UNIVERSITY OF
GLOUCESTERSHIRE

PLEASE SCROLL DOWN FOR TEXT.

Prediction of the distribution of Arctic-nesting pink-footed geese under a warmer climate scenario

RIKKE A. JENSEN *, JESPER MADSEN *, MARK O'CONNELL w, MARY S. WISZ*, HANS TØMMERVIK z and FRIDTJOF MEHLUM § 2

*Department of Arctic Environment, National Environmental Research Institute, University of Aarhus, Frederiksborgvej 399, PO Box 358, DK-4000 Roskilde, Denmark, wDepartment of Biology and Biochemistry, University of Bath, Claverton Down, Bath, BA2 7AY, zDivision of Arctic Ecology, Norwegian Institute for Nature Research, The Polar Environmental Centre, N-9296 Troms, Norway, §Natural History Museum, University of Oslo, PO Box 1172, Blindern, N-0318 Oslo, Norway

Abstract

Global climate change is expected to shift species ranges polewards, with a risk of range contractions and population declines of especially high-Arctic species. We built species distribution models for Svalbard-nesting pink-footed geese to relate their occurrence to environmental and climatic variables, and used the models to predict their distribution under a warmer climate scenario. The most parsimonious model included mean May temperature, the number of frost-free months and the proportion of moist and wet moss-dominated vegetation in the area. The two climate variables are indicators for whether geese can physiologically fulfil the breeding cycle or not and the moss vegetation is an indicator of suitable feeding conditions. Projections of the distribution to warmer climate scenarios propose a large north- and eastward expansion of the potential breeding range on Svalbard even at modest temperature increases (1 and 2°C increase in summer temperature, respectively). Contrary to recent suggestions regarding future distributions of Arctic wildlife, we predict that warming may lead to a further growth in population size of, at least some, Arctic breeding geese.

Correspondence: Rikke A. Jensen, tel. 145 46301940, fax 145 45301914, e-mail: raj@dmu.dk
1 Present address: Hartpury College, University of West England, GL19 3BE Gloucestershire, UK.
2 Present address: Research Council of Norway, PO Box 2700, St Hanshaugen, N-0131 Oslo, Norway.

Introduction

Global climate change is predicted to have strong effects on the distribution and abundance of Arctic animal and plant populations. Ranges of individual species may move polewards, expand or decline in extent, and in mountain areas, move towards higher elevations (Boyd & Madsen, 1997; Parmesan et al., 1999; Thomas & Lennon, 1999; Hickling et al., 2006). Particularly in the high-Arctic regions and islands where the range of species is limited by the Arctic ocean, it is predicted that effects will be mostly negative because the habitats of tundra living species will be squeezed by higher vegetation (Zöckler & Lysenko, 2000; ACIA, 2005).

Migratory, Arctic-nesting birds have a narrow time window for breeding, moulting and preparation for return migration between the time of thaw and before the Arctic winter sets in. The northern limits of breeding range are largely determined by the minimum period physiologically required to complete the breeding cycle (e.g. Newton, 1977), provided that suitable habitat is present. In Svalbard, nesting goose species (i.e. the brent goose, Branta bernicla, barnacle goose, Branta leucopsis and pink-footed goose, Anser brachyrhynchus), arrive late May to early June and

migrate south around mid September, a period of <4 months which coincides with the time of frost-free and snow-free conditions (Prop & De Vries, 1993; Madsen et al., 1998). Their timing and success of breeding are highly variable, depending on snow and ice conditions on arrival, summer and premigratory weather conditions (Owen & Black, 1989; Prop & De Vries, 1993; Madsen et al., 2007). The size of all three Svalbard goose populations has increased in recent decades. In barnacle and pink-footed geese, the proportions of successful breeding pairs and brood sizes have declined with increasing population sizes (Trinder et al., 2005; M. Trinder & J. Madsen, unpublished data), suggesting that density-dependent factors are now affecting their productivity. In barnacle geese, the available area for brood rearing appears to be a limiting factor (Drent et al., 1998). In pink-footed geese, it is more likely that availability of suitable nest sites is limiting (Madsen et al., 2007), possibly in combination with availability of spring staging feeding habitat in which the geese gain body reserves of critical importance for the subsequent breeding success.

The growing goose populations give rise to management concerns in their wintering range due to conflicts with agriculture (e.g. Van Eerden et al., 1996) and, increasingly, in the Arctic due to potential grazing effects on the fragile tundra ecosystems (e.g. Loonen & Solheim, 1998; Abraham et al., 2005; Van der Wal et al., 2007). Therefore, to inform management about the expected future directions of these conflicts, it is important to assess the impacts of warming of the Arctic. We examine whether warming will have a pronounced effect on the potential breeding range of the geese in the Svalbard archipelago compared with their present distribution, focussing on the pink-footed goose which has the widest distribution of the three species. A landscape based nesting habitat suitability model (resolution 15 m) for a central part of its breeding range showed that pink-footed geese prefer to nest on south facing slopes in the lowland, in close connection to suitable feeding sites which are wet moss-dominated areas (Wisz et al., in press). Upscaling the model to cover entire Svalbard (resolution 1 km), we hypothesize that at the regional scale the present distribution of pink-footed geese is determined by (1) the length of the season with frost-free conditions, which sets the limit for whether geese can physiologically fulfil the breeding cycle or not, (2) the temperature in May which indicates availability of areas providing geese with early feeding and nesting opportunities, (3) suitable feeding habitats and (4) elevation.

