

Landscape selection by migratory geese: implications for hunting organisation

Authors: Jensen, Gitte Høj, Pellissier, Loïc, Tombre, Ingunn M., and

Madsen, Jesper

Source: Wildlife Biology, 2017(1)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00192

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

doi: 10.2981/wlb.00192

© 2016 The Authors. This is an Open Access article

Subject Editor: Hans Pedersen. Editor-in-Chief: Ilse Storch. Accepted 4 June 2016

Landscape selection by migratory geese: implications for hunting organisation

Gitte Høj Jensen, Loïc Pellissier, Ingunn M. Tombre and Jesper Madsen

G. H. Jensen (gitte.h.j@gmail.com) and J. Madsen, Dept of Bioscience, Aarhus Univ., Grenåvej 14, DK-8410 Rønde, Denmark. – L. Pellissier, Landscape Ecology, Inst. of Terrestrial Ecosystems, ETH Zürich, Zürich, Switzerland, and: Swiss Federal Inst. for Forest, Snow and Landscape Research, Birmensdorf, Switzerland. – I. M. Tombre, Norwegian Inst. for Nature Research, Dept of Arctic Ecology, The Fram Centre, Tromsø, Norway

Over the last decades, many wild goose populations have increased significantly and are now causing conflicts with socioeconomic and biological interests. To mitigate impacts of rapid population increases, population control by increasing harvest has been attempted. In this study we seek to guide the design of a regional autumn goose hunting organisation in agricultural landscapes by identifying areas suitable for hunting, which have high probability of occurrence of pink-footed geese *Anser brachyrhynchus* and/or a short return time by geese to fields subject to hunting. To identify areas suitable for hunting in Nord-Trøndelag County, mid-Norway, we used species distributions models (SDMs), a broadly accepted tool in conservation planning for spatial refuge organisation. The prediction was that the highest probability of goose occurrence exists for large fields, away from small roads and near water bodies serving as safe roosting sites. Additionally, return time was predicted to be shortest for large fields near roosting sites and away from big roads. A combined map of goose occurrence and return time showed similar prediction for high goose occurrence and short return time; hence areas most suitable for hunting are large fields, close to roost sites and away from roads. If hunters and landowners are willing to coordinate goose hunting at a landscape level, they can use the prediction maps as guidance, with the likely benefit that they collectively can shoot more geese. Such local and regional organisation can become a powerful tool in the harvest management of geese.

An increasing proportion of land surface areas are used for agricultural production, which is often accompanied with intensive management through irrigation and the application of fertilisers and pesticides. The cost is, among others, a decrease in many natural habitats used by birds and reduced wildlife value (Tilman et al. 2001). This, however, does not apply for the majority of goose populations breeding or wintering in western Europe, which have increased considerably in numbers during recent decades (Madsen et al. 1999, Fox et al. 2010). Opposite to many bird species, geese have benefitted from the efficiency in agricultural practices and most species have now almost completely shifted to forage on agricultural lands during the wintering period (Van Eerden et al. 1996). As a consequence of improved agricultural food conditions, the creation of refuge areas, a decreased hunting pressure and climate change effects, most of the populations continue to increase (Ebbinge 1991, Fox et al. 2010). This has led to escalating conflicts with agricultural interests (van Roomen and Madsen 1992, Bruggers et al. 2002, Tombre et al. 2013).

This work is licensed under a Creative Commons Attribution-NoDerivatives 4.0 International License (CC-BY-ND) http://creativecommons.org/licenses/by-nd/4.0/>.

The Svalbard breeding population of pink-footed geese Anser brachyrhynchus, wintering in Norway, Denmark, the Netherlands and Belgium, has increased substantially in recent decades. From 1990 to 2010, the population increased from around 30 000 to 80 000 and now constitutes a management challenge (Madsen and Williams 2012). Accordingly, the population has been selected as the first test case for development of an international species management plan under the African-Eurasian Waterbird Agreement (AEWA). The goal of the plan is to maintain the favourable conservation status of the population, while taking into account economic and recreational interests. To attain this goal, the management plan seeks to maintain a population size of around 60 000 individuals through optimisation of recreational hunting which is currently allowed in two of the four range states: Norway and Denmark (Madsen and Williams 2012).

In order to regulate the population, the harvest rate must increase as the population is currently above its target (Johnson et al. 2014). This can be achieved by liberalising hunting regulations, such as extending the hunting season. The effectiveness of current hunting practices may also be increased by an optimal use of decoys, the hunting intensity, and/or the distribution of hunters in the landscape. The key

is to reduce the level of disturbance preventing the geese from abandoning the area and thereby jeopardising the chances of harvest success. While some information exists on how to optimise temporal hunting structure (Bregnballe and Madsen 2004, Jensen et al. 2016a), to our knowledge there are no studies documenting how to optimise the spatial hunting structure at the landscape level. Importantly, large-scale hunting organisation may potentially conflict with favourable goose foraging areas so that hunting of a few individuals may cause undesired disturbance and negatively affect a large proportion of the entire population. Indeed, hunting in an area may cause a temporary abandonment by geese (Bregnballe and Madsen 2004). By balancing hunting and feeding areas for geese, it will be possible to optimise the spatial hunting organisation, mitigate the disturbance from hunters, potentially increase the number of harvested geese and thereby contribute to the control of the population size to meet overall management objectives.

Interdisciplinary studies of landscape ecology may be used for linking ecological processes and spatial patterns influenced by humans. Knowledge gained from landscape ecology may facilitate an effective conservation planning, as it can identify areas of interest and integrate the use and protection across the landscape (Hansson and Angelstam 1991, Dunning 1995, Sanderson et al. 2002, Morris 2003). Currently, the focus in landscape ecology has been on wildlife populations of conservation concern, whereas it has more rarely been applied to abundant or increasing wildlife populations that may conflict with landscape use by humans (Hansson and Angelstam 1991, Sanderson et al. 2002).

