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For huntable waterbird species, the autumn migration strategy may be important for their fitness, as their behaviour and environmental factors may influence their exposure to hunting mortality. Hunting activity may also reduce the access to food resources which may be limited in the wintering areas, thereby affecting winter survival. In this study we assessed the possible influence of food resources, weather conditions, inter-specific competition and hunting intensity (as a measure of possible disturbance) on abundance and distribution of pink-footed geese *Anser brachyrhynchus* at their main autumn stopover site in Norway. The results show that food resources in term of spilt cereal grain were abundant, even by the time the geese had moved on. Snow cover did not limit the food availability during the main migratory period. Inter-specific competition with greylag geese *Anser anser* reduced food supplies locally and appeared to be increasing. Goose hunting intensity varied among sites and our data indicate a negative relationship between hunting intensity and the rate at which geese consumed the food resources. Collectively, our results suggest that the majority of pink-footed geese leave the stopover area earlier than they would otherwise, when hunting intensities are high. In the case of pink-footed geese, population consequences of disturbance is not a concern at present; however, an international species management plan calls for 1) keeping disturbance low in areas where geese do not cause conflicts with agriculture to prevent them being pushed to areas with problems, and 2) increased harvest to reduce and stabilise the population size. Both objectives can be met by reducing hunting disturbance in mid-Norway and it is recommended that a better local organisation of hunting is implemented.

The migratory phases of the annual cycle of birds may be hazardous, both because of adverse weather encountered during migration with consequent mass mortality, and because limited resources on stopover sites may have repercussions on the ability of birds to refuel and to make it to the next target area on the migration route (Newton 2006). While there are several studies on spring migration ecology and how the behaviour of birds and environmental conditions may influence fitness in terms of subsequent breeding success (Drent et al. 2003, Morrison et al. 2007, Inger et al. 2008, Trinder et al. 2009), relatively little attention has been paid to autumn migration.

For Arctic breeding migratory birds, an optimal timing of departure from the breeding grounds is critical to ensure survival back to temperate regions (Owen and Black 1999). Once they reach their staging and wintering areas, however, their movements may be more flexible in timing and extent, depending on local food availability, predation risk and weather conditions (Madsen 1988). Staging for an extended period in an autumn stopover site with high food abundance may be advantageous, as conditions further south are

unpredictable and with a risk of being less profitable in terms of food availability (Newton 2004). Extra reserves gained at one site will therefore be an insurance against food shortages and/or bad weather later in the season and, hence, increase the survival probability (Newton 2008). For species which are hunted, the autumn migration may be extraordinarily stressful because their behaviour and the environmental factors which they encounter en route may influence their exposure to hunting, and hence affect their survival (Menu et al. 2005). Furthermore, in cases where there is evidence of limited resources on the wintering grounds, disturbance caused by hunting (together with other sources of disturbance) on stopover sites may push birds down the migration corridor, to encounter density-dependent depletion of food supplies and starvation on the wintering grounds (Madsen and Fox 1997). Hunting may also cause disruption of pair bonds and hence potentially affect fitness (Nicolai et al. 2012).

A number of factors control the availability of food along the migration route. For geese breeding in the Arctic and migrating over northern Europe, split grain on stubble fields, root crops and intensively managed grasslands are important food resources (Gill et al. 1996, Fox et al. 2005). As long as the crops are harvested and thereby provide spilt grain or root crop remains as food, and the foraging habitats are

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not covered by snow, the food accessibility may be good for staging and overwintering geese. Spilt grain and root crop remains are finite resources, however, and along with the timing of harvest (determining when food becomes available), intra- and interspecific competition may affect resource availability (Kotrschal et al. 1993, Madsen 2001). Moreover, as geese are a popular target for recreational hunting in many countries, the hunting activity, or other disturbances caused by humans, may influence their habitat preferences, forcing them to leave an area even though the weather conditions may be favourable and food resources still plentiful (Bell and Owen 1990, Madsen and Fox 1995). For example, it has been shown that in areas with hunting, geese will relocate their distribution and not return to the hunting area within the same day. With frequent hunting, resources, which otherwise would have been available under undisturbed conditions, were therefore under-exploited (Madsen 2001). An increased predator risk/disturbance may also lead to reduced foraging time (Ely 1992), or more time spent on less preferred feeding habitats (Béchet et al. 2004, Tombre et al. 2005).

In the present study, we evaluate environmental factors affecting the number of pink-footed geese Anser brachyrhynchus utilising an autumn stopover site, Nord-Trøndelag county in mid-Norway. The population stops in Norway on their way back from their breeding areas in Svalbard to wintering grounds in Denmark, the Netherlands and Belgium. There is an open season for pink-footed goose in Norway, and 80% of the pink-footed geese shot are harvested in Nord-Trøndelag (Statistics Norway, <www.ssb.no>). We hypothesise that disturbance, in terms of hunting, will have a negative effect on goose numbers and influence their distribution in the area. Hunting on pink-footed geese has increased in mid-Norway over the last decade (Tombre et al. 2009, 2011) but hunting that is too intense may push the geese further south on their migration route. We further hypothesise that weather parameters, like snow, rain and temperature, will have indirect effects via the agricultural practice and food accessibility. Snow cover will be a negative factor, as the accessibility of food will be greatly reduced with a snow layer on top. Whether, heavy rainfall and/or low temperatures in August and September may delay the timing of harvest, resulting in fewer harvested fields with accessible grain for the geese when they arrive. Although an early harvest is positive for the geese, a subsequent early ploughing will be negative, as this will reduce the number of available stubble fields. Another goose species, the greylag goose Anser anser (the northwest European population), also utilises this staging site, with numbers peaking in early and mid-September corresponding to the time of arrival of the pink-footed geese. Hence, due to this spatial, and partly temporal, overlap with the pink-footed geese, they may affect the pink-footed geese negatively either directly or indirectly via resource competition. The northwest European greylag goose population has increased dramatically during recent decades (Fox et al. 2010), which may increase the local competition for food resources.

