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Status and population viability analyses of geese in Scotland

(ROAME No. F03AC302)

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Status and population viability analyses of geese in Scotland

Commissioned Report No. 107 (ROAME No. F03AC302)

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Background

This report summarises the analysis of census and productivity data collected for the Scottish wintering populations of pink-footed goose (*Anser brachyrhynchus*), Greenland white-fronted goose (*Anser albifrons flavirostris*), Icelandic greylag goose (*Anser anser*), Greenland barnacle goose (*Branta leucopsis*) and Svalbard barnacle goose (*Branta leucopsis*). Trends in the population counts and derived demographic rates are described, along with the outputs from population viability models developed using the demographic rates. Factors which may influence the future growth of the populations are discussed.

The results are compared with a previous set of PVA analyses for these populations carried out in the 1990s. The outcomes and predictions are used to inform a review of goose policy in Scotland.

Main findings

- Pink-footed goose. The current (2002) population of about 230,000 individuals is continuing to rise and the long-term likelihood of decline under current conditions is very small. The risk from any catastrophic events is also very low, except in the most extreme conditions modelled.
- Greenland white-fronted goose. Following a period of steady growth through to the mid 1990s the overall population had stabilised but is now showing signs of a more recent decline to a current Scottish level of 17,500. These changes appear to have been driven by a reduction in the proportion of birds breeding successfully, rather than any changes in the mean brood size or adult survival rate.
- Greylag goose (Icelandic). The autumn counts have described a sustained period of population growth in the GB wintering population peaking at around 100,000 birds in the early 1990s, followed by a decline to about 73,000 in 2002. There is currently a great deal of uncertainty in the PVA estimates, with suggestions that these counts underestimate the full size of the population, that there are problems with estimating the proportions of juvenile birds, and that it is getting increasingly difficult to distinguish between Icelandic greylags and the resident native and reintroduced greylag populations.

- Barnacle goose (Greenland). The current size of the Greenland barnacle goose population (56,400 globally with 47,300 in Scotland) appears reasonably secure in the long term. Under current conditions the population is predicted to continue to grow, though rates of growth may vary between different wintering locations.
- Barnacle goose (Svalbard). The current population of 27,000 barnacle geese wintering on the Solway has increased from a very low level in the 1940s (ca 300 birds). There is currently no evidence to suggest the population has reached the carrying capacity of either the summer or winter range. However, there is evidence that reproductive output has declined with increasing population size.

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1 STATUS AND POPULATION VIABILITY OF THE PINK-FOOTED GOOSE IN THE UK

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1.1 Introduction

This report summarises analysis of data for the pink-footed goose *Anser brachyrhynchus* population which over-winters in the UK, predominantly in eastern Scotland and northern England. While the majority of this population breeds in Iceland, some breeding is also known to take place on the east coast of Greenland, although very little information exists concerning the numbers involved. Prior to the 1970s no more than 1,000 birds were thought to breed there (Kerbes *et al.*, 1971), with this figure rising to around 10,000 by the mid 1990s (Boertmann, 1994). Much greater numbers undertake a moult migration to Greenland in late June (mostly non-breeding birds), with total estimates of up to 26,500 reported there during the 1980s and 90s (Mitchell *et al.*, 1999).

The data used for this analysis consist of counts, age ratios and mean brood size estimates made in Scotland each autumn since 1950, and Icelandic shooting bag data collected since 1995. Trends in the population counts and demographic variables are discussed, together with the outputs from a population model developed from the data, which has been used to explore a range of possible scenarios.

1.2 Methods and results

During the early part of each winter the majority of the population roosts at relatively few sites in north and east Scotland, before dispersing more widely as the winter progresses. Coordinated population censuses have been conducted each November since the 1950s, taking advantage of the restricted distribution during early autumn. Since 1990 a count has also been undertaken in October, as it became apparent that in some years considerable onward movement had already occurred by November. Age ratio and mean brood size estimates are also collected in Scotland during the autumn, with efforts made to collect the data in as robust a fashion as possible (ie from a range of sites, flock sizes etc.). Using the counts, age ratios and brood size estimates three further demographic parameters have been derived:

1. the annual (crude) survival rate (the proportion of the population surviving from one year to the next),
2. the productivity rate (the number of young produced per breeding age adult on arrival in Scotland),
3. the proportion breeding (the proportion of breeding age birds returning to Scotland with young).

See Appendix 1 for the derivation of these parameters.