In this study, we use predictions of goose landscape use to investigate the potential of a large-scale spatial hunting organisation. We used records of pink-footed goose occurrence while staging at their first stopover area during autumn migration in mid-Norway, and employed a modelling approach that relates pattern of goose occurrence with environmental variables, hypothesised to explain landscape selection.

Material and methods

Study population and area

The Svalbard breeding population of pink-footed geese departs Svalbard in mid-September towards their wintering grounds in Denmark, the Netherlands and Belgium. During migration pink-footed geese make a stopover in mid-Norway, the first and most important stopover area for pink-footed geese on their autumn migration (Madsen et al. 1999). This study was carried out in the County of Nord-Trøndelag in mid-Norway (64°30′0″N, 11°40′0″E) in 2011-2013. Nord-Trøndelag is semi-mountainous and the lowlands along Trondheimsfjorden are characterised by a mosaic of agricultural fields, mainly cereal fields, grass fields, potato and carrot fields, where geese can forage. The sheltered bays of Trondheimsfjorden as well as numerous lakes and rivers provide roosting sites for the geese from where they fly into the adjacent farmland to feed during daytime (Jensen et al. 2008).

The pink-footed geese arrive in Nord-Trøndelag in mid-September and stay until November depending on a combination of food availability, timing of snow fall and levels of disturbance (Jensen et al. 2016b).

Norway has an open hunting season for pink-footed geese from 10 August to 23 December and Denmark from 1 September to 31 December (on land). The species is protected in the Netherlands and Belgium. Around 80% of pink-footed geese reported shot in Norway are harvested in Nord-Trøndelag (Statistics Norway, https://statbank.ssb.no/en/statistikkbanken).

Study design and data collection

This study was carried out at two areas in Nord-Trøndelag; Skogn and Nesset in Levanger Municipality. Both areas represent important goose staging and hunting areas and cover approximately 35 km² and 10 km², respectively (Fig. 1). The local data from Skogn and Nesset was used to evaluate the regional models built for areas not surveyed in Nord-Trøndelag. Data was collected for the entire autumn stopover period and for every field.

At Skogn, hunting is performed on private properties, and the landowners can decide 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 (approximately 5 km²) of the Skogn area. Hunting was further restricted to a maximum of two hunting days per week in each of the six areas. At Nesset, hunting has been administrated through the local landowner association until 2011, but there have been no restrictions to the hunting intensity. Further, no organisation of shooting existed between groups of hunters, except for an agreement about one shooting-free day per week. In 2011-2013, the hunting was organised through this research project aiming towards investigating optimal organisation of local goose hunting (Jensen et al. 2016a).

To assess abundance and distribution of pink-footed geese on fields and roost sites, flocks of geese were counted and the approximate center position of flocks were mapped and coordinates were established in ArcGIS for each flock. For all years, surveys were systematically conducted on a daily basis between 08:00-18:00 hours and it was ensured that all fields and roosting sites were visited at different times during the study period. The surveys were conducted by one person, from a car and done by driving on all concrete roads at Skogn and Nesset, approximately 120 km per day. The daily observations commenced on the first pinkfooted geese arriving in the study area each autumn, and continued until most had left the area. Hence, the survey 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. To assess the influence of environmental variables, average, maximum number and total sum of geese per field throughout the whole registration period were used for all fields at Nesset and Skogn. The goose abundance estimates during the study period and areas ranged from 0-2900 for average number

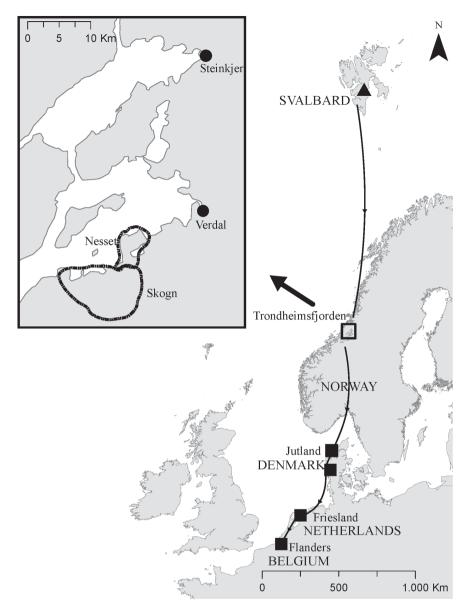


Figure 1. The Svalbard pink-footed goose flyway, major autumn/winter staging areas (squares) and breeding area (triangle). The insert map shows the two study areas in mid-Norway, Skogn and Nesset (open square).

of geese observed per field, 0–5000 for maximum number of geese observed per field and 0–38 488 for the total sum of geese observed per field.

Hunting data, date and location, from Skogn and Nesset was collected during the same period as the goose counts. This was used to calculate the numbers of days between a hunting event and until geese were observed on the field again; hereafter referred to as 'return time'. The return time, which is a proxy for sensitivity of a field exposed to hunting, ranged from 1–39 days. At Skogn we only have return time from 2011 and 2013, as we do not have the hunting locations in 2012. In 2011, the hunting data was derived from the webpage <www.gasejakt.no>; however, we do not have data from hunts performed by landowners in the Skogn area. In terms of calculating return time, we assumed that landowners did not hunt unless they had observed geese on one of their fields, which is a reasonable assumption based on communication with landowners. Hence, since surveys

of geese were done for the entire area every day, landowners would never hunt between a registered hunt and the first observation of geese on a given field. In 2013, the data was either collected through a social media group or directly from the hunters. From Nesset return time is available for all three years. To assess the influence of the environmental variables on the return time, the estimated return time for all possible fields within Nesset and Skogn was used. Since hunting is not conducted on all fields, the data is limited to those fields where hunting has been conducted. When several hunts (1–16) have been performed on the same field during the study period, an average of return time was calculated and used.

