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Commissioned Report No. 362

Status and Population Viability of Greenland White-fronted Geese in Scotland

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Summary

Status and Population Viability of Greenland White-fronted Geese in Scotland

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Background
This report updates the demographic analysis and population modelling for the Greenland white-fronted goose population provided by Trinder et al. (2005). The Scottish population peaked in size in 1998 at 21,600 but has fallen steadily since then, reaching 13,000 in 2007.

Main findings

• The overall downward trend in the Scottish population has been reflected by the majority of Scottish flocks. The proportion of flocks which have peaked in size and since declined has increased since the previous PVA from one third to two thirds, accounting for 95% of the Scottish population.

• A moratorium on shooting was introduced in Iceland in 2006. In the preceding decade an average of 3,000 geese were shot in Iceland each autumn. Since the ban around 300 have been shot (illegally or accidentally) each year. A shooting ban was also introduced in Greenland in 2009. Prior to this around 100-200 were thought to have been shot illegally in Greenland each year, although no reliable records are available.

• A significant positive relationship between the average summer temperature on the breeding grounds and reproduction was identified. However, the average demographic rates for the last five years (2003-2007) have not changed significantly from those estimated using the preceding five years (1998-2002), as used for the previous PVA.

• Evidence for density-dependent regulation in this population is equivocal: using all years of data the proportion of breeding birds was negatively related to the population size. However in recent years the increase in breeding predicted by this relationship has not been seen.

• Two population models were developed. The first was a modified version of the density-dependent model developed by Trinder et al. (2005). The second model was density-independent, based on the recent low breeding rate.
• In both models, survival rates were adjusted to account for shooting, using data from the years 1995–2006, while the mean brood size was estimated from the whole time series (1982–2007). The proportion of breeders in the density-independent model was also adjusted to account for shooting and was estimated across the same span of years (1995-2006). The density-dependent model used the relationship between the proportion of breeding birds and the number of adults in the previous year, calculated across all years (1982-2007).

• The comparative fit of the two models to historical data was assessed to determine which provided the more reliable predictions.

• Neither model gave a significantly better fit to the historical population data than the other, although the density-independent model offered a slightly better fit to the known shooting data. Thus, both models were retained and used to generate predictions for the population resulting from possible future scenarios.

• In the absence of a return to recent shooting levels, both models predicted a slow recovery, with median population predictions reaching 25,000 to 30,000 within 25 years (density-dependent and independent, respectively).

• In contrast, if shooting returns to the previous level (c. 3,000pa, 60% of which winter in Scotland), all simulated populations from both models become extinct within 25 years.

• In order for more than 95% of simulated populations to have positive population growth, the density-dependent model predicted that no more than 500 additional birds could be shot each year (above the current illegal bag of approx. 500), while for 95% of density-independent simulations to have positive growth a further reduction in (illegal) shooting of 150 was necessary.

• Changes in breeding habitat availability due to competition with Canada geese (potential reduction) or climate change (potential increase) are also likely to affect the status of this population, although the extent to which either may occur is currently unknown.

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1. INTRODUCTION

The Greenland white-fronted goose (*Anser albifrons flavirostris*) is a discrete population of white-fronted geese which breeds along the western coast of Greenland, over-winters in the UK and Ireland and stages on migration in south-west Iceland in spring and autumn.

Few data were collected for this population prior to the initiation of the Greenland White-fronted Goose Study (GWGS) in 1982, although Ruttledge and Ogilvie (1979) estimated that the population had declined from around 17,500-23,000 in the 1950s to 14,300-16,600 in the 1970s. Between 1982 and 1998 the combined British and Irish population underwent sustained growth, doubling in size from 16,000 to over 35,000. Since then, however, the population has fallen, reaching 23,000 in the winter of 2007/08. The Scottish component of the population has followed a similar path, with a 2007 population estimate of just over 13,000 (Figure 1).