By quantifying and collecting data on hunting activity, weather parameters, agricultural practice, food abundance and occurrence of greylag geese as a measure of competition, we evaluate factors influencing the numbers and

distribution of pink-footed geese utilising the stopover site in mid-Norway. Data presented in this study stem from three years of study and from three different study areas with varying data availability, such as detailed information about hunting positions. Due to the patchiness of the data we were not able to conduct a detailed multifactorial statistical analysis, but had to resort to a descriptive site-based assessment of the importance of each of the variables in question.

Material and methods

Study population and study area

The population of pink-footed geese breeds on the high-Arctic archipelago of Svalbard and winters in Denmark, the Netherlands and Belgium. Over the last decades, it has expanded its use of farmland areas along the flyway due to improved feeding conditions (Therkildsen and Madsen 2000, Fox et al. 2005). Due to a combination of increased protection from hunting in the 1970s, warmer winters, better winter food supplies as well as improved breeding conditions due to a warmer climate, adult survival and breeding success have increased (Ebbinge et al. 1991, Kery et al. 2006, Jensen et al. 2014). This has led to a population increase from ca 20 000 birds in the 1970s to more than 80 000 in 2010-12 (Madsen and Williams 2012). Because of the increase in goose numbers and their concentration on farmland, especially in spring, there has been an increase in conflicts with agricultural interest (Tombre et al. 2013, Madsen et al. 2014). Moreover, on the breeding grounds, increasing grazing pressure by the geese has been suggested to cause a degradation of tundra vegetation at several locations (Speed et al. 2009, Pedersen et al. 2013a, b). Collectively, the continued population growth and management concerns led to the development of an international species management plan for the population, under the African-Eurasian Waterbird Agreement (AEWA). As a first European test case, a population target has been set to 60 000 individuals, which is to be achieved by an optimisation of hunting regulations and practices in Norway and Denmark (Madsen and Williams 2012).

The pink-footed geese depart Svalbard in mid-September. During migration, they stop primarily along the Trondheimsfjorden, Nord-Trøndelag County in mid-Norway and along the west coast of Jutland in Denmark (Madsen et al. 1999). Smaller flocks have also been reported in northern and southern parts of Norway, as well as in southern Sweden (Madsen and Williams 2012, Nilsson 2013).

The present study was carried out during 2011–2013 at three study areas along the Trondheimsfjorden in Nord-Trøndelag, Norway; Skogn, Nesset and Egge (Fig. 1). These areas are mixed farmlands with growth of spring cereals, pastures and potatoes, and represent three different areas in terms of hunting regimes. By the time of arrival of the pink-footed geese in September, the majority of the cereal fields are harvested. Pink-footed geese and greylag geese use all three sites in the autumn, and they are both quarry species in Norway as well as in Denmark. In Norway there is an open hunting season from 10 August to 23 December and in Denmark from 1 September to 31 December (on land).

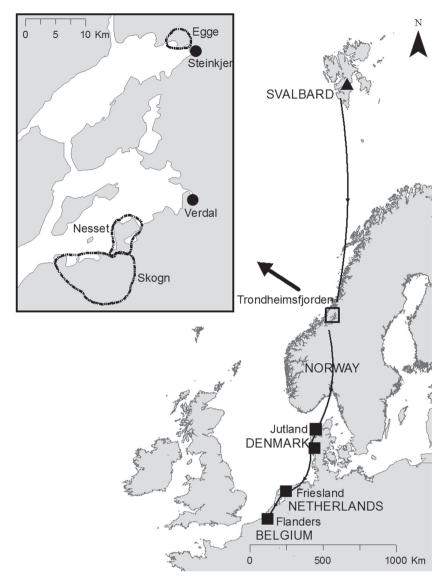


Figure 1. The Svalbard pink-footed goose flyway, major autumn/winter staging areas (squares) and breeding area (triangle). The insert map shows the region containing the three study areas in mid-Norway, Skogn, Nesset and Egge (open square) and the two weather stations (black dots), Verdal and Steinkjer.

Pink-footed geese are protected in the Netherlands and Belgium.

Goose numbers and distribution

To assess abundance and distribution of geese in the three study areas and their among site and year variation, flocks of pink-footed geese and greylag geese were counted, and their positions in the fields were mapped. For all years, field observations were conducted on a daily and systematic basis between 8.00 and 18.00 hours. The goose counts at Skogn and Nesset started from the first arriving pink-footed goose and until most of them had departed the areas. The observation period ranged from 17 September to 3 November in 2011, from 18 September to 24 October in 2012 and from 16 September to 24 October in 2013. For Egge, counts were conducted in one year only, in 2012 from 14 September to 4 October, the main period when geese were observed in the area. In addition, individually

neck-banded pink-footed geese and their habitat use were recorded by scanning through the goose flocks when they were found. This was conducted in all years at Skogn and Nesset.