In order to explore the spatial variation in areas with high goose probability combined with a short return time, a combined map of probability of occurrence of pink-footed geese and return time was produced by merging the two layers produced as explained below.

Environmental variables

In this study we investigated the following environmental variables, hypothesised to explain landscape selection by geese.

- 1) Field size (Abbr.: Field size; unit: km²). Goose abundance and distribution may be influenced by predation risk or disturbance (Madsen 1995, Vickery and Gill 1999, Jonker et al. 2010, Chudzinska et al. 2013), and as a response geese tend to congregate on larger fields (Amano et al. 2006, Jensen et al. 2008, Rosin et al. 2012). As our study is conducted during the hunting season, we expect geese to be sensitive to disturbance, and field size to be an important explanatory variable. Field size is based on areas with no physical boundaries like roads, streams, hedgerows etc. The field size ranged from 0.001 to 2.554 km². We assume geese to perceive these fields as independent foraging areas.
- 2) Distance to human infrastructure (Abbr.: Big road, Small road, Forest, Build; unit: m). Human infrastructure such as roads, railroads and buildings, as well as hedgerows and woodlands, are associated with perceived predation risk (Madsen 1985, Keller 1991, Gill 1996, Rosin et al. 2012) and the probability of goose occurrence is expected to be related to distance to these elements. The road variable is categorised in distances to small and big roads, as we expect small roads to have a larger effect due to unpredictable and irregular traffic, whereas birds are believed to habituate more easily to a frequent and directional disturbance such as densely trafficked roads (Rees et al. 2005). Based on existing spatial layers from regional authorities (Agricultural Department, County of Nord-Trøndelag) distance to roads, buildings and forests were calculated. The distance was defined as the shortest distance from the field centre to the nearest variable of each type. The road variable was divided into big roads consisting of main roads in the national road grid, whereas small roads consisted of municipality roads, private roads and dirt roads. The distances to the nearest small road ranged from 5 to 519 m, for big roads from 18 to 2157 m; for buildings the range was 20 to 542 m and for forests 5 to 620 m. For predictions outside Nesset and Skogn, distance to buildings and distance to forest were not available and therefore not used in the model for the projections.
- 3) Distance to roost site (Abbr.: Roost; unit: m). Energy use related to flight searching for suitable foraging fields is likewise expected to affect goose abundance and distribution. Most migratory geese congregate at roosting sites during night and some periods of the day, and to save energy, they forage in adjacent open landscapes (Owen et al. 1987, Vickery and Gill 1999, Jensen et al. 2008, Si et al. 2011, Patterson 2013). Therefore, we expect that the probability of occurrence of geese is inversely related to the distance to roost sites. Distance to roost sites were found on existing spatial layers and distances were calculated from field centre to nearest known night roost, based on mapping of roosting site recordings in spring and autumn (Supplementary material Appendix 1 Fig. A1). The distances for known roosts sites ranged from 261 to 7427 m.
- 4) Size of harvested area within a field (Abbr.: Harvested area; unit: km²). A common strategy for migratory geese is

- to build up and maintain sufficient nutritional reserves by intensive foraging on stopover areas (Drent et al. 1980, Klaassen et al. 2006, Stephens et al. 2014). For the pink-footed geese during autumn migration, spilt grain on stubble fields is the main food resource (Madsen 1985, Fox et al. 2005, Jensen et al. 2016b). In this study we therefore included size of harvested area within each field, and hypothesise that there is a higher probability of occurrence of geese on fields with a higher degree of harvested area. Within each field the harvested area was estimated based on surveys of field types (categorised as: unharvested cereal, stubble, ploughed, pasture, potato, carrot), which were carried out on 8 or 9 October each year. The harvest area per field ranged from 0 to 1.491 km².
- 5) Year (Abbr.: Year; unit: year). In most heterogeneous landscapes the availability and quality of food resources varies both spatially and temporally. In Nord-Trøndelag, habitats are available from the time of harvest and for as long as they are not ploughed or covered by snow. The cereal grain is harvested during late summer/early autumn, and, depending on weather conditions, the harvest date may vary by weeks. The timing of harvest and ploughing could be another factor controlling goose distribution. To account for this, the goose distribution is investigated between years, with varying timing of harvest and ploughing.

Statistical analysis

To identify fields with high probability of occurrence of geese and/or a short return time, we used a broadly accepted tool in conservation planning for spatial refuge organisation, species distributions models (SDMs). SDMs are empirical models quantifying the relationship between field observations and environmental predictor variables, hence explaining how the environmental predictors control the distribution of field observations (Guisan and Zimmermann 2000), using a selection of environmental variables hypothesised to affect distribution of species (Guisan and Thuiller 2005, Guisan et al. 2013). The procedure consisted of five steps:

Step 1 - Selecting environmental predictor variables. To produce parsimonious models for goose occurrence and return time, respectively, we included only five environmental variables showing the strongest individual correlation to goose abundance and return time, while not being strongly correlated with each other.

- Step 2 Making the data ready for model building. As the hunting intensity at Nesset has been lower than usual during the study period and lower compared to Skogn, the goose abundance dataset was transformed to a probability of occurrence dataset, to avoid potential bias from the different hunting regimes at Nesset and Skogn. The presence of geese represents any use of a given field during the study period (observation value 1), versus no observed use of a field (0). Hence, the correlation analysis was done on the abundance dataset, but the model was built on the occurrence dataset.
- Step 3 Building the models. To predict probability of occurrence of pink-footed geese we fitted a generalised linear model (GLM) with a binomial distribution. We related the

presence—absence of pink-footed geese in fields to the top five environmental predictors. To predict return time we fitted a linear model (LM), relating return time to the top five environmental predictors and specifying our model with a gaussian distribution. In addition to predictions of goose occurrence and return time, we predicted goose abundance by fitting a generalised linear model (GLM) with a quasi-poisson distribution using the same explanatory variable as in the goose occurrence model. This was done to compare the prediction made by the goose occurrence model and the goose abundance model.