![Figure 1. Scottish population of Greenland white-fronted goose, best-fit trend line and Iceland shooting bag.](image)

This report presents analysis of the count and demographic data for the Scottish population, collected since 1982 by the GWGS, and summarises predictions obtained from population models developed using these data. This provides an update of the analysis by Trinder *et al.* (2005).
2. DATA AND METHODS

2.1 Demographic data

Wintering flocks of Greenland white-fronted geese are distributed widely across western Scotland. Counts have been collected at over 40 Scottish sites since 1982, although not all of these sites have retained geese for the entire period (Appendix 1). The geese are highly site faithful in winter (Norriss & Wilson 1988), thus counts made at this time can provide a good indication of the population size. At a subset of the Scottish sites the proportion of juveniles in the flocks and the average brood size have also been estimated. In combination, the count \((N)\), age-ratio \((PJ)\) and brood size \((BS)\) data permit calculation of estimates of annual survival \((CS)\) and the minimum proportion of adults needed to have bred \((PB)\) in order to account for the estimated number of young present in the flocks (see Appendix 2 for details). Combined estimates of the proportion of juveniles and mean brood size for the whole Scottish population were calculated from all the values recorded at the local sites, weighted by flock size. These combined mean rates were then used to estimate survival and the proportion of breeders for the Scottish population. The mean demographic rates for the most recent five year period (2003-2007), the preceding five years (1998-2002), and across all years (1982-2007) are provided in Table 1. None of the demographic rates have changed significantly from those reported in the previous PVA (Trinder et al. 2005).

<table>
<thead>
<tr>
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</thead>
<tbody>
<tr>
<td>Survival</td>
<td>0.87 (0.11)</td>
<td>0.85 (0.08)</td>
<td>0.88 (0.07)</td>
</tr>
<tr>
<td>Proportion juveniles</td>
<td>0.12 (0.04)</td>
<td>0.09 (0.01)</td>
<td>0.14 (0.05)</td>
</tr>
<tr>
<td>Mean brood size</td>
<td>3.37 (0.45)</td>
<td>3.47 (0.17)</td>
<td>3.37 (0.33)</td>
</tr>
<tr>
<td>Productivity</td>
<td>0.13 (0.06)</td>
<td>0.1 (0.02)</td>
<td>0.16 (0.07)</td>
</tr>
<tr>
<td>Proportion breeders</td>
<td>0.09 (0.03)</td>
<td>0.06 (0.01)</td>
<td>0.11 (0.05)</td>
</tr>
</tbody>
</table>

Greenland white-fronted geese have been protected from hunting in the UK and Ireland since 1982 (although small numbers were shot under licence at Wexford in Ireland in 1985 and 1989). However, until 2006 they were legal quarry in Iceland in the autumn, when a ban was introduced. Since 1995 Icelandic hunters wishing to renew their firearms licence have been required to report their previous year’s shooting bag. Prior to the ban, on average 3,300 geese were reported shot in Iceland each autumn (Figure 1). Hunters provide these data anonymously, and they are considered to be reliable (Frederiksen & Sigfusson, unpubl. report), which is supported by the fact that around 300 geese have still been reported shot in the two years since the ban. A small number are also thought to have been shot in Greenland each year prior to 2009 (approx. 100-200). A ban was introduced in Greenland in 2009, although no figures are available to indicate the extent to which this has been adhered to.

2.2 Relationships between demographic rates and Greenland climate

Reproductive success in Arctic breeding geese is strongly influenced by weather conditions experienced before and during breeding (e.g. Alisauskas 2002, Trinder et al. 2009). The brief Arctic summer requires geese to begin nesting as soon as conditions permit. Therefore, any delays, caused for example by a late spring thaw, can reduce
overall productivity (Madsen et al. 2007). Boyd and Fox (2008) found evidence for changing relationships between temperature and precipitation in Greenland in summer and the proportion of juveniles recorded on Islay and at Wexford (Ireland) in the following autumn, over the period 1968 and 2007. Using their analysis as a guide, we undertook a similar analysis on the data for the combined Scottish population for the period 1982-2007.

Two climate variables were tested: daily total precipitation for April and May (summed) and mean daily temperature between May and July (inclusive). Climate data were recorded at Kangerlussuaq (67°04'N, 50°42'W), which lies within the population’s breeding range.

Climate data frequently contain both inter-annual variability and long-term temporal trends. To minimise the risk of confounding long-term trends in the climate data with those in the demographic rates during analysis, both datasets were de-trended prior to analysis. This process removes long-term changes (trends) present in the data while retaining the between-year variability. In addition, prior to de-trending the spring precipitation data were square-root transformed in order to normalise the residuals.