Neckbands were registered to assess the individual length of stay, estimated by the number of days between the first and last individual neckband observation. Differences between the areas (Skogn and Nesset) and between years were assessed with non-parametric tests (Mann–Whitney or Kruskal–Wallis) followed by Dunn's post hoc test when a significant result was found. Habitat use of observed flocks of geese was registered to assess changes among areas and time of season.

The season length was divided in three roughly equally long periods; S1) 16–30 September, S2) 1–15 October and S3) 16 October to 3 November. Within each period, the habitat use was estimated by the number of geese using a given habitat, divided by the total number of geese in the given period. Goose numbers were defined as the maximum number of geese counted per day.

Environmental factors influencing goose numbers

Hunting activity

The Skogn site is a mixed farmland area covering approximately 35 km², where more than 16 km² are used for hunting. Hunting is carried out on private properties, and the landowners can decide for themselves how to arrange the hunting activities as long as it follows the general regulations set by the national environmental authority (Tombre et al. 2009). In 2011 and 2012, hunting was open to individual agreements between landowners and hunters, whereas in 2013 the hunting was organised and restricted to six hunting groups, each controlling part of the area. In 2013, hunting was also restricted to a maximum of two hunting days per week and unit.

The Nesset site is a mixed farmland area covering approximately 10 km². Until 2011 the hunting was administrated through the local landowner association, but there were no restrictions on the hunting intensity and no organisation of shooting existed between groups of hunters except for an agreement about one shooting-free day per week. During the study period, the hunting was administrated by a research project (Jensen et al. 2012) and the intensity was kept low for experimental purposes and hunting always finished before noon. Hence, compared to Skogn in 2011 and 2012, the hunting intensity at Nesset was generally low.

The Egge site is a mixed farmland area, covering approximately 3 km². Since 2008, a local landowner association has administrated the goose hunting (http://home.online.no/~o-jerpst/gas.html), but with no organisation of shooting between groups of hunters. In 2013, only morning hunt was allowed.

For each site, information on the number of harvested pink-footed geese and the number of hunting trips was collected. For 2011 and 2012, we do not have data on the number of hunting trips performed by landowners in the Skogn area, only their hunting bag. If we assume that landowners had the same shooting efficiency as hunters renting the hunt, we can estimate the number of hunting trips by landowners from their bag and the ratio between numbers of geese shot per hunting trip for external hunters. In 2013 the data was collected either through a private social media group, which also included information from the landowners who had hunted, or directly from the hunters. For Nesset, the hunting data was directly collected from the hunters in the research project, and for Egge the information from all the hunters was available from the local hunting administrator.

We expressed hunting intensity per site and year as an index, using the ratio between the number of hunting trips per season and the area of stubble field and root crops available at the start of the season (around 20 September).

Weather

Data on weather parameters was derived from the nearest weather stations of the Norwegian Meteorological Institute, in the municipalities of Verdal and Steinkjer (snow depth only available from Verdal, <www.eklima.met.no>) (Fig. 1). To make a qualitative assessment of the effect of snow cover on food availability, weather conditions from 1 August to 31 December, 2011–2013, in terms of daily mean snow

depth, were used. To assess the timing of harvest, the mean temperature and the cumulative precipitation were used, as especially cold, but also very wet months, will result in a slow maturation of the grain and thereby forcing farmers to postpone harvest. Additionally, the number of periods with two or more days in a row with less than 1 mm precipitation per day, was counted, as the farmers also rely on dry periods to harvest. The monthly mean temperature, monthly cumulative precipitation and periods with less than 1 mm precipitation per day were extracted from 1 July to 31 October, 2011–2013.

Weather data from the two stations was strongly correlated (precipitation: $r_{1010} = 0.76$, p < 0.01; mean temperature: $r_{1010} = 0.99$, p < 0.01). We therefore used averages between the two weather stations in the analyses.

Agricultural practice and food availability

To assess variation in food availability among areas and years, field types and status, whether they were harvested or ploughed, were visually registered on a map in the field and plotted in ArcGIS. All agricultural fields at the three sites were registered. At Skogn and Nesset, registrations were made every second week in 2011 (11 and 23 September, 9 and 23 October, 3 November) and on a daily basis in 2012 and 2013 (18 September to 24 October, and 16 September to 24 October, respectively). At Egge in 2012, registrations were made before the main arrival of pink-footed geese, and after the departure of the majority of pink-footed geese. To assess the food availability in the three season periods (S1–S3), the food resource data was extracted from the mid-point of the three season periods (S1–S3).

The availability of food resources, and the depletion due to goose feeding, was assessed by spilt grain counts on randomly selected stubble fields. The counts were conducted before the main arrival of pink-footed geese and/or when the cereal fields were harvested (14 September to 2 October). A second count was made after the departure of the majority of pink-footed geese and/or before the field was ploughed (8 October to 4 November). For each field, grain density was recorded in three randomly selected plots of 0.16 m² (Madsen 2001). Based on the densities of spilt grain in the selected fields, the total amount of spilt grain available before the pink-footed geese arrived (early grain counts) was estimated for each area, as well as the remaining amount when the geese had departed (late grain counts). To assess differences among areas, periods and years respectively ANOVA and t-test were used.