Step 4 - Evaluating the models. We used a repeated (10 times) split sample approach for evaluating the goose occurrence model. The model was fitted using 70% of the data and evaluated using the area under the curve (AUC) of a receiver-operating characteristics (ROC) plot (Fielding and Bell 1997) calculated on the excluded 30%. An AUC score between 0.8 and 0.9 indicated good discrimination capacity, an above 0.9 excellent discrimination capacity (Thuiller et al. 2005). This approach provides a good evaluation of the model performance beyond the calibration dataset and is used regularly in SDMs to predict beyond the calibrated geographic area (Petitpierre et al. 2012). For evaluating the return time model, we used a repeated split sample and for each split-sample repetition and for each model, a Spearman rank correlation between observed and predicted was calculated using the evaluation dataset, as recommended by Zheng and Agresti (2000). In addition to the general model evaluation, we calculated the importance of each explanatory variables in the model, by quantifying how much information was lost by randomising one variable at a time. We quantify the difference between the variance from standard predictions and the predictions obtained when the variable under investigation is randomized. Thus, a large reduction in explained deviance suggests that the variable in question is of high importance in the model.

Step 5 - Production of map. Maps were produced by basic model projection.

We used R statistical software (<www.r-project.org>) along with ArcGIS (ESRI 2013) for all statistical analyses and spatial predictions.

Results

Field size and harvested field size were strongly correlated for both goose abundance (r = 0.861, n = 657, p < 0.01) and return time (r = 0.941, n = 42, p < 0.01) (Table 1) and since field size is available for Nord-Trøndelag as a whole while harvested field size is not, field size was used in further analysis. Predictions of goose occurrence and distribution were consistent across all three years, independent of varying timing of harvest and ploughing (Supplementary material Appendix 2 Fig. A2a–c). Therefore, in the following sections, we only present results based on models excluding year effects.

Model for goose occurrence

For the goose occurrence model, we first identified the top five environmental variables which correlated the most with goose abundance. The estimate of goose abundance (average, sum and maximum), which had the highest correlation with the explanatory variables, was maximum number of geese per field (r = 0.295). However, all three estimates of goose abundance were highly correlated and provided similar results (Table 1a). The environmental variables which correlated the most with goose abundance, and which were

Table 1. Correlations matrix for explanatory variables including the dependent variables for a) pink-footed goose abundance and b) return time. See Methods section for explanation of the variables. * p < 0.10, **p < 0.05, ***p < 0.01.

1)	Goose abundance			Explanatory variables						
	Max	Sum	Average	Field size	Harvested area	Big road	Small road	Roost	Build	Forest
Max	1.000	0.787	0.848	0.512***	0.502	0.117	0.245***	-0.155***	0.297***	0.265***
Sum		1.000	0.540	0.531***	0.535	0.128	0.141***	-0.110***	0.256***	0.219***
Average			1.000	0.378***	0.331	0.074	0.251***	-0.141***	0.271***	0.205***
Field size				1.000	0.861***	0.130	0.448	-0.004	0.552	0.366
Harvested area					1.000	0.130	0.379	-0.072	0.473	0.379
Big road						1.000	-0.036	-0.089	0.173	0.105
Small road							1.000	0.112	0.659	0.251
Roost								1.000	0.038	-0.210
Build									1.000	0.279
Forest										1.000
2)	Explanatory variables									
	Return time		Field size H		rvested area	Big road	Small road	Roost	Build	Forest
Return time	1.000		-0.26	2* -	0.306	-0.202	-0.085	0.276*	-0.254	-0.191
Field size			1.00	0	0.941***	0.185	-0.075	-0.044	0.403	0.351
Harvested area					1.000	0.177	-0.036	-0.106	0.460	0.429
Big road						1.000	-0.017	0.147	0.290	0.293
Small road							1.000	0.516	0.180	0.184
Roost								1.000	-0.017	0.0560
Build									1.000	0.662
Forest										1.000

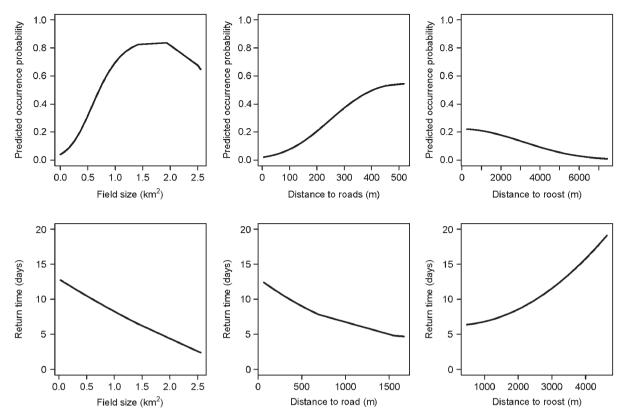


Figure 2. (upper row) Predicted occurrence probability of pink-footed goose versus left) field size, central) distance to roads and right) distance to roost in Nord-Trøndelag, mid-Norway. (lower row) Return time (days) of pink-footed goose versus left) field size, central) distance to roads and right) distance to roost in Nord-Trøndelag, mid-Norway. See Methods section for explanation of the variables.

subsequently used in the occurrence model for Nesset and Skogn were: field size, distance to buildings, distance to forest, distance to small roads and distance to roost (Field size: r = 0.512, n = 657, p < 0.01; Build: r = 0.297, n = 657, p < 0.01; Forest: r = 0.265, n = 657, p < 0.01; Small road: r = 0.245, n = 657, p < 0.01; Roost: r = -0.155, n = 657, p < 0.01; Table 1a). The response curves for the predictors were consistent with hypothesised predictions (Fig. 2, upper row).

