box) which split, at the start of the tracking period, and following each subsequent juvenile split (numbers in circles).
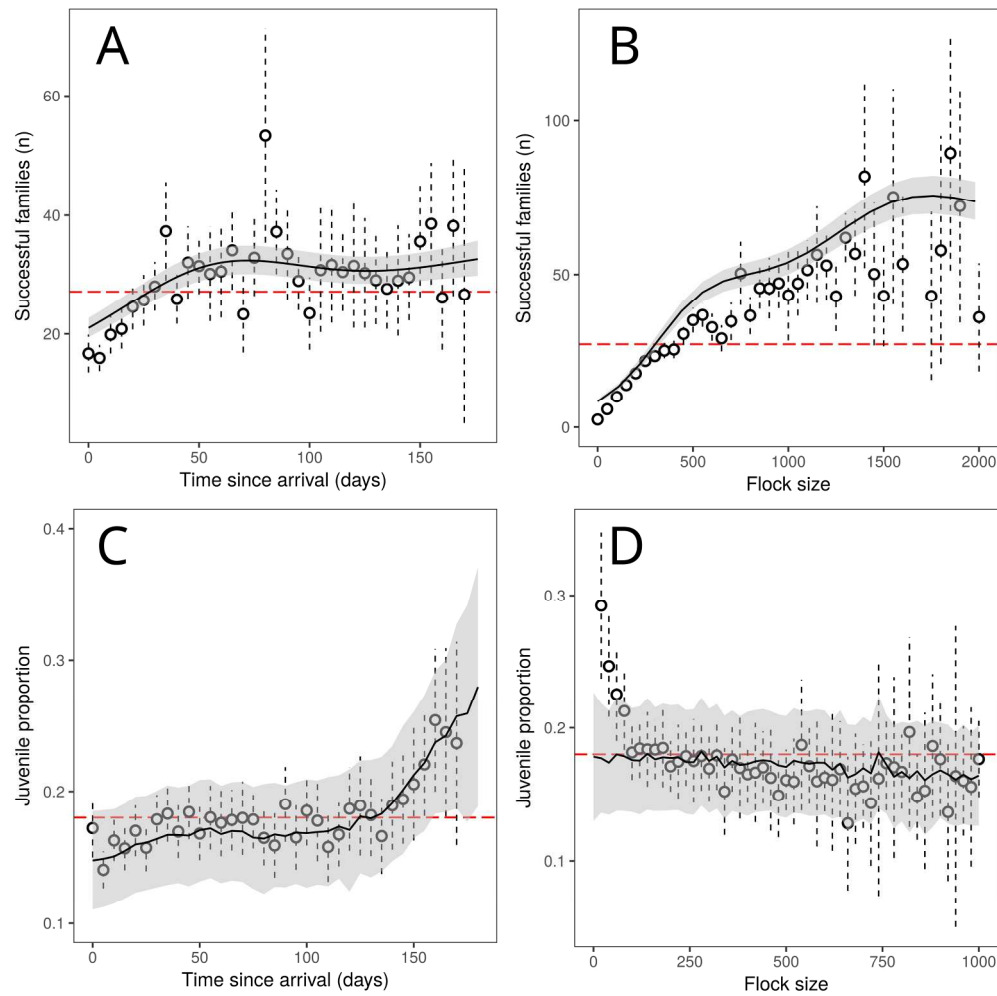
Fig. 4: GAMM fits (solid black lines), data (circles), 95% confidence intervals for data (vertical dashed lines) and fits (shaded grey areas), and overall observed mean response value (horizontal dashed red line) for:
A. Mean number of successful families in flocks every 5 days after autumn arrival;
B. Mean number of families in flocks, in increments of 50 individuals;
C. Mean proportion of first-winter juveniles in flocks every 5 days;
D. Mean juvenile proportion of flocks, in increments of 20 individuals.