In 1995 the Icelandic Institute of Natural History (IINH) and the Wildfowl and Wetlands Trust (WWT) initiated research into the dynamics of the Icelandic breeding populations of both the greylag and pink-footed goose, with a particular emphasis on improving understanding of the impact of shooting on the two

populations. Between 1996–2000 over 1,200 pink-footed geese were fitted with individually identifiable colour rings in Iceland. Colour rings have also been fitted to a comparable number of geese caught in Scotland each winter since 1987. Combined analysis of both live re-sightings and dead recoveries of these ringed geese have provided adult and juvenile survival rate estimates which, unlike the crude survival rate described above, are independent of population counts (Frederiksen *et al.*, 2004).

Since 1995 hunters in Iceland wishing to renew their shooting licences have been required to submit a report of the number of each species they shot in the previous season, and this shooting bag data has been made widely available (<http://www.ust.is/Veidistjornun/Almennt/Veiditolur/>). Analysis of these data suggests that, while a small amount of over-reporting may occur, this is unlikely to be significant (Frederiksen *et al.*, 2004). The number of shot pink-footed geese reported to the scheme has varied by only a few thousand each year, with an average of just over 13,000 (1995–2002; Figure 1). Currently there is no equivalent bag reporting scheme for hunters in the UK. A pilot study based on independent surveys of both British Association for Shooting and Conservation (BASC) members and firearm licence holders in selected Scottish police force regions, provided a preliminary estimate that 25,000 Icelandic pink-footed geese are shot in Scotland each year (Hart & Harradine, 2003). Frederiksen (2002) used the Icelandic bag data, together with the estimated probability that shot, ringed geese will be reported, to estimate that 25,000 pink-footed geese are shot in the UK each winter (assuming similar shooting conditions to those found in Iceland). Since these two independently derived UK bag estimates are in close agreement we have a high degree of confidence that a UK bag of 25,000 is close to the true value. In addition to total bag estimates, between 1993–2000 the IINH collected goose and duck wings from hunters. Analysis of these data revealed that on average just over 33% of the pink-footed geese shot each year in Iceland were juveniles (Frederiksen *et al.*, 2004).

1.2.1 Analysis of population count data

Analysis of the ringing and shooting data for the Icelandic breeding populations of both greylag goose and pink-footed goose revealed that the autumn greylag population estimates made in the UK were too low to account for the apparent level of shooting experienced by this population (Frederiksen *et al.*, 2004). In contrast, no such mismatch was identified for the pink-footed goose data, and therefore analysis of the population counts and reproductive estimates was conducted without undue concern over their reliability. The population grew gradually from less than 10,000 in 1950 to around 100,000 in the mid 1980s, before rising sharply to around 200,000 by 1990. Since then the population has fluctuated between 160,000–260,000 (Figure 2), and while the October estimates have tended to be higher than the November ones (in 8 out of 11 years), both counts suggest a continuing upward trend. The gradual increase in the population size seen up until the early 1980s has been attributed to site safeguards which led to reduced mortality (Fox *et al.*, 1989). However, the mechanisms underlying the sudden increase in the population during the 1980s are not well understood, although it seems likely that density-dependent regulation of breeding was eased at this time (Pettifor *et al.*, 1997).

In order to determine if there is any evidence for a decline in the population growth rate as the population has increased, tests for the presence of density-dependence in the population time series were conducted using the randomisation test of Pollard *et al.* (1987) and the boot-strap test of Dennis & Taper (1994). Both tests yield non-significant p-values (Pollard *et al.*: $p = 0.081$; Dennis & Taper: $p = 0.18$), thus based on the count data alone there is no suggestion that population growth has been regulated by density-dependence. However, further testing for density-dependence in the demographic rates is detailed in the following section.

1.2.2 Analysis of demographic data

The mean annual demographic rates (and their standard deviations) derived using data for the population collected between 1950–2002 are provided in Table 1, together with the rates calculated using the data available for the previous PVA (1950–1992; Pettifor *et al.*, 1997) and those for the years since (1993–2002), in order to highlight where changes have occurred. None of the rates has changed significantly since the previous PVA was developed for this population. Investigation of changes in the demographic rates in relation to the current and previous year's population density and environmental conditions was conducted using both Generalised Linear Models (GLMs) and Robust Regression. In contrast to standard (ordinary least squares) linear regression, where outlying data points can disproportionately influence the results obtained, Robust Regression methods weight data points according to their proximity to the fitted regression line: points which lie further from the fitted trend consequently have a reduced influence. While GLMs enable interactions between population density and environmental variables to be tested, they are sensitive to the presence of outliers in the data. Conversely, Robust Regression minimises sensitivity to outliers, but cannot handle interactions between parameters. The two methods therefore complement one another.