Since distance to buildings and distance to forest were not available for predictions outside Nesset and Skogn, those variables were not used in the model for the projections. However, neither of these showed strong variance importance (Fig. 3a).

The prediction of goose occurrence for Nesset and Skogn using field size, distance to buildings, distance to forest, distance to small roads and distance to roost achieved an AUC of 0.89. The prediction of goose occurrence for Nesset and Skogn using only field size, distance to small roads and distance to roost achieved an AUC of 0.87, nearly identical. Due to minor variance importance of the excluded

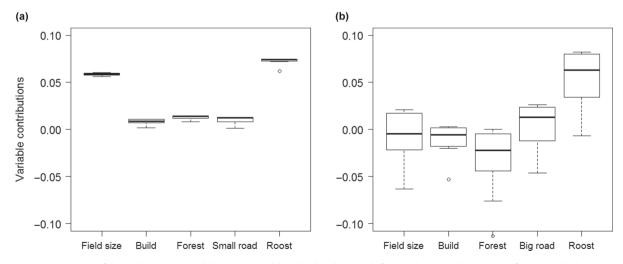


Figure 3. Importance of the explanatory variables in the models, calculated as the difference between the variance from standard predictions and the predictions obtained when the variable under investigation is randomized in the (a) pink-footed goose occurrence model and (b) return time model for Nord-Trøndelag, mid-Norway. See Methods section for explanation of the variables.

environmental variables and the identical prediction power, we used the model excluding distance to buildings and distance to forest to make our spatial predictions for Nord-Trøndelag. The predicted highest probability of goose occurrence exists for large fields, away from small roads and near roosting sites (Fig. 4; Supplementary material Appendix 3 Fig. A3). The predicted highest goose abundance provided similar results, but with a positive bias for Nesset, presumably because of a lower hunting intensity during the study period (Supplementary material Appendix 4 Fig. A4).

Model for return time

The environmental variables with the highest correlation with return time, and hence included in the model for Nesset and Skogn, were: distance to roost, field size, distance to buildings, distance to big roads and distance to forest

(roost: r=0.276, n=42, p<0.1; field size: r=-0.262, n=42, p<0.1; build: r=-0.254, n=42, p>0.1; big road: r=-0.202, n=42, p>0.1; forest: r=-0.191, n=42, p>0.1; Table 1b). The response curves for the predictors were consistent with the hypothesised predictions (Fig. 2, lower row).

For predictions outside Nesset and Skogn, distance to buildings and distance to forest were not available and therefore not used in the model for the projections. However, these variables neither showed a significant effect on return time in the LM model (p > 0.1), nor did they have strong variance importance (Fig. 3b).

The prediction of return time for Nesset and Skogn using distance to roost, field size, distance to buildings, distance to big roads and distance to forest achieved a median Spearman rank correlation of 0.293 with the observed return time. The predictions for Nesset and Skogn only using distance to

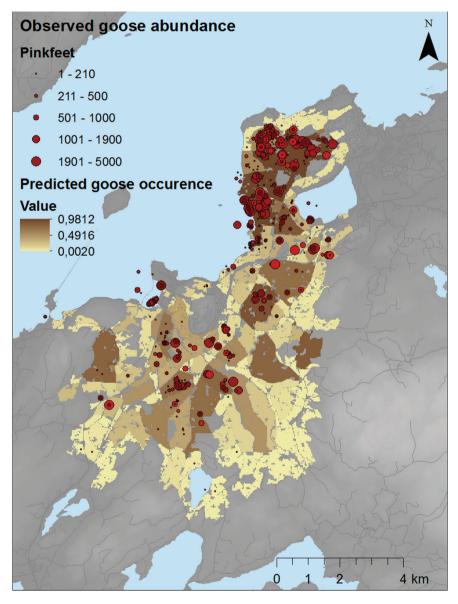


Figure 4. Field observations (dots) and predictions of the probability of occurrence of pink-footed goose at Nesset and Skogn, mid-Norway. The predictions were computed using a GLM model and values of field size, distance to the nearest small road and to the nearest roosting site.

roost, field size and distance to big roads had a correlation of 0.458 (Supplementary material Appendix 5 Fig. A5).

Due to increased prediction power for the limited model and minor variance importance of the excluded variables, we feel comfortable excluding distance to buildings and distance to forest in the model for Nord-Trøndelag and predictions outside the study area. The predicted lowest return times were found for large fields near roosting sites and away from big roads (Fig. 5; Supplementary material Appendix 6 Fig. A6).

Sensitive/non-sensitive areas

The combined map of goose occurrence and return time showed similar prediction for high goose occurrence and short return time (Fig. 6; Supplementary material Appendix 7 Fig. A7); hence areas most sensitive to hunting are relatively

small fields away from the roosts and in proximity to roads.

Discussion

In this study we predicted that the highest probability of goose occurrence exists for large fields, away from small roads and near water bodies serving as safe roosting sites. Additionally, return time was predicted to be shortest for large fields near roosting sites and away from big roads. A combined map of goose occurrence and return time showed similar predictions for high goose occurrence and short return time; hence, fields most suitable for hunting are large fields, close to roost sites and away from roads.

We found that field size was a main explanatory variable to predict goose landscape use. This may simply be because

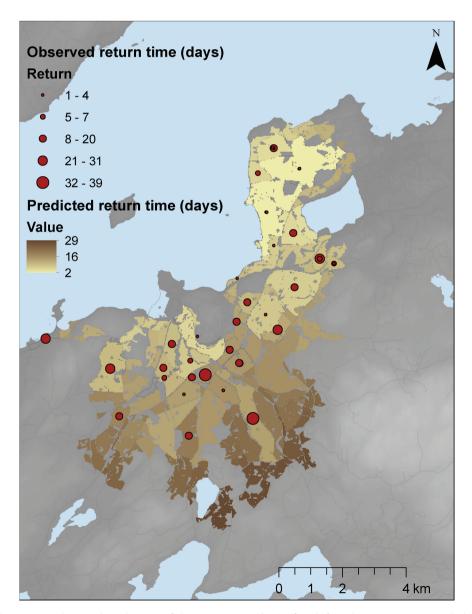


Figure 5. Field observations (dots) and predictions of the return time (days) of pink-footed goose at Nesset and Skogn, mid-Norway. The predictions were computed using a LM model and values of distance to the nearest roosting site, field size and distance to nearest big road.