Means and proportions were pooled across all years. Note that in C days since arrival was modelled as a smoothed covariate using thin plate splines, and 4 knots. C and D show conditional fits.
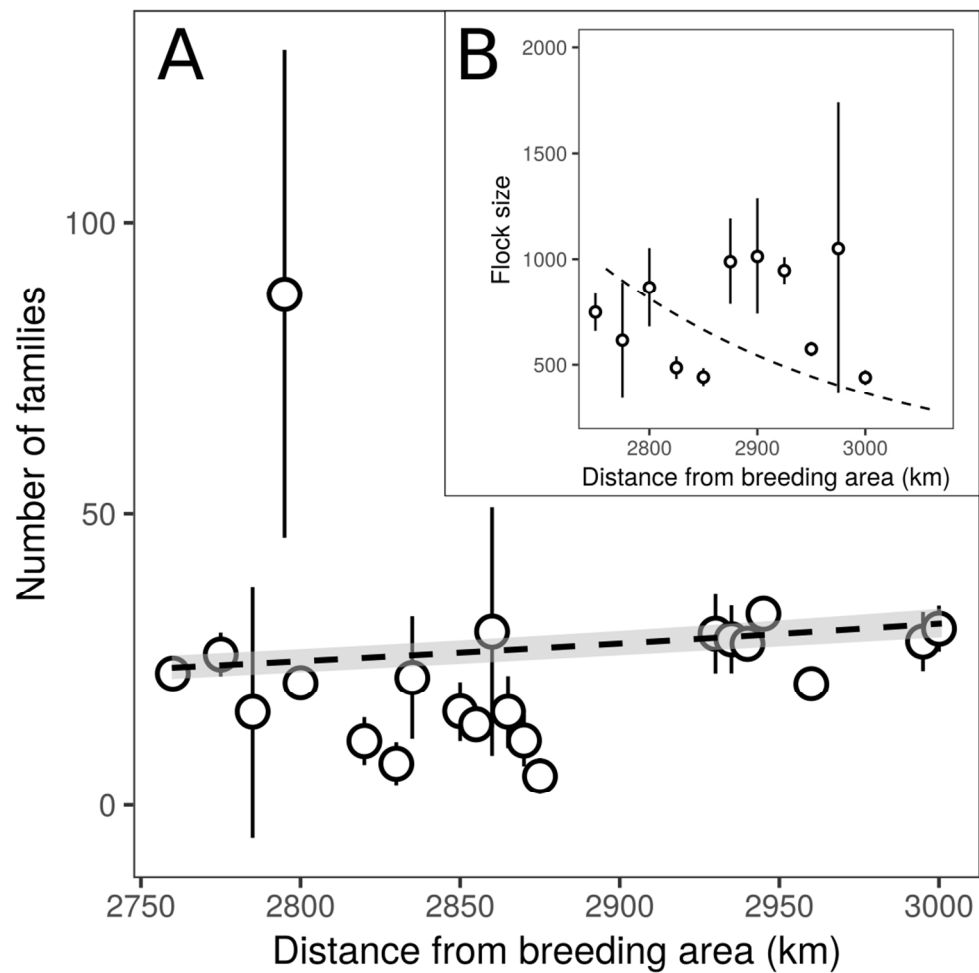
Fig. 5. GAMM fit (dashed line), data (circles), and 95% confidence intervals for data (vertical lines) and fits (shaded grey area) for:
A: Mean number of families in flocks at distances from Kolguyev Island, in increments of 5km;
B: Mean flock size at distances from Kolguyev Island, in increments of 25km.
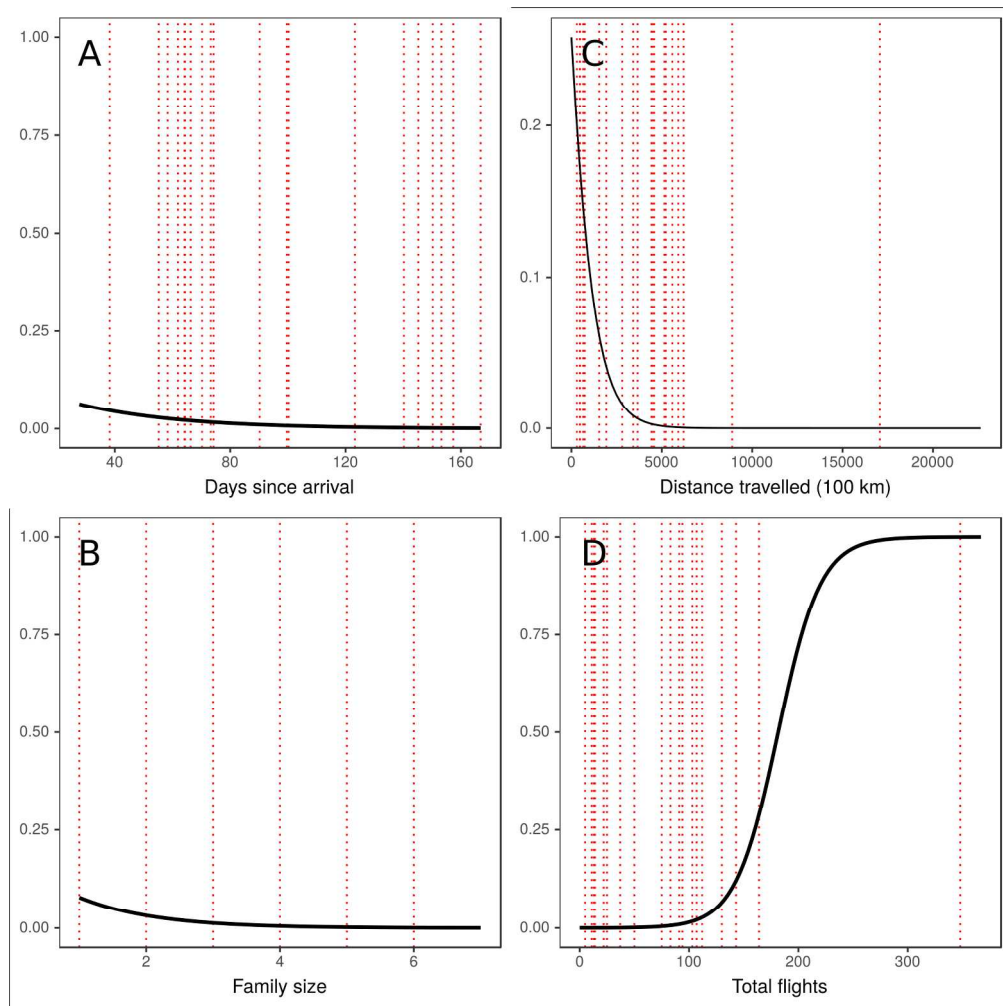Sites to the north-east of the study site are approximately 500 km nearer to Kolguyev than sites in the south-west.