Based on the present potential distribution, we predict future distributions of pink-footed geese under a warmer climate scenario.

Materials and methods

Study population

The Svalbard-breeding population of the pink-footed goose winters in Denmark, the Netherlands and Belgium, with autumn and spring stopover sites in Norway. The population has increased from approximately 15 000 individuals in the 1960s to more than 50 000 in 2003 (Fox et al., 2005). The pink-footed goose breeds in loosely aggregated colonies, mainly along the west coast and in the interior lowlands of the western parts of Svalbard. It breeds on small islands, as well as on the open tundra, being capable of defending its nest against avian predators, as well as Arctic foxes, *Alopex lagopus* (Mehlum, 1998).

Spatial data layers

For modelling the potential distribution of nesting pinkfooted geese, we used known presence of nests, environmental and climatic predictors. Our sample units consist of grid cells of 926.6 m by 926.6 m. For simplicity we refer to these as grid cells of 1 km^2. As large parts of Svalbard is covered with glacier (approximately 55 000 km^2) only cells with no glacier were considered in the analysis.

This area consists of 10 498 cells. Areas disturbed by human activity are included in the analysis, but their extent is negligible compared with the total area.

Nest records. Data were derived from: (1) The database of the Norwegian Polar Institute with records from 1962 to 1996. Only data with geographical coordinates and records of nests were used, whereas records of broods were not used. The accuracy of the coordinates is generally within 1 km^2. (2) Recent nest surveys in different parts of Nordenskiöldland: (a) Sassendalen in the interior of Isfjorden, 2003–2004 (Wisz et al., in press); (b) Nordenskiöldkysten, 2004 (J. Prop, unpublished data), (c) Reindalen, 2004 (J. U. Jepsen, unpublished data); (d) Vårsolbukta, 2004 (C. Hübner, unpublished data) and (e) Adventdalen, 2004 (D. Kuijper, unpublished data) (Fig. 1). In the recent studies, nest positions were recorded with a GPS with an accuracy of c. 50 m.

From these sources 692 nest records and accurate coordinates could be derived. After relating these to a 1 km^2 grid and assigning one presence record for each cell containing one or more nests, 111 records of nest presences were available for analysis.

Vegetation. A vegetation cover map with four major classes relevant for geese was developed for entire Svalbard, based on Landsat Thematic Mapper with a 28 m spatial resolution (H. Tømmervik, in preparation, see Wisz et al., in press). The relevant classes are (1) dry heath dominated by *Dryas octopetala*, *Cassiope tetragona* and *Carex* spp., (2) bare ground with sparsely vegetated patches dominated by *Saxifraga oppositifolia*, (3) moist moss dominated fen with mixed coverage of
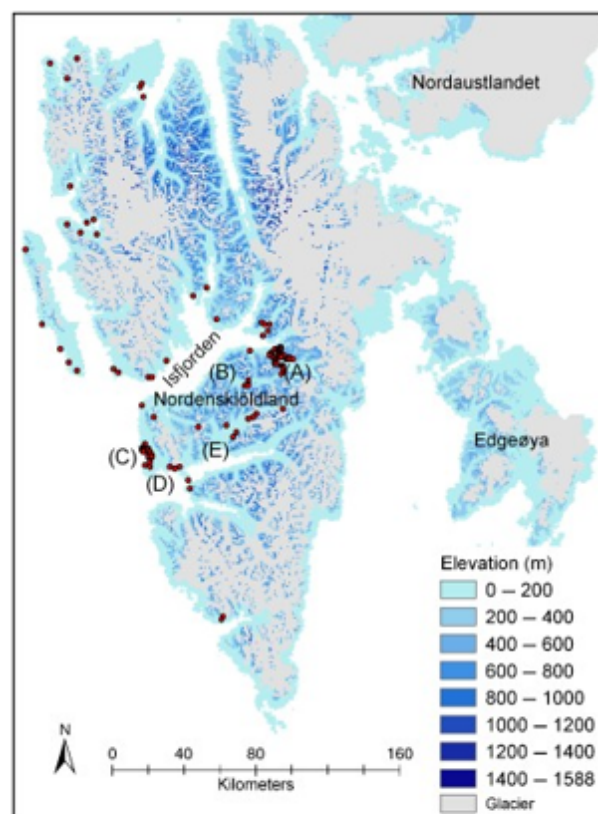

Fig. 1 Elevation map of Svalbard with pink-footed goose nest presences shown by red dots. Localities where detailed nest surveys were carried out: (a) Sasssendalen, (b) Adventdalen, (c) Nordenskiöldkysten, (d) Vårsolbukta, (E) Reindalen.

Bistorta vivipara, Salix polaris, Equisetum spp., *Eriophorum* spp. and *Carex* spp. and (4) wet moss carpet, dominated by mosses and *Dupontia* spp. For the purpose of the present analysis, we only used the area of moist- and wet moss-dominated habitat, expressed as proportion for each 1 km^2 grid cell, which is the preferred feeding habitat during the prenesting and nesting period and a significant predictor in the landscape nest site model (Wisz et al., in press). Nest presences were observed at proportions of moist/wet moss in a range from 0.0 to 0.85.