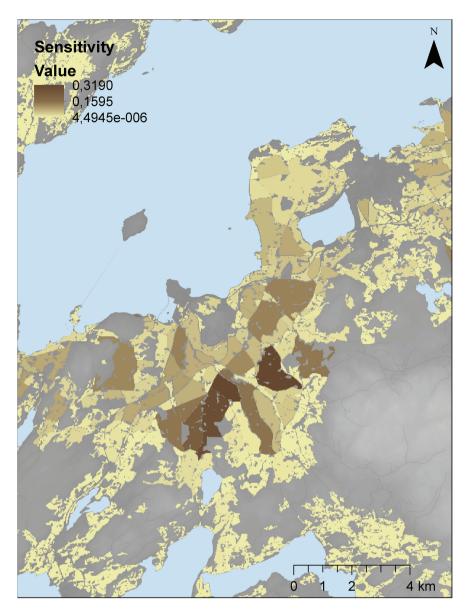


Figure 6. Predictions of hunting sensitivity at Nesset and Skogn, mid-Norway. The predictions were based on combined results from pink-footed goose occurrence and return time; high numbers indicate a long return time and high probability of goose occurrence.

bigger fields can sustain more geese. However, other studies at this stopover area have found that during spring migration the behaviour of pink-footed geese is strongly influenced by disturbance (Chudzinska et al. 2013, Simonsen 2014). As the disturbance during autumn migration is likely to be even higher due to hunting activities and because autumn is a busy time for farmers in the fields, it is reasonable to assume that field size, as a proxy for sensitivity to disturbance, is an important explanatory variable for predicting goose occurrence. Other forms of disturbance, which could be reasons for geese to choose larger fields, are small roads, buildings and forest, which were all found to have a significant effect on goose occurrence, but nevertheless with minor variance importance. Rosin et al. (2012) found that geese prefer large fields that are remote from forests and human settlements. Additionally, Chudzinska et al. (2013) found that sporadic and unpredictable disturbance associated with traffic on small roads had a higher effect on geese in terms of behavioural responses, opposite to a predictable source of disturbance, such as large roads with constant traffic. Madsen (1985) also investigated the effect of roads on goose usage of fields, and found that roads with a traffic volume of 20–50 cars (or equivalent) per day had a depressing effect on goose utilisation in a range of 0–500 m from the road. The reason why small roads are more disturbing compared to large roads is probably that geese habituate to constant traffic while they are more wary of sporadic passage of vehicles. In terms of hunting organisation this means that it is more important to stay away from smaller roads than large roads.

Distance to roost was also selected as an important predictor of goose landscape use, which is supported by previous work on the pink-footed goose (Jensen et al. 2008, Wisz et al. 2008, Chudzinska et al. 2013). This may be explained by the energetic flight costs involved in reaching fields further away, but also exacerbated by effects of disturbance in the fields. When geese are disturbed (by humans or

natural avian predators such as eagles), they often move back to the roost sites to find peaceful conditions (Jensen and Madsen unpubl.); and, if geese have to make several foraging flights per day, distant fields become even less attractive. Therefore, the prediction was that geese will deplete the spilt grain resources faster in fields close to the roosts. However, repeated counts of densities of grain in fields over the course of the autumn staging period of geese suggest that in the majority of fields, including those close to the roost sites, food supplies remain plentiful throughout the autumn (Jensen et al. 2016b).

An area with a short return time is characterised by many of the same features as a field with high probability of goose occurrence; however, distance to roosting sites was the only critical predictor. Potential disturbance or predation risk in terms of field size, distance to buildings, big roads and forest had minor importance. This indicates that disturbance itself is less important for when geese decide to return, but rather that return time is governed by 1) the potential escape routes from the disturbance, 2) proximity to roosting sites 3) minimising energy cost by first revisiting areas closest to the roosting sites. In other words the effect of hunting is primarily caused by spatial effect rather than temporal effects. In an experimental study conducted at the Nesset study area in mid-Norway (Jensen et al. 2016a) it was found that geese returned to the same fields two days after a hunting event. In the present study, we found that the predicted return time for the study area ranged from 1.5 up to 18.6 days, dependent on the distance to roosting sites. The experimental study was conducted within four km from the nearest roost site, and within this distance, return time was not important as a predictor of goose usage. This is in accordance with the spatial prediction from the SDM models. Beyond four km the return time increases dramatically. Additionally, big roads with constant traffic have a higher influence on return time than small roads with only irregular traffic. This may be because, if a hunt is conducted close to a big road, hunting will reduce the habituation by geese to the constant traffic.

We found that in Nord-Trøndelag there is not a big environmental difference between areas with high probability of goose occurrence and a short return time. This may be because of the flocking behaviour as geese are more likely to return quicker to areas with high probability of goose occurrence. Nevertheless, this is an important finding in terms of a sustainable large-scale hunting organisation, as it shows that there is not a strong conflict between hunting locations and feeding areas, since geese return faster to preferred areas than less preferred areas after a hunt. For none of the fields, however, did geese return on the same day as hunting was conducted, hence, even for the most preferred goose fields, the geese needed a minimum of two days to return and resume foraging. The two days return time is based on the predicted return time and results from experimental work looking at temporal responses by geese to hunting (Jensen et al. 2016a). In terms of maximising the hunting bag, this means that hunting should be conducted on large fields, which are located close to a goose roost and away from roads. On these fields, hunters will have a greater chance of encountering geese on a given hunt. Additionally, more hunting events can be arranged, since geese quickly return to these fields. Therefore, for these field types we expect a bigger hunting bag per hunt and in total for the season.