Table 1 Pink-footed goose demographic parameters derived from the population counts, proportion of juveniles and mean brood size estimates made in Scotland each autumn since 1950. The previous estimates (1950–1992) represent those available for the last PVA exercise (Pettifor *et al.*, 1997) and are included for comparison with the more recent estimates. The survival rate is a combined estimate for all birds older than c.6 months, calculated as the number of adults in the current year divided by the total population in the previous year; productivity is the ratio of juveniles to breeding age adults; mean brood size is the estimated family size in a sample of Scottish flocks; proportion of juveniles is the percentage of juveniles in a sample of Scottish flocks; proportion breeders is the minimum number of adults required to have bred (in order to account for the estimated number of juveniles) divided by the total adult population. See Appendix 2 for further details.

	Previous estimate (1950–1992)	Current estimate (1993–2002)	Overall estimate (1950–2002)
Parameter	Mean (St. dev)	Mean (St. dev)	Mean (St. dev)
Survival	0.87 (0.15)	0.84 (0.14)	0.86 (0.15)
Productivity	0.34 (0.18)	0.27 (0.04)	0.33 (0.16)
Mean brood size	2.42 (0.62)	2.29 (0.15)	2.39 (0.56)
Proportion juveniles	0.21 (0.08)	0.18 (0.02)	0.20 (0.08)
Proportion breeders	0.29 (0.12)	0.24 (0.03)	0.28 (0.11)

The environmental variables investigated were: mean monthly temperatures (May–August) recorded at a weather station located within the breeding range in Iceland (Grímsstaðir, North-east Iceland, 17.8W, 64.4N), and the North Atlantic Oscillation (NAO) index for the main migration months (April, September and October). The NAO index is a measure of the relative difference in sea-level atmospheric pressure recorded at the Azores and Iceland, and provides an indication of the prevailing weather conditions in the North Atlantic. Positive values of the NAO index are associated with enhanced westerly winds, and higher than average temperatures and precipitation, while negative ones are an indication of less windy conditions

and below average temperatures and precipitation. Three sets of tests were conducted: the demographic and count data were analysed for the whole time series (1950–2002), the run of years until the sudden population increase (1950–1984) and the years after the increase (1987–2002). In addition, when the population sequence included data collected since 1990 (when counting in both October and November began) the analysis was repeated using both sets of counts.

No significant interactions between population density and environmental variables were revealed by GLMs, and the results of Robust Regression are therefore reported here. Very similar results were obtained when the November counts were replaced with the October ones for the years since 1990, therefore only the November results are discussed here. Using the data for the early years (1950–1984), analysis revealed that all the reproductive parameters declined significantly with increasing population density over this time (Table 2). However, there were no detectable trends with either the NAO index or the average monthly temperatures recorded on the breeding grounds between May–August. Similar results were obtained when the analysis was conducted using data for all years (1950–2002), with the addition that the proportion of juveniles had a significant positive relationship with the average May temperature ($t=2.04$, $p=0.046$). Analysis of data for the years since 1987 failed to identify any significant relationships between the reproductive parameters and population density. In contrast, the crude survival rate, which showed no detectable pattern over either the whole period or just the early years, has declined significantly with population size since 1987. The best explanatory population density variable in all cases is the natural log of the population size in the previous year, indicating that the decline in each rate with increasing population has not been linear, but instead has tended to level off as the population size has grown.

Table 2 Significant results of statistical analysis of the pink-footed goose demographic data. The explanatory population variable is: $\log_e(N_{t-1})$ – natural log of total population size in the previous year. In all instances Generalised Linear Models (GLM) were used first to check for the presence of significant interaction terms. None were identified so the remaining model refinement was performed using Robust Regression, which is less sensitive to outliers in the data. All tests were conducted using Matlab (MathWorks, Inc.). Note: NS = non-significant.

		1950–1984			1987–2002		
Test rate (transformation)	Explanatory variables	t	p	Parameter estimate (s.e.)	t	p	Parameter estimate (s.e.)
Mean brood size	Constant	6.32	<0.001	10.2 (1.6)		NS	
	$\log_e(N_{t-1})$	-4.82	<0.001	-0.71 (0.1)		NS	
Proportion breeders (sqrt)	Constant	3.56	0.001	1.5 (0.4)		NS	
	$\log_e(N_{t-1})$	-2.31	0.027	-0.09 (0.4)		NS	
Proportion juveniles	Constant	4.11	<0.001	0.95 (0.2)		NS	
	$\log_e(N_{t-1})$	-3.23	0.003	-0.07 (0.02)		NS	
Productivity (cuberoot)	Constant	5.93	<0.001	2.08 (0.3)		NS	
	$\log_e(N_{t-1})$	-3.97	<0.001	-0.13 (0.03)		NS	
Survival (\log_e)	Constant		NS		2.87	0.013	9.92 (3.4)
	$\log_e(N_{t-1})$		NS		-2.93	0.012	-0.83 (0.3)