Competition

Resource competition between pink-footed geese and greylag geese was assessed by counting the number of droppings from greylag geese in a 2-m radius around the grain count plots before the pink-footed geese arrived (the first grain count). In the grain count analyses, it was therefore considered whether there had been any greylag geese at sites where pink-footed geese were observed later. Counts of greylag geese were only conducted in the same period as the pink-footed geese. Pink-footed geese and greylag geese were the only goose species observed in the study area, although a few single individuals of Canada geese *Branta canadensis* may be seen in some years (Jensen et al. unpubl.).

Food consumption

The consumption of spilt grain in stubble fields by geese was estimated for each of the three study areas on the basis of 1) the recorded total amount of grain available in the start of the season, expressed by the area of stubble multiplied by the average density of grain in the start of the season, 2) total number of goose-days spent by pink-footed geese and greylag geese, respectively, and 3) their daily grain intake rates. We collected data to calculate the total amount of grain for Nesset and Skogn 2011–2013 and Egge 2012. For Skogn in 2013, we lacked data on grain densities but knew the area of stubble; we have assumed that grain densities were similar to those recorded on Nesset (which was the case in 2011 and 2012).

To estimate food consumption rates (in terms of cereal grains per day) and hence the possible degree of exploitation competition of the two goose species, we derived intake rates under various assumptions. Estimates of grain intake rates exist for pink-footed geese foraging on newly sown barley fields where grain was partly visible on the surface, viz. 4625 barley grains per day (Madsen 1985); that study was carried out in early spring when geese start accumulating body reserves. We assume the results are comparable to the autumn situation where geese also accumulate body reserves (based on weight measurements of locally shot geese which were also sexed and aged; Gundersen 2013). For greylag geese, no field data on grain intake rates were available. To estimate their food intake, we scaled the consumption by pink-footed geese to greylag geese by the difference in basal metabolic rate (BMR), using the equation for BMR in Lasiewski and Dawson (1967). To calculate BMR, we used body mass of pink-footed geese shot in mid-Norway (Gundersen 2013) and we took an average mass of adult males, adult females and juveniles, assuming a juvenile ratio of 33% in the field, which is realistic for the stopover site in mid-Norway (J. Madsen unpubl. data). This gives an average mass of 2325 g. The mass of greylag geese (adults as well as juveniles) were derived from measurements of Scottish birds shot in autumn (Matthews and Campbell 1969). Assuming a juvenile ratio of 33% in the field, this gave an average body mass of 3098 g. Scaled to BMR, greylag geese have a 23% higher daily consumption than pink-footed geese, equivalent to a total of 5684 grains per day.

The relationship between goose consumption rate and hunting intensity was investigated using a locally weighted polynomial regression (Cleveland 1979).

Results

Goose abundance

The abundance of pink-footed geese, expressed by numbers of goose-days in each period, varied between areas, years and period (Fig. 2). The total number of goose-days spent by pink-footed geese ranged from 30 286 (in 2013) to 116 071 (in 2012) at Nesset, and from 26 655 (in 2012) to 54 643 (in 2011) at Skogn. At Nesset the highest number of pink-footed geese was registered in S2 for all years. At Skogn the highest number of pink-footed geese was registered in S3 in 2011, S1 in 2012 and S2 in 2013 (Fig. 2). At Egge in 2012, the total number of goose-days spent by pink-footed geese was registered in S1 The highest numbers counted at any one

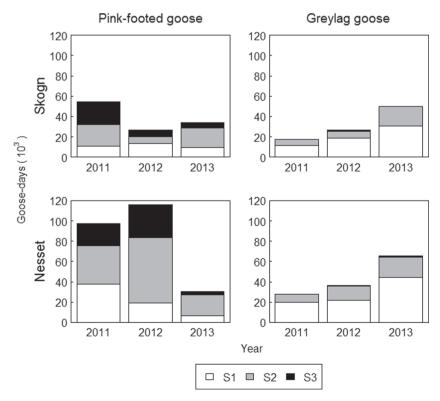


Figure 2. The cumulative number of pink-footed geese (10³) and greylag geese (10³) in two study areas in mid-Norway, Skogn and Nesset, during the three season periods S1) 16–30 September, S2) 1–15 October, S3) 16 October to 3 November, in 2011–2013.

Table 1. Length of stay (number of days) based on observations of individually neck-banded pink-footed geese (n total) at two study sites in mid-Norway, Skogn and Nesset, during the autumn migration in 2011–2013

| | 2011 | 2012 | 2013 |
|-------------------|---------------|----------------|---------------|
| Skogn | | | |
| Min | 1 | 1 | 1 |
| Max | 17 | 28 | 23 |
| Mean ± SE | 4.1 ± 0.7 | 5.7 ± 0.8 | 5.9 ± 2.9 |
| % staying one day | 44.7 | 40.0 | 66.7 |
| n total | 38 | 85 | 9 |
| Nesset | | | |
| Min | 1 | 1 | 1 |
| Max | 29 | 41 | 9 |
| Mean ± SE | 3.8 ± 1.0 | 13.2 ± 1.3 | 3.3 ± 0.8 |
| % staying one day | 78.7 | 30.7 | 62.5 |
| n total | 47 | 75 | 16 |

day at Nesset were 6904 pink-footed geese on 24 September 2011, at Skogn 3670 pink-footed geese on 16 October 2011 and at Egge 672 pink-footed geese on 19 September 2012. For greylag geese, numbers increased over the three study years, both in Skogn and at Nesset and, in terms of goosedays, greylag geese outnumbered pink-footed geese in 2013 in both areas (Fig. 2).