Linear models were used to test for the presence of relationships between the de-trended demographic rates and the climate data. Once an acceptable fit for each initial model to the data had been determined (i.e. the residuals were confirmed as being normally distributed), model refinement was performed until only significant explanatory variables remained (at a significance of at least $\alpha<0.05$). All model fitting was conducted using R (http://www.R-project.org).

The proportion of juveniles, mean brood size and proportion of breeding birds were all significantly, positively related to the de-trended average summer temperature, while the proportion of juveniles and mean brood size were both significantly negatively related to the de-trended total spring precipitation (Table 2, Figure 2). There was no evidence for relationships between survival and either summer temperature or spring precipitation.

Table 2 – Significant relationships between de-trended Greenland summer temperature and spring precipitation and demographic rates for the Scottish population of Greenland white-fronted geese, 1982-2007

<table>
<thead>
<tr>
<th>Demographic rate</th>
<th>Explanatory variable</th>
<th>Coefficients (SE)</th>
<th>$F$</th>
<th>$p$</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proportion juveniles</td>
<td>Summer temperature</td>
<td>0.0244 (0.007)</td>
<td>11.9</td>
<td>0.002</td>
<td>0.3</td>
</tr>
<tr>
<td>Proportion juveniles</td>
<td>Spring precipitation</td>
<td>-0.015 (0.005)</td>
<td>7.5</td>
<td>0.01</td>
<td>0.21</td>
</tr>
<tr>
<td>Proportion breeders</td>
<td>Summer temperature</td>
<td>0.02 (0.0057)</td>
<td>12.5</td>
<td>0.002</td>
<td>0.32</td>
</tr>
<tr>
<td>Mean brood size</td>
<td>Summer temperature</td>
<td>0.145 (0.0053)</td>
<td>7.47</td>
<td>0.01</td>
<td>0.21</td>
</tr>
<tr>
<td>Mean brood size</td>
<td>Spring precipitation</td>
<td>-0.131 (0.034)</td>
<td>14.5</td>
<td>&gt;0.001</td>
<td>0.36</td>
</tr>
</tbody>
</table>

Since 1995 there has been an increase in spring snow cover on Greenland, associated with a shift towards positive values of the spring Atlantic Multidecadal Oscillation (AMO). Boyd and Fox (2008) suggested this has had a negative influence on reproduction due to the delaying effect of snow on the onset of breeding. It is worth noting that the values of a
long-term index such as this would be expected to switch back at some point in the future, which would manifest as reduced snow cover in spring and thus be expected to lead to an increase in reproduction.

![Graphs showing relationships between Greenland white-fronted goose reproduction and spring and summer climate in Greenland.](image)

Figure 2. Relationships between Greenland white-fronted goose reproduction and spring and summer climate in Greenland. All data were de-trended prior to analysis. The spring precipitation data were also square-root transformed prior to analysis.

### 2.3 Tests for density-dependence in reproduction

Trinder et al. (2005) presented evidence for an apparent density-dependent decline in reproduction, most evident in a significant negative relationship between the population size in the previous autumn and the proportion of breeding adults in the current one (i.e. a delayed effect). A mechanistic model to describe this relationship was developed by Trinder et al. (2005) to provide a biological explanation for the relationship. This model, which fitted the data slightly better than a simple linear regression, had two parameters:
The proportion of birds which breed had a maximum value \((maxPB)\) which was achieved when the number of breeding age birds was below a threshold size \((maxN)\). Above \(maxN\) the proportion of birds able to breed declines at a constant rate (see Appendix 2 for details).

A significant relationship between the proportion of breeding birds and the previous year’s population size was still present with the additional five years of data collected since the original analysis (linear model: \(F = 12.3, p = 0.002\), Figure 3). With small adjustments to the estimates of \(maxPB\) and \(maxN\) the mechanistic model still fitted the data better than the linear regression.

![Figure 3. Relationship between the proportion of breeding birds and the number of adults in the previous year. The red line is the best-fit least squares regression, the blue line the best-fit mechanistic threshold model. The maximum proportion of breeding birds \((maxPB)\) is 0.158, achieved below the threshold size \((maxN)\) of 7,740, indicated by the dashed grey lines.](image)

However, there is some evidence that this apparent density-dependent relationship may have broken down in recent years. Thus, while the population size has fallen, the proportion of breeding birds has not risen as predicted by this model. Since 2001 the proportion of breeding birds has not exceeded 7.5% (average = 6.4%), whereas the density-dependent model predicts that the proportion should have increased to around 12% over this period.