1.3 Population model

A partially age-structured population model was developed for the pink-footed goose population using the overall crude survival and reproductive rates calculated above, incorporating three age classes: juveniles, second years and third years and older. In each year of a population simulation the survival rate and mean brood size are drawn at random from appropriate probability distributions derived from the observed data. The proportion of the adult population which breeds is dependent on the population size in the previous year, using a threshold model developed to explain the observed relationship in mechanistic biological terms. The model has two parameters estimated from the data: a maximum proportion of breeding birds and a threshold number of breeding age birds. When the population is below the threshold, the maximum proportion of breeding birds is achieved, above it the proportion breeding declines at a constant rate with increasing population size. This model was fitted initially to the data collected before the large population increase (ie pre-1985), yielding a maximum proportion of 0.368 and a threshold of 35,000. However, using these estimates the threshold model performs poorly for the data collected since 1985. A second threshold population size (80,605) was identified through further fitting of the model to the data collected after 1987, thus enabling the same model structure to accommodate the substantial increase observed in the breeding population (at a number of newly colonised (and re-colonised) breeding sites in Iceland the breeding population more than doubled during the 1980s; Mitchell *et al.*, 1999). The population projections presented here are obtained using this second threshold estimate and the maximum proportion of breeding birds. See appendix 2 for further details of this threshold model.

Using this model, we have investigated the risk of population decline below specific thresholds (quasi-extinction) within the short to medium term, resulting from changes in conditions which may affect the population. The term quasi-extinction probability as used here refers to the likelihood that the population will fall below a specific size within a particular period of time (eg the chance that the population will fall below 25,000 in the next 25 years), expressed as a proportional (or percentage) probability.

1.3.1 Baseline model outputs

With the initial population size set to the 1950 count the model produces a good fit to the observed data, with a close match between the predicted 2002 median population size and the observed population in that year (Figure 3). Simulations starting from an initial population size taken after the sharp increase (eg the 1988 population count, 176,210) produce a similarly close match between the observed and simulated populations (Figure 4). Thus it appears that the density-dependent threshold model for the proportion of breeders provides a good means to explain the observed population trend. If the current conditions are maintained the median equilibrium population size predicted by the model is approximately 220,000, the probability that the population will decline below 50,000 individuals within the next 25 years is 2%, and below 25,000 is less than 0.1% (Figure 5). The most sensitive demographic rate in terms of its influence on the likelihood of population decline is adult survival, with a reduction of 8% in adult survival yielding a 25% risk of decline below 50,000 in 25 years. In contrast, the juvenile survival and mean brood size need to be reduced by 44% and 46% respectively in order to observe the same 25% risk of decline below 50,000.

1.3.2 Risk analysis

1.3.2.1 Changes to the current level of shooting

The probability that the population will decline below key thresholds (10,000, 25,000, 50,000) in response to changes to the current level of shooting mortality are provided in Table 3, and Figure 6. Between 1995–2002, an average of 13,000 pink-footed geese were shot each year in Iceland, and an estimated 25,000 were shot each year in the UK (Frederiksen, 2002) thus, overall approximately 38,000 pink-footed geese are shot annually. This level of shooting is implicitly included in the model structure, and changes to this are modelled simply as an increase or decrease in the size of the shooting bag. To simulate the different levels of shooting mortality, the appropriate number of geese are either removed (representing an increase in shooting) or added (representing a reduction in shooting) during the post-breeding period each year. The bag consists of both juveniles and adults, with the juvenile proportion of the bag set at 0.33, corresponding to the reported proportion of juveniles in the Iceland bag (Frederiksen and Sigfússon, unpubl. report). If the current level of shooting is maintained, the probability of the population falling below 50,000 within 25 years is 2%. As the additional number shot each year increases, the probability of population decline rises. For example, the risk of decline below 50,000 increases to 11% if 5,000 extra birds are shot each winter, and is over 34% if 10,000 extra birds are shot. A reduction in shooting reduces the likelihood of significant population decline; if 5000 less birds are shot each winter then the probability of decline below 50,000 is reduced to 0.4%.

Table 3 Quasi-extinction probabilities and median population size in 25 years for Iceland pink-footed geese in response to change to the current level of shooting mortality. The probability of the population declining below specific levels (10,000, 25,000, 50,000) within 25 years resulting from change to the current annual shooting mortality (ie current shooting bag –5,000 to +15,000). When the additional number shot/yr equals zero, shooting mortality is maintained at its current level (c. 38,000/yr). Negative additional shooting represents a reduction in the current level and positive values indicate an increase above the current level.