The length of stay for individual neck-banded pink-footed geese varied significantly between Nesset and Skogn in 2011 and 2012 (2011: U=639.5, p<0.05, r=0.25; 2012: U=4305.5, p<0.05, r=0.63; 2013: U=70.5, p>0.05, r=0.30) and between years for Nesset (H=31.7, DF=2, p<0.01). Further, the Dunn's post hoc test showed significant variation between 2011 and 2012, and 2013 and 2012 (p<0.01) (Table 1). At Nesset the mean length of stay varied from 3.3 days (SE=0.8) in 2013 to 13.2 days (SE=1.3) in 2012. The maximum length of stay was observed in 2012, with 41 days at Nesset and 28 days at Skogn. A high proportion of geese were only observed once, ranging from 31% at Nesset in 2012 to 79% at Nesset in 2011.

The habitat use by pink-footed geese (average for 2011–2013) varied between areas and periods within the season. The main habitat used for foraging was stubble fields (86.8% at Skogn and 74.8% at Nesset), followed by root crops, which mainly consisted of potato and carrot fields (9.5% at Skogn and 20.3% at Nesset). For root crops, the mid-season was most used by the geese (Fig. 3).

Hunting activity

The total hunting bag per year in the three areas ranged from 11 pink-footed geese shot at Egge in 2012 to 284 pinkfooted geese shot at Skogn in 2011 (Table 2). The exceptionally high harvest in Egge in 2011 was due to a skilled team of goose hunters shooting nearly 200 pink-footed geese in few days. The number of hunting trips ranged from 15 trips at Nesset in 2012 and 2013 to 97 trips at Skogn in 2011 (Table 2). The hunting intensity index, expressed by the number of hunting trips per unit area, was highest in Egge, intermediate in Skogn in 2010, 2011 and lowest at Nesset 2010–2013 and Skogn 2013 (Table 2). In the Skogn area in 2010 and 2011 as well as in Egge in 2012, hunters were active almost every day during the period when geese were observed. At Nesset in 2011, hunting alternated between one and two consecutive days followed by one to eight hunting-free days. In 2012, hunting was never conducted on two consecutive days, but carried out on every second day, alternating between two zones giving a hunting free period of three days per zone. In 2013, hunting was conducted every second day in the northern half of Nesset, whereas it was less intense in the southern half (hunting only every five to six day).

Weather conditions

The first record of snow for each year was 28 November 2011 (2 cm), 26 October 2012 (25 cm) and 20 November 2013 (5 cm). The late first snowfall in 2011 and 2013 had no effect on the goose abundance as most geese had already departed by that date. In 2012, the snow cover in late October may explain the rapid decrease in goose numbers at Nesset and Skogn, declining from 2800 geese on 24 October to 705 geese on 26 October.

The temperature and precipitation data offers rather conflicting results in terms of the maturity of the grain, as the year (2011) with highest mean temperature (12.4°C) is also the year with highest precipitation (243.6 mm). Additionally, the year (2012) with lowest mean temperature (10.2°C) is also the year with lowest precipitation (164.6 mm). Nevertheless, as most of the periods with less than 1 mm precipitation per day in 2012 falls in August, presumably before the grain is mature and as July was especially wet in 2012 (253.7 mm), the farmers have not been able to take

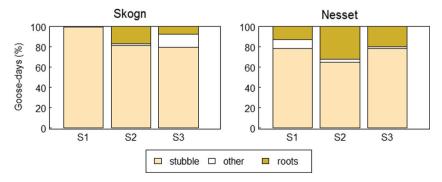


Figure 3. The feeding habitat distribution of pink-footed geese in two study areas in mid-Norway, Skogn and Nesset, from September–November, average for 2011–2013, during three periods in the season S1) 16–30 September, S2) 1–15 October, S3) 16 October to 3 November, expressed as the proportion of goose numbers in each habitat type.

Table 2. Hunting data from three study sites in mid-Norway, Skogn, Nesset and Egge, during 2011–2013, in terms of number of pink-footed geese shot, the number of hunting trips and hunting intensity index calculated as the number of hunting trips divided by the area with stubble and root crops.

| | 2011 | 2012 | 2013 |
|----------------------------------|------|------|------|
| Number of pink-footed geese shot | | | |
| Skogn | 284 | 249 | 196 |
| Nesset | 133 | 205 | 103 |
| Egge | 209 | 11 | 71 |
| Number of hunting trips | | | |
| Skogn | 97 | 76 | 35 |
| Nesset | 16 | 15 | 15 |
| Egge | 82 | 39 | 65 |
| Hunting intensity index | | | |
| Skogn | 5.1 | 7.0 | 1.9 |
| Nesset | 2.2 | 3.5 | 2.0 |
| Egge | | 14.3 | |

advantage of these periods, resulting in the lowest proportion of harvest fields in 2012 in Nesset and Skogn (Fig. 4).