Therefore, two population models were developed, a density-dependent one and a density-independent one. The use of these two models is precautionary, since the different formulations are likely to give rise to different levels of associated risk with the different scenarios.
2.4 Variations between local Scottish populations

The Scottish population increased in size between 1982 and 1998 and has subsequently declined to a similar size (in 2007) to that seen during the 1980s. This trend has been reflected across most of the flocks for which annual data are available (Appendix 1, Table 4). A regional breakdown performed for the previous PVA (Trinder et al. 2005) found that around one third of flocks (accounting for almost 70% of the Scottish population) had initially grown and subsequently declined. In 2007 this category accounted for over 95% of the population and almost two thirds of the flocks. Only three flocks have undergone linear growth over the whole period, and these accounted for only 1.5% of the 2007 Scottish population. A further five flocks have shown no clear trend between 1982 and 2007, accounting for 2.6% of the 2007 population size. Thus the majority of flocks in Scotland which increased during the 1980s and 1990s have since declined.
3. POPULATION MODELS

Two population simulation models were developed for the Scottish population of the Greenland white-fronted goose. The density-dependent one was largely unchanged from that developed by Trinder et al. (2005). In its baseline form, this model assumed there would be no change in the level of shooting experienced by this population. The density-independent model was similar in structure; however the proportion of breeding birds was no longer linked to the population size. Instead, this was generated as a random variable in each year of a simulation using the mean and variance calculated from the last five years of data, during which time the value has not exceeded 7.5%.

Trinder et al. (2005) reported that the density-dependent model gave a reasonable fit to the observed population counts (1982-2002). However, their baseline prediction suggested that the Scottish population would stabilise at around 20,000 by 2030 while the population in fact declined, falling to approximately 13,000 by 2007. In the light of the mismatch between the prediction and the actual population trajectory the assumption of constant shooting was reinvestigated, using both models.

The moratorium on shooting in Iceland introduced in 2006 meant the rates of survival and reproduction needed to be re-estimated, taking shooting into account for the period 1995-2006. The amended demographic rates were effectively ‘pre-shooting’ estimates, obtained by adding the reported number of shot birds back to the count data prior to the calculations (Table 3). In doing this it is assumed that the alternative sources of mortality in this population are additive, rather than compensatory. In other words, a reduction in shooting mortality is not cancelled out by a corresponding increase in natural mortality (or vice versa). This assumption is not unreasonable as there is evidence that shooting mortality in this population is additive (Fox, 2003). The mean brood size has remained very consistent over the complete period of data (e.g. Table 1). Thus the average and standard deviation were calculated across the entire time series. The extent to which the mean brood size may be influenced by shooting is dependent on the proportion of families which are partially reduced by shooting. This rate is not known and thus the mean brood size was not adjusted for shooting.

Table 3 – Demographic rates used in the population models. Survival and proportion of breeders were estimated taking shooting into account (see text for details). Years over which rates estimated provided.

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<tr>
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<tbody>
<tr>
<td></td>
<td>Mean Standard deviation</td>
<td>Mean Standard deviation</td>
<td>Mean Standard deviation</td>
</tr>
<tr>
<td>Density-dependent</td>
<td>0.93 0.086</td>
<td>3.368 0.332</td>
<td>NA*</td>
</tr>
<tr>
<td>Density-independent</td>
<td></td>
<td></td>
<td>0.08 45 0.02</td>
</tr>
</tbody>
</table>

* The density-dependent model used the function and parameters illustrated in Figure 3.
There are no reliable data on the number of geese shot in Greenland, although a figure of 100-200 has been suggested (Fox & Stroud 2002), while around 300 have been reported shot in Iceland in the two years since the ban. Neither of these two figures could be straightforwardly incorporated into the amended demographic rates, thus the current population model’s baseline outputs implicitly include these levels of off-take (i.e. a shooting rate of ‘zero’ actually includes this low level of shooting).

Two starting years were used in the model; 1982 and 2006, depending on whether the model was being run for validation or prediction purposes respectively. The starting population size in each case was the observed population size in that year (i.e. 7,141 in 1982, 12,530 in 2006).