Elevation. A digital elevation model DEM with a 20 m spatial resolution was made available for the project from the Norwegian Polar Institute (Fig. 1). From this map mean elevation was calculated in the coarser resolution of 1 km^2 grid cells. Elevation was a significant predictor in the landscape nest site model (Wisz et al., in press). Nest presences were observed at elevations ranging from 0 to 632m.

Surface temperature. We used MODIS satellite imager-derived land surface temperature and emissivity (Friedl et al., 2002; Petitcollin & Vermote, 2002) at a spatial resolution of 1 km^2 grid cells. We chose a temporal resolution averaging values across the middle 8 days of each month. Monthly temperature values for the years 2001–2004 were obtained, and subsequently reprojected using bespoke MODIS data manipulation tools (USGS EROS Data Center, 2002). Pixel values were averaged across all available years (two to four) to create a single mean monthly value (to nearest 0.5°C) for each 1 km^2 grid cell over the entire area of Svalbard (Fig. 2). Thus, a frost-free month is defined as a month where the average temperature across the middle 8 days is above 0°C. The cells with three frost-free months are concentrated along the west coast, in the valleys that debouch into the western fiords and in the western lowlands of Edgeøya. Nordenskiöldland has some of the largest continuous areas with three or four frost-free months. Nest presences were observed in cells with a
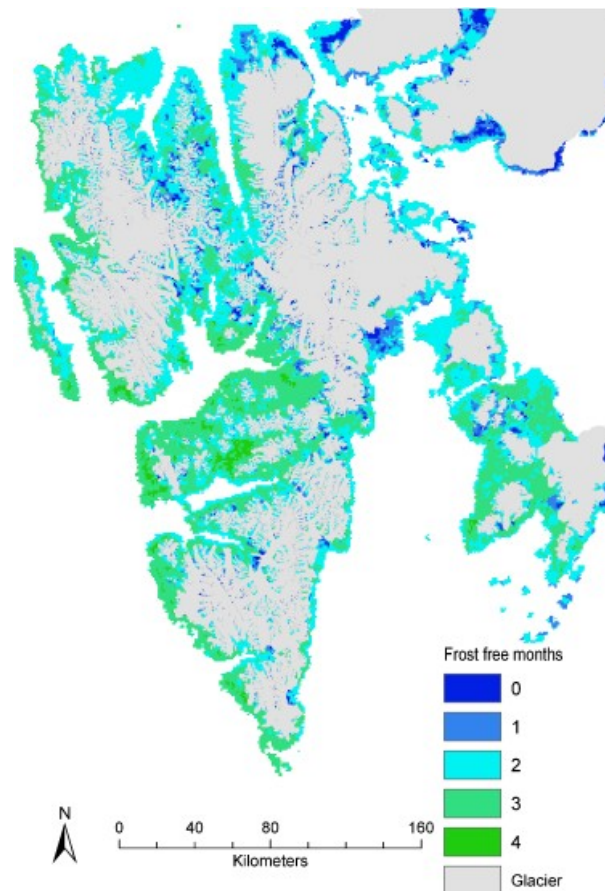
Fig. 2 Current surface map of frost-free months on Svalbard.

mean May temperature ranging from -8.87 to -1.59°C, and in areas with two to four frost-free months. Very few nest records were recorded in areas with two frost-free months.

Future climate scenarios. Future distributions of pink-footed geese are predicted using an increase of the mean May temperature of 1 and 2°C, respectively, and an increase of the frost-free period derived from a scenario where the mean temperatures of May, June, July, August and September, are elevated by 1 and 2°C, respectively. These scenarios are supported by the temperature increase predicted by Førland et al. (2004), who downscaled a temperature scenario (based on ECHAM4/OPYC3 AOGCM with the transient GSDIO integration), predicting that in 2050 the mean summer temperatures at Svalbard airport in the central part of Isfjorden will have increased approximately 1°C compared with the 1961–1990 normal period and that this will cause an increase of 2 months for the frost-free period. Our predictions for the warmer climate scenarios do not take into account that glaciers are likely to decrease in size and expose new potential nest sites.

Modelling framework

We used generalized additive models (GAM) (Hastie & Tibshirani, 1990) to model the probability of finding pink-footed goose nests within the 1 km^2 grid cells as a function of four environmental predictors (all continuous variables): number of frost-free months, mean May temperature (°C), proportion of moist/wet moss vegetation cover and elevation (m). Unlike regression models, GAMs do not force a parametric relationship (e.g. linear, parabolic, etc.) between the response and the predictors. Instead, GAMs implement nonparametric smoothers in regression models. GAMs have been shown to be particularly useful in modelling species distributions (e.g. Austin, 2002; Elith et al., 2006) because the smoothing functions can describe the complex nonlinear relationships often seen in ecology (e.g. Guisan & Zimmermann, 2000). The statistical analysis was performed in R 2.2.0 statistical software (http:// www.R-project.org), using the GRASP v2.5 library (Lehmann et al., 2002) for R. We used a binomial error family with a logit link function. Predictions to the entire Svalbard archipelago were calculated in R and illustrated on maps using ArcGIS 9.2.