Food resources

The food resources available for geese varied between areas and time of the season. At Skogn, Nesset and Egge the main field types were (in descending order) spring cereal fields (either harvested, un-harvested or ploughed), grass fields, root crops and winter cereal fields. The variation in food availability for geese between years was mainly due to the variation in the timing of harvest, reflected in the proportion of harvested and un-harvested fields when the geese arrived to the area. In particular, at Skogn and Nesset in 2012 the harvest was late with only about half of the cereal fields harvested (Skogn: 57% and Nesset: 59%) at the time when pink-footed geese arrived in mid-September. Between the different periods of the season, the variability in field availability was determined by the timing of ploughing. Especially at Egge and Skogn, the ploughing started early, and by the time that most pink-footed geese had left in late October, between 20% (Skogn 2012) and 41% (Egge 2011) of the stubble fields had been ploughed. At Nesset ploughing was less frequent (Fig. 4).

At the time the pink-footed geese arrived in mid-September, the average density of spilt grain on stubble fields ranged from 162 (SE = 37) grains m⁻² (in 2011) to 785 (SE = 489) grains m⁻² (in 2013), both counts from Egge (Fig. 5). Within each area, there was only significant differences in grain densities between years at Nesset (Nesset: $F_{2,230} = 5.39$, p < 0.01; Egge: $F_{2,59} = 2.88$, p = 0.06; Skogn: $t_{1,137} = -1,30$, p = 0.20). Over the three years, there were only significant differences in grain densities between sites in 2011 (2011: $F_{2,170} = 4.44$, p = 0.01; 2012: $F_{2,119} = 1.91$,

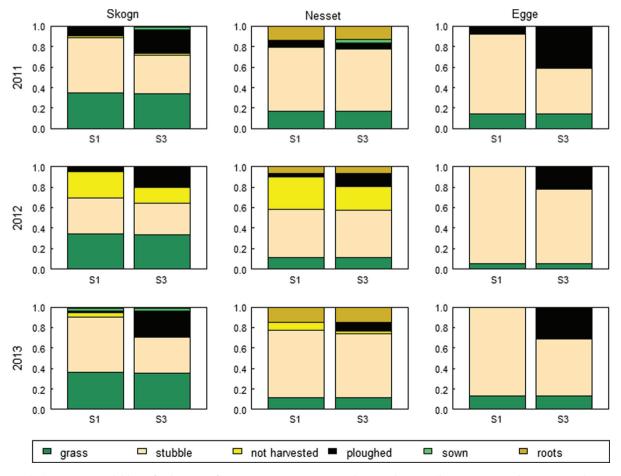


Figure 4. Crop types available as food sources for autumn-staging geese in three study sites, Skogn, Nesset and Egge, in mid-Norway, expressed as the proportion of the total area used by geese from September to November, 2011–2013, at two times during the season; midpoint for respectively S1 (23 September) and S3 (23 October).

p=0.15; 2013: $t_{1,137}=1.17$, p=0.27). On fields used by greylag geese prior to arrival of pink-footed geese, the grain density was significantly lower than on fields without greylag geese ($t_{1,383}=3.68$, p<0.01). In late October/early November when most geese had left the area, the average density of grain ranged from 72 (SE = 25) grains m⁻² to 336 (SE = 254) grains m⁻² (data from Nesset in 2011 and Egge in 2013, respectively). There were no significant differences in grain densities in these late counts between areas in any year (all p-values > 0.4) (Fig. 5).

At Skogn and Nesset in 2011 and 2012 there was a significant reduction in grain densities from the early to the late grain counts (Skogn 2011: $t_{1,111} = 5.07$, p < 0.01; 2012: $t_{1,97} = 3.48$, p < 0.01; Nesset 2011: $t_{1,57} = 3.54$, p < 0.01; 2012: $t_{1,67} = 1.76$, p < 0.01). At Nesset in 2013 and at Egge in 2011 and 2013 there were no significant differences in grain densities from the early to the late grain counts (all p-values > 0.1).

The relationship between the total amount of grain available and the number of pink-footed goose days spent at the three areas differed greatly. At Skogn there was a high amount of spilt grain but relatively few goose-days (30 000–50 000) compared to Nesset, which had a lower amount of spilt grain but relatively more goose-days (100 000–120 000).

Similarly, the estimated rate of consumption of the spilt grain by pink-footed geese and greylag geese varied between areas. It was highest at Nesset in all years, ranging between 28 and 42% of the total amount of spilt grain available in mid-September; between 9 and 23% at Skogn, while only 1% was consumed by geese at Egge in 2012. The consumption by greylag geese more than doubled over the three years in both Skogn and at Nesset, and at Nesset in 2013, greylag geese were responsible for the consumption of 73% of the grain consumed by geese after mid-September.

When hunting intensity was related to rate of consumption across years and sites (n = 7), the locally weighted regression showed a negative relationship (Fig. 6).