3.1 Model validation

Prior to the introduction of the reporting system in Iceland, no data were collected on the number of geese shot. Two alternative models of how the number shot in Iceland may have changed between 1982 and 2005 were developed; a linear-threshold one and a logistic one. These made use of the bag data from 1995, from which estimates of the number shot were extrapolated backwards to 1982, according to the following rules.

The linear model had three parameters;
- the proportion of the Iceland shooting bag made up of Scottish birds between 1995-2006 (PropScot, between 0 - 1);
- the year in which shooting began (BagStart, between 1982 and 1994) and,
- the size of the bag in the BagStart year relative to that of the known data between 1995-2006 (StartProp, between 0 -1).

The increase in the number shot each year between BagStart year and 1995 (when the Iceland shooting bag data begins) was modelled as a straight line. Thereafter shooting was maintained at a constant (threshold) value.

The logistic model had two parameters;
- the asymptotic level for the number of Scottish birds shot each year (Smax) and,
- the year when shooting began (S1).

Each shooting model was used to generate simulated Scottish bag sizes between 1982 and 2006 across a range of parameter values. The population models were then run from the 1982 population size, with the simulated shooting bag for each year removed from the population at the appropriate time step. The rate of reproduction in the density-dependent model was calculated using the relationship between population size and the proportion of breeders described above. In contrast, in the density-independent model the proportion of breeding birds was set at year-specific constant values, obtained from the linear regression of the proportion of breeding birds against year

\(\text{Proportion breeding} = -0.00454 \times \text{year} + 9.173; F = 18, p <0.001\).

In this way the observed decline in reproduction was also incorporated into the backwards predictions.
The relative fit of the median population size generated by the models under each shooting scenario was then compared to the observed population counts over the same period, and the best-fit parameters for each combination of population model (density-dependent / density-independent) and shooting model (linear / logistic) were identified by least squares.

The closest correspondence (i.e. best-fit) between the projected median population trend and the actual population counts were obtained when the logistic shooting model was used in conjunction with the density-dependent model (Figure 4) and when the linear shooting model was used in conjunction with the density-independent model (Figure 5). In both these figures (4 and 5) the lower panel indicates the actual total number shot between 1995 and 2007 (red dots), the estimated number of Scottish geese shot between 1982 and 2007 (dashed line; estimated using either the logistic or linear shooting model), while the upper panel provides the corresponding population model output resulting from the estimated level of shooting (dashed line) in the lower panel.

Figure 4. Population projection (upper panel) and simulated number of Scottish birds shot in Iceland (lower panel) using the logistic shooting model and density-dependent reproduction. The population plot shows the median population simulation (black line), 95% confidence intervals (dashed red lines) and the observed time series (grey line). The shooting plot shows the total Iceland bag data, including Irish birds, (red dots) and the simulated number of Scottish birds shot (dashed line). The plot shown was derived using the best-fit logistic model parameters.
Figure 5. Population projection (upper panel) and simulated number of Scottish birds shot in Iceland (lower panel) using the linear shooting model and density-independent reproduction. The population plot shows the median population simulation (black line), 95% confidence intervals (dashed red lines) and the observed time series (grey line). The shooting plot shows the Iceland bag data (red dots) and the simulated number of Scottish birds shot (dashed line). The plot shown was derived using the best-fit linear model parameters.

In both cases the median population prediction (upper panel, black line) lies close to the observed population trend. The 95% confidence intervals follow the density-dependent median trend quite closely (Figure 4). However the confidence intervals around the density-independent median prediction are much wider, with a population range of 0 – 50,000 after 25 years (such large uncertainty in outputs is a common feature of density-independent models). Therefore, on the grounds of median model fit to the observed population trend there is little difference between the two population models. However, the shooting bags implied by these models represent very different historical trends in the shooting of the Scottish population. The density-dependent model implies that the number of Scottish birds shot has increased gradually from a very low level prior to 1990 to over 2,000 by 2005. This contrasts with the known Iceland bag in the mid 1990s which was comparatively level at around 3,000 (Figure 4). In contrast, the density-independent model implies that shooting increased rapidly during the early 1990s before attaining a constant level of approx. 1,300, equating to 40% of the average total number shot.
The two models provide different estimates for the total number of Scottish birds shot prior to 1995 and of the proportion of birds in the post-1995 shooting bag which came from the Scottish population. The density-dependent model implies that shooting of Scottish birds was comparatively low during the mid 1990s but increased steadily to account for around 2/3rds of the total shooting bag by 2007. By contrast, the density-independent model suggests that, since 1995 a constant 40% of the total shooting bag was derived from the Scottish population. While Irish and Scottish birds are thought to use different areas for staging in Iceland, possibly leading to different levels of exposure to shooting (Tony Fox, pers. comm.), the model prediction seems on the low side when compared to the fact that Scotland accounted for around 60% of the total population.