In this study we have used a number of environmental variables to make predictions of goose occurrence and return time. This is done in order to investigate the potential of a large-scale spatial hunting organisation. A limitation of such a model is, however, that predictions done outside the realm of the data includes further uncertainties. Hence, e.g. knowledge of the influence of potentially increased hunting intensity on goose occurrence and return time is limited and there is a possibility that frequent, consequently repeated hunting events on a given field, will lead to abandonment of this field by geese. Such a reaction will have a negative effect on the hunting bag, but in addition, when geese are driven off their favourite grounds, they will search for other fields which involve additional energy expenditure and exploitation of fields of minor quality. Demonstrating such an effect, however, would require a spatially explicit and complete record of hunting in the region, which was not available in this study. Additionally, in this study it was shown that the return time is short, especially in large fields, which are relatively close to the goose roost sites. It is therefore expected that hunting has a spatial effect which in turn affects the temporal accessibility of geese to hunting.

A second limitation of the study is the spatial predictions outside our study area. We do, however, not expect the projection of the model to the larger area to be problematic, because the location for the prediction was close by and similar to the location where the data was collected. Therefore, we feel comfortable extrapolating our predicting for Skogn and Nesset to the Nord-Trøndelag County.

Species distribution models are useful for optimising management decisions (Guisan et al. 2013) and to our knowledge this is the first attempt to provide a model for regional scale hunting organisation. The study, focusing on optimising goose harvest management, brings valuable input to the international species management plan currently seeking to stabilise the population of the pink-footed goose. The model and the recommendations of coordinating hunting events with neighbouring hunters (Jensen et al. 2016a), can be used as a tool by managers, private landowners or consortia of hunters to optimise hunting activity based on first principles of goose behaviour. Currently the adaptive harvest management plan for the pink-footed goose sets an annual harvest quota with little regards and limited knowledge of how the quota is regulated or shall be reached at the local level. However, through an adaptive hunting organisation, which regulates size and/or place of the hunting areas combined with monitoring of the hunting bag in the same areas, it is possible to link the overall hunting quota with the local hunting activities. However, as the target population size is reached, it will be important to continue monitoring how the hunting bag is affected. Apart from using statutory tools such as season length to regulate harvest, a novel avenue would be to make voluntary regional regulations with temporal and spatial limitations on hunting based on probabilities for harvesting geese. If hunters and landowners are willing to coordinate the goose hunting at a landscape level, they can use the large-scale spatial hunting organisation to plan their activity, with the likely benefit that they collectively harvest geese sustainably in the long-term. Such

local and regional organisation can become a powerful tool in the management of goose harvest.

Acknowledgements —We thank landowners and hunters at the two study areas for making their land accessible for the study and contributing with data on hunting activities. We especially acknowledge Ove Martin Gundersen, Lars Waade (Skogn), Olav-Arne Gilstad, John Bakken and Ole Jørstad (all Nesset). We would also like to thank a number of field assistants for help, in particular Ove Martin Gundersen, Paul Shimmings, Conny and Frank Høj Jensen, Jens Korsgaard Skriver and Tore Reinsborg. The authors declare that they have no conflict of interest.

Funding – This study was financed by the Norwegian Research Council (project GOOSEHUNT), Aarhus University, the County Governor in Nord-Trøndelag, the Fram Centre in Tromsø (Terrestrial Flagship) and the Trygve Gotaas Foundation.

References

- Amano, T. et al. 2006. Foraging patch selection and departure by non-omniscient foragers: a field example in white-fronted geese. Ethology 112: 544–553.
- Bregnballe, T. and Madsen, J. 2004. Tools in waterfowl reserve management: effects of intermittent hunting adjacent to a shooting-free core area. Wildl. Biol. 10: 261–268.
- Bruggers, R. L. et al. 2002. Wildlife damage management research needs: perceptions of scientists, wildlife managers, and stakeholders of the USDA/Wildlife Services program. Int. Biodeterior. Biodegrad. 49: 213–223.
- Chudzinska, M. et al. 2013. Diurnal variation in the behaviour of the pink-footed goose *Anser brachyrhynchus* during the spring stopover in Trøndelag, Norway. J. Ornithol. 154: 645–654.
- Drent, R. H. et al. 1980. Balancing the energy budgets of Arctic-breeding geese throughout the annual cycle: a progress report.
 Verh. Orn. Ges. Bayern 23: 239–264.
- Dunning, J. B. 1995. Spatially explicit population models: current forms and future uses. Ecol. Appl. 5: 3–11.
- Ebbinge, B. S. 1991. The impact of hunting on mortality-rates and spatial-distribution of geese wintering in the western Palearctic. Ardea 79: 197–209.
- ESRI 2013. ArcGIS Desktop: rel. 10.2. Redlands CA.
- Fielding, A. H. and Bell, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/ absence models. Environ. Conserv. 24: 38–49.
- Fox, A. D. et al. 2005. Effects of agricultural change on abundance, fitness components and distribution of two Arctic-nesting goose populations. Global Change Biol. 11: 881–893.
- Fox, A. D. et al. 2010. Current estimates of goose population sizes in western Europe, a gap analysis and an assessment of trends. Ornis Svec. 20: 115–127.
- Gill, J. A. 1996. Habitat choice in pink-footed geese: quantifying the constraints determining winter site use. J. Appl. Ecol. 33: 884–892.
- Guisan, A. and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. – Ecol. Modell. 135: 147–186
- Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8: 993–1009.
- Guisan, A. et al. 2013. Predicting species distributions for conservation decisions. Ecol. Lett. 16: 1424–1435.
- Hansson, L. and Angelstam, P. 1991. Landscape ecology as a theoretical basis for nature conservation. – Landscape Ecol. 5: 191–201.