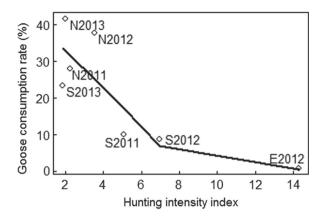


Figure 6. Relationship between goose consumptions rate (pink-footed goose and greylag goose summed) and hunting intensity index at three study areas in mid-Norway, Skogn (S), Nesset (N) and Egge (E) from mid-September-November, in 2011–2013.

Discussion

In this paper we have assessed the possible influence of availability of food resources, weather conditions, interspecific competition and hunting intensity (as a measure of possible disturbance) on abundance and distribution of pink-footed geese at autumn staging areas in mid-Norway.

Autumn staging geese in mid-Norway appear to have plentiful food resources in terms of spilt grain in harvested cereal fields. Spilt grain densities are comparable to conditions found in Denmark further south along the migration route (Madsen 2001). When the geese leave the area for their southward migration, there were still substantial amounts of spilt grain on the stubble fields although some fields were ploughed before goose departure. Nevertheless, grain is a finite resource and could potentially be exhausted, which would force the geese to leave the area, a pattern found in Denmark on fields with low shooting intensity (Madsen 2001). Hence, in Danish autumn-staging sites with

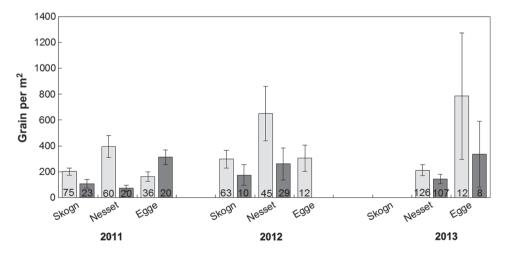


Figure 5. Average density of grain on stubble fields in three study areas in mid-Norway, Skogn, Nesset and Egge, at the time when pink-footed geese arrive in the area in mid-September (light grey) and at the time when most of the geese have left the area in late October/early November (dark grey), in 2011–2013. There was no data available for Egge in late October 2012 and no data available from Skogn in 2013. Numbers in columns represent the numbers of plots where grains have been counted. Vertical lines show standard error.

low hunting intensity, pink-footed geese and greylag geese almost completely depleted the available spilt grain resources and then moved on to other sites, while in sites with higher hunting intensity, geese abandoned the sites when there were still ample food resources available.

In this paper we showed that the presence of greylag geese prior to the arrival of the pink-footed geese may locally cause a major reduction in the resource availability for the pink-footed geese. Nevertheless, our assessment suggests that, at the moment, there is still a surplus amount of food available for geese in all three sites, with a potential to host more geese than observed at present. However, if the greylag goose population continues to increase in mid-Norway, this may be a future resource challenge for the pink-footed geese.

It cannot be expected that geese will empty all available resources. Because geese keep a distance to physical landscape elements such as buildings, roads and forests, certain parts of the fields will not be used by the geese. In terms of field sizes, the three study areas do not differ (Jensen 2014) and the differences in consumption rates cannot be explained by physical properties of the landscapes.

In addition to the inter-species competition effect, weather and farming practices may have an influence on food availability. The timing of harvesting and ploughing of fields in mid-Norway is affected by the weather, in terms of temperature and precipitation. The autumn of 2012 was a relatively cold but dry year; the cold weather resulted in a slow maturation of the grain, forcing farmers to postpone harvest; as a result, fewer stubble fields were available for the geese to forage in on arrival. Further north in Nord-Trøndelag as much as 80% of the fields were not harvested by the time of arrival of pink-footed geese, and geese were observed to pass over the area (Jensen 2014). In our study area the postponed harvest did not manifest in fewer geese; on the contrary, high numbers of geese remained and they stayed for longer compared to the other years. One explanation for this is that cereal fields were gradually harvested in late September through early October, gradually opening new foraging areas with high food abundances. Additionally, during a late harvest there is a higher likelihood of harsh weather blowing the grain of the grain plant or crack the fruiting body of the grain plant, which will result in even higher food abundance, of which the geese can take advantage.

Snow conditions did not affect the occurrence of geese in the main migration period in September–October. Only in one year (2012), did snow cause an exodus of geese in late October; Hence, when the weather allows for it, flocks of up to 500 geese have been observed staying until late November (O. M. Gundersen pers. comm).

As there was plenty of resources left when the geese had moved on and no significant snow cover to reduce its availability, there were apparently other reasons for the departure of the geese. The general farming activity is a source of disturbance for the geese, but this is more or less evenly distributed over the whole staging period. Superior conditions, in terms of food resources and/or low levels of hunting disturbance, in Denmark, which is the next staging site on the autumn migration route of pink-footed geese, could be an explanation for the early departure from mid-Norway. However, both grain densities and hunting intensities in Denmark are comparable to the Norwegian

situation, and inter-specific competition may be even more pronounced in Denmark with increasing numbers of greylag geese and barnacle geese *Branta leucopsis* overlapping in autumn distribution and habitat use (Madsen 2001; J. Madsen unpubl.).