Statistical methods

GAM procedures require absences, as well as presences for inference, so we computed so-called pseudo-absences randomly from the background area not covered by glacier. The pseudo-absences were not intended as a sample of sites with true absences but as a sample of all sites potentially available to nesting geese in Svalbard. Because of the random procedure, pseudo-absences may coincide with observed presences. Pseudo-absence records along with presence records have been widely used as a reliable surrogate for true presence/absence data (e.g. Ferrier et al., 2002; Elith et al., 2006). We generated 10 times more pseudo-absence records than the number of presences in order to ensure sufficient landscape variety in the pseudo-absences. To ensure that the presences and pseudo-absences contributed equally to the model and to avoid bias towards the larger sample (Sokal & Rohlf, 1995), we weighted each pseudo-absence as 1/10 in the model. Model selection was based on Akaike's Information Criterion (AIC), by backwards model simplification, dropping terms from the full model. Smoothing parameters were also selected using AIC.

To account for spatial auto-correlation in the data, we also fitted a model that included all the environmental predictors and an auto-covariate. This method is recommended by Augustin et al. (1996) to avoid inflation of the significance of the selected predictors. In our study the auto-covariate was the sum of the eight nearest neighbouring cells where nests have been recorded. The inclusion of the auto-covariate did not change the selected predictors, nor did it seem to inflate their significance. Model performance was slightly better than the model without the auto-covariate, and

we concluded that spatial auto-correlation did not seriously inflate the significance of the selected predictors, and we do not address the subject further in this analysis.

Model evaluation

To assess the amount of deviance the model could explain, we used D^2, defined as D^2 = (null deviance − residual deviance)/null deviance. This measure is equivalent to the R^2 value known from ordinary regression (Guisan & Zimmermann, 2000). In order to evaluate the overall predictive performance of our model, we examined the model's ability to discriminate between occupied and unoccupied sites and the reliability with which it predicts the probability of a site being occupied.

To assess our model's discriminatory ability, we calculated the threshold-independent Area Under the Receiver Operating Characteristic Curve (AUC) (e.g. Pearce & Ferrier, 2000). The Receiver Operating Characteristic Curve (ROC) is plotted on a unit square as sensitivity against (1- specificity) for a range of increasing threshold values. Sensitivity is defined as the proportion of sites correctly predicted to be occupied out of the total number of occupied sites in the sample. Specificity is defined as the proportion of sites correctly predicted to be unoccupied out of the total number of unoccupied sites in the sample. The AUC describes the discrimination capacity ranging from 0.5 for models with no discrimination ability, to 1 for a model with perfect discrimination (Pearce & Ferrier, 2000). An AUC score between 0.8 and 0.9 indicates good discrimination capacity, and above 0.9 an excellent discrimination capacity (Thuiller et al., 2005). We assessed the predictive reliability, also known as calibration (Pearce & Ferrier, 2000), using the correlation coefficient (COR) describing the simple correlation between the observed and predicted response, as recommended by Zheng & Agresti (2000).

AUC and COR was calculated from a cross-validation based on five randomly selected subsets of the entire dataset. Each subset contained 20% of the data points. The subsets were dropped from the model one at a time, and the model was refitted to the remaining 80% of the data and finally predictions were made for the omitted data points.

The threshold, discriminating between predicted occupied and unoccupied sites, was set by calculating the maximum (k) (Cohen, 1960). k is a measure of agreement, considering both omission and commission errors (Elith et al., 2006) and is useful for setting a nonarbitrary threshold for the predicted response.

Results

The most parsimonious GAM model incorporated mean May temperature, number of frost-free months, and proportion of moist and wet moss vegetation (Table 1). Elevation was not selected by the model. The probability of nest occurrence increased with number of frost-free months (Fig. 3a) and with mean May temperature (Fig. 3b). Probability of nest occurrence also increased with increasing moist and wet moss vegetation coverage (Fig. 3c). The confidence intervals around the additive contribution of each predictor suggest that the increase in the response was significant for all the selected predictors (Fig. 3d–f). The model had a reasonable fit to the data as D^2 was 0.34, indicating that we can explain 34% of the total deviance. AUC was 0.86, indicating that the model predicts higher where the species is present than where it is absent in 86% of the locations used for predictions. The model was well calibrated as the COR for the cross-validation was 0.42 (P<0.001).

We calculated the maximum (k) to be 0.75. This was used as the objective threshold, when discriminating between occupied and unoccupied areas from the predictions.

Table 1 Table of the predictors for nest distribution of the pink-footed goose in Svalbard and specifications of the selected model, based on 111 nest presences and 1110 pseudoabsences

	Smoothing	
	df	*p*
Predictors		
Mean May temperature	1	0.014
Number of frost-free months	1	<0.001
Proportion of wet and moist moss vegetation	1	0.039
Elevation	Not selected	
Specifications		
Null deviance		308
Explained deviance		104
D2		0.34
AUC		0.86
COR		0.41

Null deviance is the total amount of deviance in the sample and explained deviance is the amount which can be accounted for by the model. D^2 is the proportion of deviance explained by the model. AUC is the Area Under the Receiver Operating curve and COR the simple correlation between observed and predicted values.

The predicted suitable nesting areas, under the current conditions, exist in the lowlands on the southwest coast of Svalbard, in some of the valleys debouching into the western fjords, as well as in the western part of Edgeøya in the southeast of Svalbard (Fig. 4a).

The predicted distribution under the 1°C increase in mean summer temperature scenario shows that there is a marked increase in possible nest site areas compared to the current distribution (Fig. 4b). Using the k of 0.75 as the critical threshold, a large part of the west coast is pointed out as suitable nesting area, as are several of the valleys that debouch into the western fjords. Under the 2°C increase scenario (Fig. 4c), most of the west coast and the majority of the western valleys are predicted to be suitable for nesting. Compared with the present potential distribution, which is approximately 1950 km², the suitable nesting area is predicted to increase by 84% and 217% under the 1 and 2°C scenario, respectively.