Thus, neither of these two scenarios appears altogether reasonable and the conclusion of this validation exercise is that, while the observed trend in the Scottish population appears to have resulted from a combination of poor reproduction and unsustainable shooting, this cannot be confirmed with the available data. Consequently, both models were used to generate future population predictions.

3.2 Baseline model predictions and changes in shooting

Projecting forward 25 years, with a constant level of shooting at the post-moratorium rate (c. 300 in total, of which 60% estimated to be Scottish birds), the density-dependent model predicted the population will recover to just over 25,000, with indications that the population will level off at a few thousand more (Figure 6a). The density-independent model predicted a slightly slower initial population recovery, but reached a slightly higher median of almost 30,000 after 25 years (Figure 6b), with further growth predicted (due to the absence of population regulation).

![Figure 6](Image)

*Figure 6: Predicted population growth with the Iceland shooting moratorium maintained, produced using the density-dependent model (a) and the density-independent model (b).*
However, if shooting were to return to the previous level of approximately 3,000 birds/year, with an estimated 60% of the bag made up of Scottish birds, all simulated populations declined to zero within 25 years, irrespective of which model was used (Figure 7a & b).

![Figure 7. Predicted population growth with Icelandic shooting at pre-moratorium level, with 60% of total bag made up of Scottish birds (= c. 2,000), produced using the density-dependent model (a) and the density-independent model (b).](image)

The risk of the population declining below specific thresholds (‘quasi-extinction’) was predicted to increase with a resumption in shooting, irrespective of which model was used (Figures 8a and b). In the absence of density-dependence the simulated populations were more sensitive to increased shooting. For example, using the density-dependent model, more than 2,000 of the Scottish population need to be shot each year before all simulated populations fall below 10,000 within 25 years (Figure 8a), whereas using the density-independent model the same risk of decline occurs when more than 1,300 are shot (Figure 8b).

Since these values are similar to, or less than, the level at which this population was shot prior to 2005, the models indicate that the current moratorium should be maintained in order to minimise the risk of further population decline.
Figure 8. Risk of population decline below specific threshold sizes in 25 years with changes in shooting, produced using the density-dependent model (a) and the density-independent model (b).

Figure 9. Average stochastic growth rate (blue dashed line) and 95% confidence intervals (dotted red lines) resulting from increases in shooting, produced using the density-dependent model (a) and the density-independent model (b).
The difference between the two models can also be seen in the relationship between the average stochastic population growth rate and the number of geese shot (Figures 9a and 9b). Using the density-dependent model the growth rate remains greater than 1 (i.e. positive population growth) until annual shooting exceeds c.1000 (Figure 9a). In contrast the equivalent threshold predicted using the density-independent model is c.400 (Figure 9b). For a minimum of 95% of simulations to have positive population growth the density-dependent simulations indicate that no more than 500 birds can be shot each year, whereas only if shooting falls further (i.e. a reduction of 150 in the number of illegally / accidentally shot birds) do 95% of the density-independent simulations have positive population growth.

3.3 Sensitivity analysis

Geese are relatively long-lived, slow breeding species, and as such the demographic rate most sensitive to change is adult survival (Figures 10 and 11). Changes to this rate have a proportionally much greater effect on the risk of population decline than changes to either juvenile survival or reproduction. This difference between demographic rates is more pronounced using the density-independent model (Figure 11). Thus, factors which affect the adult survival rate (e.g. shooting) will have the greatest relative influence on the population growth rate.

*Figure 10. Twenty five year quasi-extinction risks resulting from proportional changes to juvenile survival, adult survival and mean brood size using the density-dependent model.*
Figure 11. Twenty five year quasi-extinction risks resulting from proportional changes to juvenile survival, adult survival and mean brood size using the density-independent model.