Fig. 6. GAMM conditional fits of split probability (solid black lines), and split occurrences (vertical red dotted lines) in relation to:
A. Days since arrival;
B. Cumulative number of flights over winter;
C. Family size;
D. Cumulative number of displacements of more than 1km.

1 **Supplementary Material**

2 ## Appendix 1

3 Here we provide representations of the distribution of filtered observation data over yearly and

4 monthly scales (Figs. A1.1 & A1.2). Arctic geese are expected to begin arriving at the eastern end of

5 the study site by late September, and are present on Dutch and northern German sites by early - mid

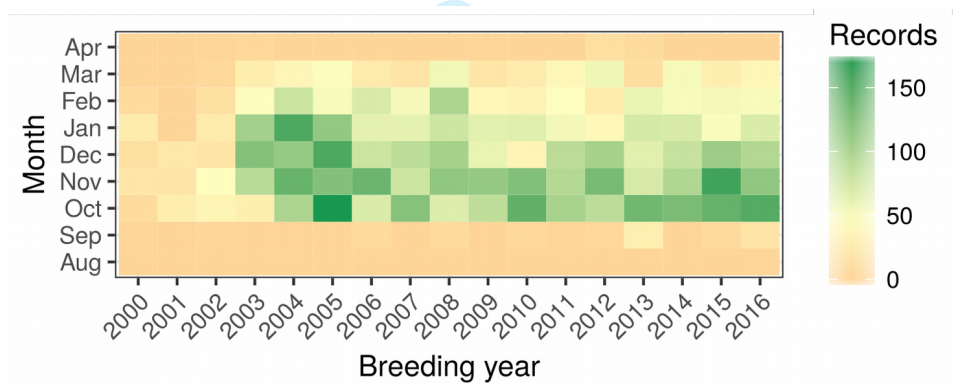6 October. The heatmaps shown reflect this pattern.