Discussion

Climate has a profound effect on species distributions, and our results show that this also applies for the distribution of pink-footed geese. Their current nesting distribution appears to be limited by climatic factors, (i.e. the number of frost-free months combined with early snow melt), which are
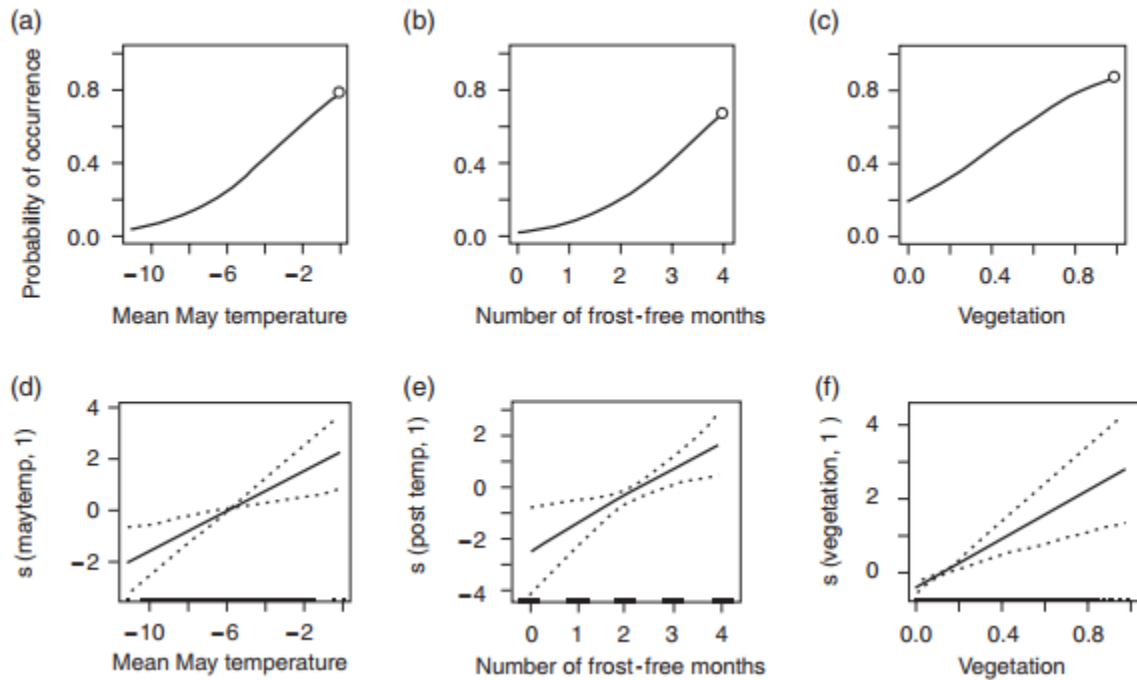
Fig. 3 Response curves from the generalized additive models (GAM) based on the 111 nest presences and 1110 pseudo-absences. (a–c): Probability of nest occurrence as a function of the selected predictor variables. The functions are generated by setting the contribution of all predictors in the model to 0, except for the predictor in question. (d–f): GAM response curves of the probability of nest occurrence as a function of the selected predictors where the y-axis can be interpreted as a transformation of the response. The GAM curves show the additive contribution of each variable to the response. Dashed lines are twice-standard-error curves. The black markings on the x-axis show observations of the predictor in question.

indicators of the physiological requirements of successfully breeding geese, and availability of suitable feeding habitat. Under scenarios of even modest warming, the range of the species is likely to increase substantially due to a north- and eastward expansion. From this analysis we cannot conclude that that range of the species will increase altitudinal because elevation is not selected as an important predictor variable in our model. Wisz et al. (in press) documented the effect of elevation on a finer scale, and we find it likely that suitable nesting areas may become available at higher altitudes as the temperature increase. Some possible limitations of nesting at higher altitudes may, however, exist due to wind exposure and longer travelling distances from nest to brood rearing areas along the coasts, lakes and rivers, increasing the risk of predation.

Although our model shows good fit and discriminatory ability, additional uncertainties arise when making predictions into the future (Araújo et al., 2005). First, in predictive habitat distribution models, species distributions are assumed to be in equilibrium with the conditions present during the sampling period (Guisan & Thuiller, 2005). This requires that the environment has not undergone dramatic changes in recent time, and thus it is a postulate that the current distribution reflects the current environmental conditions. In support of the equilibrium assumption, historical records of the breeding areas of pink-footed geese indicate that the range and key nesting areas have not changed from the 1960s to the 1990s (Mehlum, 1998), in spite of a threefold increase in population size. If the distribution of the pink-footed goose is not in equilibrium, our predictions may be an underestimate of the true potential range (Guisan & Thuiller, 2005).

Second, effects of predictor variables can be confounded with interactions between species and in consequence bias predictions into the future (Loehle & Leblanc, 1996). An increase in numbers of pink-footed geese may potentially lead to increased competition for resources with

barnacle geese. However, the two species partly occupy different niches and show different feeding habits and food plant selectivity when occurring sympatrically (Madsen & Mortensen, 1987; Fox & Bergersen, 2005; Fox et al., 2007). Hence, we expect that competitive interactions between the two species are not likely to affect substantially the overall distribution of the two species in Svalbard.