The hunting activity varied between the different areas and years, presumably causing variable disturbance to the goose flocks in each area. From 2011-2013 a hunting experiment was carried out at Nesset (Jensen 2014), with low hunting disturbance following an organised experimental design. Hence, only one hunting team was active per hunting day, and there was always one hunting-free zone, an area of more than two km². With the exception of 2011, there was always a hunting-free period after a hunting day. This is in contrast to Skogn in 2011–2012 and Egge, where none, or only small areas, were hunting-free (less than 0.15 km² per hunting-free area). Here, several hunting teams were active per day and hunting took place on several consecutive days. Results from the experiments suggest that the reduced disturbance level at Nesset in 2011-2012 resulted in geese staying at higher abundance and for longer, expressed by the maximum length of stay for both 2011 and 2012 and the mean length of stay in 2012. The geese also stayed at higher abundance and longer at Nesset even though the food resources were more plentiful elsewhere, suggesting that a reduced hunting intensity, providing more safe areas to feed in, is more important than the total amount of food available. Similar conclusions were made by Madsen (2001), who examined the effect of diurnal regulation of goose shooting on the behaviour and site use of geese in Denmark.

At Nesset, the hunting disturbance, expressed by the number of hunting trips, was the same in 2011 and 2012, but lower in 2013; nevertheless, the number of pinkfooted geese was lower in 2013 than in the preceding years. One explanation for the decrease in pink-footed goose numbers could be the large increase in the number of greylag geese, hence increasing the competition for fields and food resources. At Skogn, the opposite pattern was observed in 2013, suggesting that it was the reduced hunting activity causing less disturbance to the geese, which was the reason for more geese, despite increasing numbers of greylag geese. One explanation can be that the Skogn area is twice as large as Nesset, leaving more room for both species and potentially reducing the competition for resources. In Egge we only had goose data from 2012, but the data supports the finding that an intense hunting disturbance had a negative effect on goose abundance and led to an early departure.

A very high proportion of neck-banded geese were only observed once suggesting that many birds stopped very briefly, either because they were motivated to move on or because they were disturbed, triggering them to depart. If the latter is the case, reducing the levels of disturbance could potentially lead to an extension of the length of stay, which will have huge implications for the volume of birds staging, expressed in goose-days. We have not performed a formal capture—mark—recapture analysis to estimate the true length of stay and volume of birds passing through the area (Frederiksen et al. 2001), and our estimates are undoubtedly too low. Nevertheless, our observations show that some birds may stay in the area for more than a month, indicating that

there is a potential for building up a local staging population of geese.

Collectively, our results suggest that geese depart from mid-Norway due to disturbance caused by too intensive goose hunting. However, it cannot be ruled out that snow might have been a factor in previous years. If snow normally arrives earlier than in our study, the early departure time of geese might be an adaptation to earlier arrival of snow and not only a response to hunting disturbance. Nevertheless, for pink-footed geese, the early departure is unlikely to have a fitness effects in terms starvation, because food conditions on the wintering grounds are suggested to be plentiful (Therkildsen and Madsen 2000, Wisz et al. 2008); hence, at least at the moment there is little conservation concern.

Implications for hunting management

Up until 2011 there was an increase in numbers of pinkfooted geese shot in mid-Norway. Since then the numbers has declined (Statistics Norway), albeit the proportion of pink-footed geese shot in Levanger, the municipality where our study areas are located, has increased in both 2012 and 2013 (Statistics Norway). The argument, that hunting disturbance is the main reason for geese leaving the area heading southwards, could potentially have implications for fulfilling two of the objectives of the international management plan for the population. Firstly, the plan recommends that levels of human activity should allow geese to stay as long as possible in areas where they do not cause conflicts with agriculture, in order to avoid them being pushed to areas where conflicts are likely to arise. For example, disturbance causing geese to depart from Norway or Denmark in autumn may lead them to migrate to the Netherlands where they cause damage to pastures before the last mowing in autumn (Madsen and Jepsen 1992). Secondly, one of the objectives is to regulate the harvest rate to reach a population target at around 60 000 individual geese. When the present study was conducted, the population was above the target of 60 000 (ca 80 000 during 2011-2013; (Madsen et al. 2015a); and the harvest had to increase in order to reduce the population size (Johnson et al. 2014). The implementation of the plan therefore called for an increase in harvest in Norway and Denmark, the two countries with an open season for pink-footed geese. As a new tool to reduce the population, a prolonged hunting season (on land) was established in Denmark, thereby opening for hunting opportunities also in January; this might be effective because in recent years increasing numbers of pink-footed geese have stayed in Denmark throughout the winter (Madsen et al. 2015b). In Norway, on the other hand, such initiatives are impossible to implement, as the geese leave the country well before the hunting season is over. In order to increase the harvest, an increase in the hunting intensity may not necessarily be efficient, because it may scare the geese away from the area; however, local agreements to reduce the hunting intensity may lead to less disturbance (Jensen 2014), enabling geese to stay longer in an area, as long as they are not forced to leave for other reasons such as limited resources, snowfall or inter-specific competition. To fulfil the two above objectives of the international management plan, we recommend that a better organisation of hunting is implemented.

As a post scriptum it should be mentioned that since this study was performed, the population of the pink-footed goose was actually reduced to the target of 60 000 individuals in spring 2015. This was possibly due to the extension of the hunting season on land in January 2015 in Denmark, which increased the overall harvest (Madsen et al. 2015a). To maintain the population at target in the coming years, the harvest has to decrease compared to previous years. As part of the adaptive process, the harvest can be intensified again if the population bounces back. Therefore, a better organisation of hunting remains an important tool to regulate the harvest of the population.

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