- Jensen, R. A. et al. 2008. Prioritizing refuge sites for migratory geese to alleviate conflicts with agriculture. – Biol. Conserv. 141: 1806–1818.
- Jensen, G. H. et al. 2016a. Hunting migratory geese: is there an optimal practice? Wildlife Biol. 22: 194–203.
- Jensen, G. H. et al. 2016b. Environmental factors affecting numbers of pink-footed geese *Anser brachyrhynchus* utilising an autumn stopover site. – Wildlife Biol. 22: 183–193.
- Johnson, F. A. et al. 2014. Adaptive harvest management for the Svalbard population of pink-footed geese. 2014 progress summary. – DCE – Danish Centre for Environmental Research, Aarhus Univ.
- Jonker, R. M. et al. 2010. Predation danger can explain changes in timing of migration: the case of the barnacle goose. – PLoS ONE 5(6): e11369
- Keller, V. E. 1991. The effect of disturbance from roads on the distribution of feeding sites of geese Anser brachyrhynchus, Anser anser, wintering in northeast Scotland. – Ardea 79: 228–231.
- Klaassen, M. et al. 2006. Modelling behavioural and fitness consequences of disturbance for geese along their spring flyway. J. Appl. Ecol. 43: 92–100.
- Madsen, J. 1985. Impact of disturbance on field utilization of pink-footed geese in West Jutland, Denmark. Biol. Conserv. 33: 53–63.
- Madsen, J. 1995. Impacts of disturbance on migratory waterfowl. Ibis 137: S67–S74.
- Madsen, J. and Williams, J. H. 2012. International species management plan for the Svalbard population of the pink-footed goose *Anser brachyrhynchus*. – AWEA Technol. Rep. No. 48. African–Eurasian Waterbird Agreement, Bonn, Germany.
- Madsen, J. et al. 1999. Pink-footed goose Anser brachyrhynchus: Svalbard. – In: Goose populations of the western Palearctic. A review of status and distribution. Wetlands Int. Publ., Wetlands Int., Wageningen, the Netherlands, Natl Environ. Res. Inst., Rønde, Denmark, pp. 344.
- Morris, D. W. 2003. How can we apply theories of habitat selection to wildlife conservation and management? Wildl. Res. 30: 303–319.
- Owen, M. et al. 1987. The use of the Solway Firth, Britain, by barnacle geese *Branta leucopsis Bechst.* in relation to refuge establishment and increases in numbers. Biol. Conserv. 39:
- Patterson, I. J. 2013. Goose distribution in relation to SPAs in Grampian. – Scott. Natural Heritage Commissioned Rep. No. 546.
- Petitpierre, B. et al. 2012. Climatic niche shifts are rare among terrestrial plant invaders. Science 335: 1344–1348.
- Rees, E. C. et al. 2005. Factors affecting the behavioural responses of whooper swans *Cygnus c. cygnus* to various human activities. Biol. Conserv. 121: 369–382.
- Rosin, Z. M. et al. 2012. Landscape structure, human disturbance and crop management affect foraging ground selection by migrating geese. – J. Ornithol. 153: 747–759.
- migrating geese. J. Ornithol. 153: 747–759.
 Sanderson, E. W. et al. 2002. A conceptual model for conservation planning based on landscape species requirements. Landscape Urban Planning 58: 41–56.
- Si, Y. et al. 2011. Distribution of barnacle geese *Branta leucopsis* in relation to food resources, distance to roosts, and the location of refuges. Neth. Ornithol. Union 99: 217–226.
- Simonsen, C. E. 2014. Goose/agricultural conflicts in Norway building species distribution models: objective tools in local management when allocating subsidies and evaluations on scaring cost effectiveness. Aarhus Univ.
- Stephens, P. A. et al. 2014. Capital and income breeding: the role of food supply. Ecology 95: 882–896.

- Thuiller, W. et al. 2005. Niche properties and geographical extent as predictors of species sensitivity to climate change. Global Ecol. Biogeogr. 14: 347–357.
- Tilman, D. et al. 2001. Forecasting agriculturally driven global environmental change. Science 292: 281–284.
- Tombre, I. M. et al. 2009. Jakt på kortnebbgjess i Nord-Trøndelag 2008. En evaluering og forslag til fremtidig forvaltningspraksis. – NINA Rep. 431 (in Norwegian with English summary).
- Tombre, I. M. et al. 2013. Towards a solution to the goose–agriculture conflict in north Norway, 1988–2012: the interplay between policy, stakeholder influence and goose population dynamics. PLoS ONE 8: e71912.
- Van Eerden, M. R. et al. 1996. The response of Anatidae to changes in agricultural practice: longterm shifts in the carrying
- Supplementary material (available online as Appendix wlb-00192 at <www.wildlifebiology.org/appendix/wlb-00192>). Appendix 1–7.

- capacity of wintering waterfowl. Gibier Faune Sauvag. 13: 681–706.
- van Roomen, M. and Madsen, J. 1992. Waterfowl and agriculture: review and future perspectives of the crop damage conflict in Europe. IWRB Spec. Publ. No. 21. Int. Waterfowl and Wetlands Research Bureau.
- Vickery, J. A. and Gill, J. A. 1999. Managing grassland for wild geese in Britain: a review. Biol. Conserv. 89: 93–106.
- Wisz, M. et al. 2008. Modelling pink-footed goose Anser brachyrhynchus wintering distributions for the year 2050: potential effects of land-use change in Europe. – Divers. Distrib. 14: 721–731.
- Zheng, B. and Agresti, A. 2000. Summarizing the predictive power of a generalized linear model. Stat. Med. 19: 1771–1781.