Third, predicting species distributions should be restricted to be inside the ranges of the observed predictor variables, because information lack about responses outside those ranges
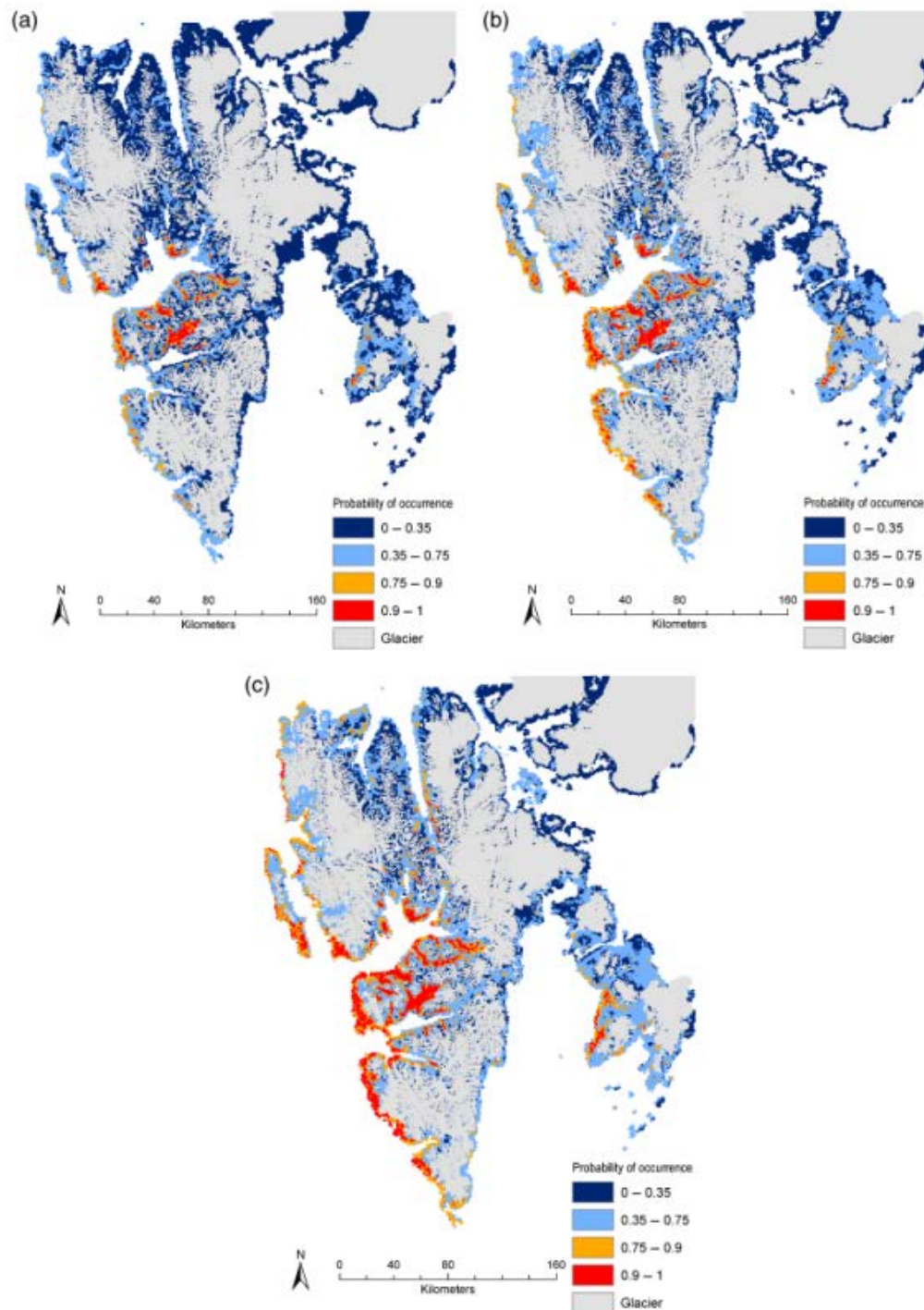
Fig. 4 Predicted nesting distribution of pink-footed geese in Svalbard: (a) at present, (b) under the 1 1 1C, and (c) under the 1 2 1C mean-summer temperature climate scenario, respectively.

(Thuiller et al., 2004). However, in this study we make predictions to areas that go beyond the observed ranges from the data. By increasing mean May temperatures by 1°C a large part of the coastal area on Svalbard will have a mean May temperature above -1.59°C which is the highest observed temperature where nests have been reported. We have no doubt that the warming will generally have a positive effect on habitat suitability for the geese and we believe that the exclusion of the areas outside the temperature range would be more confounding to the analysis than retaining them in the predictions. The area with frost-free months, proportion of moist/wet moss vegetation or elevation outside observed ranges is negligible (at +2°C nest presences were predicted in 159 cells with 5 frost-free months, 15 cells outside the elevation range, and 219 cells outside the vegetation range) and we do not find it necessary to exclude these from the analysis.

Fourth, the absence of important predictor variables in a model may lead to unrealistic predictions. Snow cover at the time of egg laying is a controlling factor of the distribution of geese (Prop & De Vries, 1993; Lepage et al., 1996; Madsen et al., 2007). Data on snow coverage for the entire Svalbard are not available and our closest approximation is the mean May temperature.