3.4 Change in number of breeding pairs

Greenland white-fronted geese have very low reproductive output compared to other populations of this species. The average percentage of juveniles recorded in the Scottish population since 1982 is 13%, but in the last nine years has been as low as 1% and no higher than 11%. This compares with three different North American populations of white-fronted geese, for which the percentage of juveniles has averaged between 25% and 33% over the same period (Boyd & Fox 2008).

One possible cause for the decline in reproductive success in the Greenland white-fronted goose population over the last twenty years has been the expansion of a breeding population of Canada geese within the breeding range of the white-fronted geese (Scribner et al. 2003). Canada geese are behaviourally dominant over white-fronted geese (Malecki et al. 2000), although direct evidence for such an effect in Greenland is lacking and the two species apparently co-exist successfully elsewhere (e.g. Carriere et al. 1999).
The most likely period for competition appears to be during the post-breeding moult, when feeding resources in proximity to lakes (which are used for predator avoidance) may become limiting (Boyd & Fox 2008). Conversely, the extent of the area favoured by the geese for breeding is predicted to increase as climate change results in retreat of the Greenland ice sheet (Joughin et al. 2008). If the availability of suitable breeding and moultng habitat is indeed limiting, climate change may therefore permit an increase in reproduction in this population. It is worth stressing, however, that any increase in the extent of breeding habitat as a result of retreating ice is likely to occur over a period of several decades.

It is difficult to determine the potential impacts of these changes on the population, since the mechanism by which competition during the post-breeding moult may reduce productivity, for example, is not currently known. However, since competition for space is a form of density-dependence, the most appropriate means to explore these effects was using the density-dependent model. This was achieved by changing the proportion of birds able to breed. Since this parameter is subject to density-dependent regulation in the model, this involved changing the value of $maxN$ applied. This can be thought of as simply extending or reducing the length of the horizontal portion of the threshold model (defined by $maxPB$, Figure 3, blue line). In the baseline form of the model, the maximum proportion of adults which can breed (0.158) is achieved only when there are fewer than 7,740 adults, while above this number the proportion of breeding birds declines at a constant rate. The rationale for setting a $maxN$ was that of a biological constraint on the maximum number of birds which can breed. Therefore, this adjustment is consistent with modelling changes in breeding habitat availability. Such changes might result from either elevated competition (i.e. a reduction in $maxN$), or reduced ice cover (i.e. an increase in $maxN$). The baseline value for $maxN$ was modified by +/-30%, giving a range of values from 5,400 to 10,000 and the risk of quasi-extinction assessed (Figure 12).

![Graph](data:image/png;base64,iVBORw0KGgoAAAANSUhEUgAAAAEAAAABCAYAAAAfFcUpwAAAAAXNSR0IArs4c6QAAAARnQU1BAACxjwv8YQUAAAAJcEhZcwAADsQAAA7EAkucXBo AAAABHJQVHJ4cAAAASUlEQVR42mP8/wAAAAASUVORK5CYII=)

*Figure 12. Change in quasi-extinction risks within 25 years resulting from change to the threshold point ($maxN$) below which the maximum proportion of adults can breed. The vertical dotted line indicates the baseline value (7,740).*
The results indicate that, while the risk of population decline below 10,000 remains low across the entire range of values tested here, change in habitat availability may affect the likelihood that the population will exceed 20,000 within 25 years. The difficulty with interpreting these results is that, while it may be possible to estimate the increased availability of breeding habitat due to reduced ice cover, the extent to which interspecific competition for breeding sites occurs is still unknown. However, this analysis does provide some guidance, should such data become available.
4. CONCLUSIONS

- Evidence for density-dependent reproduction in this population is equivocal, therefore two population models were developed, a density-dependent one and a density-independent one.

- The two population models generated different estimates for the historical level of shooting experienced by the Scottish population since the early 1980s.

- Using the density-dependent model and assuming that shooting was solely responsible for the observed population trend, the proportion of shot geese originating from the Scottish population was estimated to have increased from a low of 20% in 1995 to around 60% by 2006.

- The density-independent model, which also allowed for the observed changes in reproduction, estimated that geese which winter in Scotland have accounted for a constant proportion (approx. 40%) of the total number shot.

- Of these backward predictions, the density-independent one appears more likely. However, neither model seems able to explain completely the trends observed. In addition, with limited shooting data it is not possible to state which set of predictions is more accurate.