7

Fig. A1.1. Heatmap of number of flock counts per month in each calendar year.
Data are sparse from the early 2000s. Data density is higher in the first three
winter months (Oct, Nov,Dec) than the following ones (Jan, Feb, Mar). A mean of
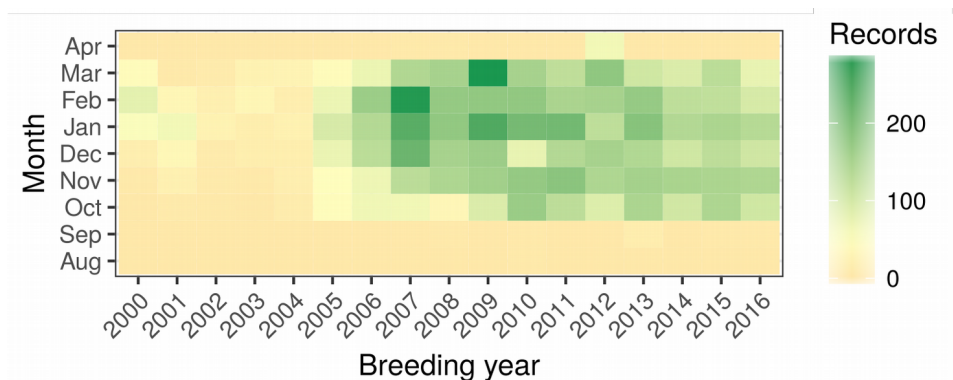47 flocks are censused per month (range: 0 - 177).

8

Fig.A

Fig. A1.2: Heatmap of number of observations of geese marked with numbered
neckbands per month in each calendar year. Data are sparse until the mid 2000s.
Marked geese are sighted in the study area earlier and later than censused flocks.
On average, 49 marked geese are seen each month (range: 0 - 294).

Model	Type	Dataset	Response	Fixed effects	Random effects	Records used
1	LMM	Family size counts	Distance to breeding area	1, 5	8, 9, 10	20,160[a]; 14,018[b]
1	LMM	Ring-sighting data	Distance to breeding area	1, 5	8, 11	3,289[a]; 7,320[b]
2.a	GLMM	Family size counts	Number of juveniles	3, 5, 7	8, 9, 10	34,179
2.a	GLMM	Ring-sighting data	Number of juveniles	5, 7	8, 11	10,426
2.b	GAMM	Age-ratio counts	Number of families	3, 5, 7	8, 9, 10	837
2.c	GLM	Family sizes on Kolguyev	Number of juveniles	Dataset		2,615
3	GAMM	Age-ratio counts	Flock size	5, 6, 7	8, 9, 10	5,700
4	GAMM	Age-ratio counts	Juvenile proportion	5, 6, 7	8, 9, 10	5,659
5	GLMM	GPS tracking of families	Split occurrence	13 - 19	20	1,009

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, 12: Split occurrence , 13: Family size, 14: Days since autumn arrival, 15: Daily number of flights, 16: Cumulative number of previous flights, 17: Daily distance travelled, 18: Cumulative distance previously travelled, 19: Time since last take-off, 20: Family identity

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

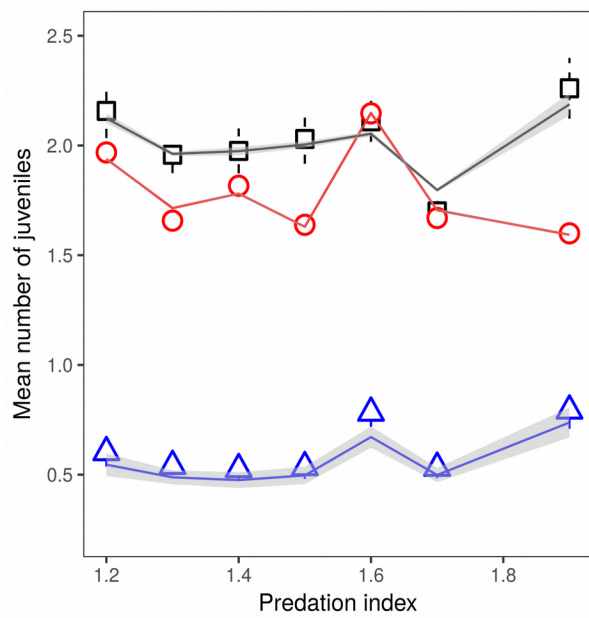Table A1: Statistical model responses, predictors, and data used.

9

Fig. A2. GLMM fits (lines), mean number of juveniles per family at levels of pooled summer predation index, in increments of 0.1 (symbols), and 95% confidence intervals for data (vertical solid lines), and fits (shaded grey area), using family size counts (red circles and line), ring-resighting data including unsuccessful families (blue triangles and line), and ring-reisighting data without unsuccessful families (black squares and line).