Fifth, in this analysis we have not considered potential climate change effects on vegetation types and primary production. It is expected that increased temperatures will lead to changes in plant community composition (polar deserts will be displaced to some extent by northward and altitudinal movement of the tundra), increase in biomass and primary production as well as drying out of wet habitats (Callaghan, 2005). It is reasonable to expect that such changes will be beneficial for the geese. In East Greenland and Iceland, pink-footed geese nest in sub and low Arctic environments (Mitchell et al., 1999). Furthermore, during recent decades, barnacle geese have successfully spread from Arctic north Russia into the temperate Baltic Sea area (Ganter et al., 1999) and pink-footed geese have spread from the highlands into the lowlands in Iceland (Mitchell et al., 1999). These examples show that goose species adapted to Arctic conditions may possess the phenotypic flexibility to exploit very successfully areas with different plant phenologies and food plant qualities (Van der Graaf et al., 2006).

Conclusions

Contrary to recent suggestions regarding effects of global warming on Arctic wildlife (ACIA, 2005) we predict that even modest temperature increases will have a positive effect on the suitability of Svalbard for nesting geese in terms of range expansion into the northern and eastern parts of Svalbard which are currently unsuitable. Hence, it is possible that increased temperatures could release the population from the suggested present density-dependent regulation during the nesting period. Furthermore, an elongation of the frost-free season in Svalbard may relax their dependence on the acquisition of body stores before arrival (so-called 'capital' breeding, *sensu* Drent & Daan, 1980), so that geese will have more time to acquire the necessary resources upon arrival and still breed successfully. Both factors are likely to have a positive effect on the population growth. Future assessments of effects of climate impacts on Arctic species should combine analyses of ecologically founded spatial predictions and population dynamics.

Acknowledgements

References

Abraham KF, Jefferies RL, Alisauskas RT (2005) The dynamics of landscape change and snow geese in mid-continent North America. Global Change Biology, 11, 841–855.

ACIA (2005) Arctic Climate Impact Assessment. Cambridge University Press, New York.

Araújo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species-climate impact models under climate change. Global Change Biology, 11, 1504–1513.

Augustin NH, Mugglestone MA, Buckland ST (1996) An autologistic model for the spatial distribution of wildlife. Journal of Applied Ecology, 33, 339–347.

Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecological Modelling, 157, 101–118.

Boyd H, Madsen J (1997) Impacts of global change on arcticbreeding bird populations and migration. In: Global Change and Arctic Terrestrial Ecosystems (eds Oechel WC, Callaghan T, Gilmanov T, Holten JI, Maxwell B, Molau U, Sveinbjo¨rnsson B), pp. 201–217. Springer-Verlag, New York.

Callaghan TV (2005) Arctic Climate Impact Assessment. Arctic Tundra and Polar Desert Ecosystems. Cambridge University Press, New York, pp. 243–352.

Cohen J (1960) A coefficient of agreement on for nominal scales. Educational and Psychological Measurement, 20, 37–46.

Drent RH, Black JM, Loonen MJJE, Prop J (1998) Barnacle geese Branta leucopsis on Nordenskio¨ldkysten, western Spitsbergen– in thirty years from colonisation to saturation. Norsk Polarinstitutt Skrifter, 200, 105–114.

Drent RH, Daan S (1980) The prudent parent: energetic adjustment in avian breeding. Ardea, 68, 225–252.

Elith J, Graham CH, Anderson RP et al. (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography, 29, 129–151.

Ferrier S, Watson G, Pearce J, Drielsma M (2002) Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling. Biodiversity and Conservation, 11, 2275–2307.

Fox AD, Bergersen E (2005) Lack of competition between barnacle geese (Branta leucopsis) and pink-footed geese (Anser brachyrhynchus) during the pre-breeding period in Svalbard. Journal of Avian Biology, 36, 173–178.

Fox AD, Bergersen E, Tombre I, Madsen J (2007) Intra-seasonal dietary overlap of barnacle and pink-footed geese on their breeding grounds in Svalbard. Polar Biology, 30, 759–768.

Fox AD, Madsen J, Boyd H, Kuijken E, Norriss DW, Tombre IM, Stroud DA (2005) Effects of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations. Global Change Biology, 11, 881–893.

Friedl MA, McIver DK, Hodges JCF et al. (2002) Global land cover mapping from MODIS: algorithms and early results. Remote Sensing of Environment, 83, 287–302.

Førland EJ, Skaugen TE, Benestad RE, Hanssen-Bauer I, Tveito OE (2004) Variations in thermal growing, heating, and freezing indices in Nordic Arctic, 1900–2050. Arctic, Antarctic, and Alpine Research, 36, 347–356.

Ganter B, Larsson K, Syroechkovsky EV, Litvin KE, Leito E, Madsen J (1999) Barnacle Goose Branta leucopsis: Russia/Baltic. In: Goose Populations of the Western Palearctic. A Review of Status and Distribution. Wetlands International Publication No. 48. Wetlands International, Wageningen, the Netherlands (eds Madsen J, Cracknell G, Fox AD), pp. 68–81. National Environmental Research Institute, Rønde, Denmark.

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecology Letters, 8, 993–1009.

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecological Modelling, 135, 147–186.

Hastie T, Tibshirani R (1990) Generalized Additive Models. Chapman and Hall, London.