- Since density-dependent and density-independent models will typically generate quite different predictions both models were retained for the remaining predictive simulations.

- If the moratorium on shooting in Iceland is maintained, the 25 year median population sizes predicted by the models were between 25,000 (density-dependent) and 30,000 (density-independent). The associated risk of decline below 10,000 for each of these simulations was 0% and 3% respectively.

- If shooting in Iceland is resumed at the 1995-2005 level both models predict that the population will decline to zero within 25 years.

- If shooting is resumed to around 1,000 birds per year, the risk of population decline below 10,000 within 25 years increases from 0% to 15% using the density-dependent model and from 3% to 97% using the density-independent one.

- Two potentially conflicting influences may affect breeding success in this population: interspecific competition with Canada geese and reduction in the extent of the Greenland ice-cap. If the density-dependent threshold number of birds which can breed at the maximum rate is reduced by 800, the probability that the population will fail to exceed 20,000 in 25 years doubles from 12% to 24%. Conversely if the threshold value is increased by 800, only 7% of simulations failed to exceed 20,000 after 25 years. The potential for either factor to affect reproduction is currently unknown.
5. ADVICE

- In the previous PVA, Trinder et al. (2005) provided recommendations which would help either safeguard the population or improve understanding of its demographic rates.

- One of the recommendations was that shooting should not increase above the (then) current level, although it now appears even that level was unsustainable. The shooting moratoria in Iceland and Greenland have addressed this concern, and the models suggest there are grounds for cautious optimism that the population will recover. However, while the population remains at a low level it is critical that additional significant mortality is avoided.

- Another recommendation was that monitoring of the population should at least be maintained at the current level, which has been achieved.

- Currently it is not possible to determine which population model (density-dependent or density-independent) offers the more reliable predictions. Thus management decisions should be based on the outputs from both models.

- In order to address the above point, further efforts should be made to estimate the role, and strength, of density-dependent regulation in the population. Determination of this aspect would greatly improve the understanding of the population’s dynamics and should enhance future predictions. In order to achieve this, greater efforts to record productivity rates at a wider range of Scottish sites should be undertaken.

- Estimation of rates of inter-change between regional flocks would also assist in determining the extent to which density-dependent regulation operates within both local populations, and the overall population.

- It is apparent that the key determinants of this population's size and conservation status lie on the breeding grounds. It is therefore imperative that improved understanding of the nature and extent of interactions between Greenland white-fronted geese and Canada geese on the breeding grounds is obtained.
6. REFERENCES


Appendix 1. Regional Greenland white-fronted goose flocks

Trends in regional Scottish Greenland white-fronted goose flocks, 1982 – 2007. Sites have been divided into linear best fit (top, 3 sites), polynomial best-fit (middle, 15 sites) and no significant trend (bottom, 5 sites), based on the trend measured over all years (1982 – 2007).

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Appendix 2 – Greenland white-fronted goose demographic rate calculations

Calculation of demographic data and age class sizes for Greenland white-fronted geese using the annual population count \((N)\), proportion of juveniles \((PJ)\) and mean brood size \((BS)\) data collected at sites around Scotland. In all of the following equations subscript ‘\(t\)’ is used to denote the current year, ‘\(t-1\)’ the previous year, etc.

Number of juveniles:

\[ J_t = PJ_t \times N_t \]

Crude annual survival rate (from year \(t-1\) to year \(t\)):

\[ CS_t = \frac{N_t - J_t}{N_{t-1}} \]

Number of birds in their second year:

\[ N2_t = J_{t-1} \times CS_t \]

Number of birds in their third year or older:

\[ N3_t = N_t - (J_t + N2_t) \]

Productivity:

\[ P_t = \frac{J_t}{N3_t} \]

Proportion of breeders:

(i.e. the minimum number of third year and older birds required to have bred to account for the estimated number of juveniles)

\[ PB_t = \frac{J_t}{0.5 \times N3_t} / BS_t \]

Threshold density-dependence:

(Parameters: \(maxN\) = threshold population size of breeding age birds; \(maxPB\) = maximum proportion of breeders)

\[ DDpropB_t = maxPB \]

If \(N3_{t-1} < maxN\)

\[ DDpropB_t = \max PB \times \frac{maxN}{N3_{t-1}} \]

If \(N3_{t-1} > maxN\)
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