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology, 12, 450–455.

Lehmann A, Overton JMcC, Leathwick JR (2002) GRASP: generalized regression analysis and spatial predictions. Ecological Modelling, 157, 189–207.

Lepage D, Gauthier G, Reed A (1996) Breeding-site infidelity in greater snow geese: a consequence of constraints on laying date? Canadian Journal of Zoology, 74, 1866–1875.

Loehle C, LeBlanc D (1996) Model based assessments of climate change effects on forests: a critical review. Ecological Modelling, 90, 1–31.

Loonen MJJE, Solheim B (1998) Does arctic vegetation change when grazed by barnacle geese? A pilot study. Norsk Polarinstitutt Skrifter, 200, 99–103.

Madsen J, Bregnballe T, Frikke J, Kristensen JB (1998) Correlates of predator abundance with snow and ice conditions and their role in determining timing of nesting and breeding success in Svalbard light-bellied brent geese (Branta bernicla hrota). Norsk Polarinstitutt Skrifter, 200, 221–234.

Madsen J, Mortensen CE (1987) Habitat exploitation and interspecific competition of moulting geese in East Greenland. Ibis, 129, 25–44.

Madsen J, Tamstorf M, Klaassen M, Eide N, Glahder C, Riget F, Nygaard H, Cottaar F (2007) Effect of snow cover on timing and reproduction in high-Arctic pink-footed geese Anser brachyrhynchus. Polar Biology, 30, 1363–1372.

Mehlum F (1998) Areas in Svalbard important for geese during the pre-breeding, breeding and post-breeding periods. Norsk Polarinstitutt Skrifter, 200, 41–55.

Mitchell CM, Fox AD, Boyd H, Sigfusson A, Boertmann D (1999) Pink-footed Goose Anser brachyrhynchus: Iceland/Greenland. In: Goose Populations of the Western Palearctic. A Review of Status and Distribution. Wetlands International Publication No. 48. Wetlands International, Wageningen, the Netherlands (eds Madsen J, Cracknell G, Fox AD), pp. 68–81. National Environmental Research Institute, Rnde, Denmark.

Newton I (1977) Timing and success of breeding in tundra nesting geese. In: Evolutionary Ecology (eds Stonehouse B, Perrins PM), pp. 113–126. Macmillan, London.

Owen M, Black JM (1989) Factors affecting the survival of barnacle geese on migration from the breeding grounds. Journal of Animal Ecology, 58, 603–617.

Parmesan C, Ryrholm N, Steefanescu C et al. (1999) Poleward shift in geographical ranges of butterfly species associated with regional warming. Nature, 399, 579–583.

Pearce JL, Ferrier S (2000) Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling, 133, 225–245.

Petitcollin F, Vermote EF (2002) Land surface reflectance, emissivity and temperature from MODIS middle and thermal infrared data. Remote Sensing of Environment, 83, 112–134.

Prop J, De Vries J (1993) Impact of snow and food conditions on the reproductive performance of barnacle geese (Branta leucopsis). Ornis Scandinavia, 24, 110–121.

Sokal RR, Rohlf FJ (1995) Biometry: The Principles and Practice of Statistics in Biological Research, 3rd edn. W.H. Freeman, New York.

Thomas CD, Lennon JJ (1999) Birds extend their ranges northwards. Nature, 399, 213.

Thuiller W, Brotons L, Arau´jo MB, Lavorel S (2004) Effects of restricting environmental range of data to project current and future species distributions. Ecography, 27, 165–172.

Thuiller W, Lavorel S, Arau´jo MB (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. Global Ecology and Biogeography, 14, 347–357.

Trinder M, Rowcliffe M, Pettifor R, Rees E, Griffin L, Ogilvie M, Percival S (2005) Commissioned Report No. 107 (ROAME No. F03AC302). Scottish Natural Heritage. Status and population viability analyses of geese in Scotland.

USGS EROS Data Center (2002) MODIS Reprojection Tool User's Manual. Department of Mathematics and Computer Science, South Dakota School of Mines and Technology, Reston, VA.

Van der Graaf AJ, Stahl J, Bakker JP, Drent RH (2006) Surfing on a green wave–How plant growth drives spring migration in the barnacle goose. Ardea, 13, 539–545.

Van der Wal R, Sjögersten S, Woodin SJ et al. (2007) Spring feeding by pink-footed geese reduces carbon stocks and sink strength in tundra ecosystems. Global Change Biology, 13, 1–7.

Van Eerden MR, Zijlstra M, Van Roomen M, Timmerman A (1996) The response of Anatidae to changes in agricultural practice: long-term shifts in the carrying capacity of wintering waterfowl. Gibier Faune Sauvage, 13, 681–707.

Wisz MS, Tamstorf M, Madsen J, Jespersen M (in press) Modelling potential distributions of nesting pink-footed geese (Anser brachyrhynchus) in western Svalbard. Diversity and Distributions, doi: 10.1111/j.1472-4642.2007.00408.x. Z

heng B, Agresti A (2000) Summarizing the predictive power of a generalized linear model. Statistics in Medicine, 19, 1771–1781.

Zöckler C, Lysenko I (2000) Water Birds on the Edge: First Circumpolar Assessment on Arctic Breeding Water Birds. WCMC Biodiversity Series No. 11. World Conservation Monitoring Centre, Cambridge, UK.