Quasi-extinction threshold		Quasi-extinction probability (25 years)			
		10000	25000	50000	Average population size in 25 years
Additional Number shot/year	-5000	0	0	0.004	277,335
	0	0	0.002	0.02	231,673
	5000	0.03	0.05	0.11	179,465
	10000	0.24	0.27	0.34	108,721
	15000	0.57	0.6	0.66	46,470

1.3.2.2 Catastrophic mortality

The aim of catastrophic event simulations is to determine the sensitivity of the population to extreme events which can give rise to rates of survival or reproduction which are outside the range encountered during the period of data collection. Over long periods, it is likely that there will be occasional “catastrophic” events, causing mortality well above the range of values observed (caused for example by severe storms in the north

Atlantic during migration). The sensitivity of the population to occasional large increases in mortality was therefore investigated by recording the quasi-extinction probability over 100 years resulting from the removal of a proportion of the population at random intervals (Figure 7). At the beginning of each simulation the average annual frequency of catastrophes (from 1 in 1,000 years to 1 in 10 years) and the proportion of the population to be removed by each event are selected (between 0–90%). The likelihood of the population falling below 10,000 individuals within 100 years is negligible, until catastrophes are either moderate but frequent (removing more than 30% of the population once every 10 years on average), or infrequent but severe (80% removal one year in 100). The baseline risk of the population declining below 50,000 within 100 years is around 20% and rises rapidly with even comparatively small losses (10–20% of the population) on a regular basis (once in 10 years); a loss of 30% on average once every 10 years gives rise to greater than a 70% risk of population decline below 50,000 in 100 years.

1.3.2.3 Loss of breeding habitat

Concerns have been raised about the possible loss of, or modification to, current pink-footed goose breeding habitat which may result from proposed hydro-power developments in the Icelandic Highlands. Currently, it is not clear how much breeding habitat may become lost or unsuitable as a consequence of the existing proposals, however it is likely to be only a small percentage of the current breeding area (2003). In order to more comprehensively assess the sensitivity of the population to breeding habitat loss, simulated reductions in the current breeding habitat of between 0–50% were undertaken. With an increasing percentage loss of habitat the risk of population decline below 50,000 within 25 years increases only gradually (Figure 8); when a quarter of the current breeding area is removed the probability of decline below 50,000 is 6.4% (from a baseline of 2.5%), rising to 25% when half the current area is lost. However, while the risk of significant population decline increases relatively modestly in the face of considerable habitat loss, the average stochastic growth rate over 25 years falls below 1 (ie more than 50% of all simulated populations decrease in size) when habitat loss exceeds 4% (Figure 9). The presence of density-dependent regulation of breeding in the model makes population decline in the longer term unlikely, instead the average simulated population path will tend to level out around a new, lower equilibrium point. Thus, a 25% reduction in habitat yields a median equilibrium population of 163,000 in 25 years, while a 50% reduction produces a median of just over 100,000 (Figure 10). However, it should be noted that the range of possible population sizes predicted by these simulations is very wide, and consequently the lower 95% confidence limit indicates that habitat losses of 25% and 50% may cause the population to fall as low as 55,000 and 37,000 respectively.

1.4. Conclusions

1.4.1 Implications of PVA results for the UK pink-footed goose population

- 1 If the current conditions and shooting regime are maintained the predicted median equilibrium pink-footed goose population size is approximately 220,000, and there is just a 2% probability the population will decline below 50,000 within 25 years.
- 2 The quasi-extinction probabilities are most sensitive to change in adult survival, however even this rate needs to be reduced quite significantly in order to obtain a 25% probability that the population will fall below 50,000; to observe this level of quasi-extinction risk reductions to the mean adult survival, juvenile survival or productivity of 8%, 44% or 46% respectively are required.
- 3 The current level of shooting appears to be sustainable. A reduction in the number shot per year of 5,000 reduces the predicted probability of population decline below 50,000 within 25 years from 2% to 0.4%. However, if an additional 10,000 geese are shot/yr the likelihood of decline below 50,000 in 25 years increases to over 34% and the average population size after 25 years falls to less than 110,000.
- 4 While the loss of breeding habitat as a consequence of the currently proposed hydropower schemes is predicted to lead to a reduction in the median population size, it is unlikely to lead to a significant increase in the risk of population decline below 50,000.

1.4.2 Advice

- 1 Simulations indicate that the current shooting regime for pink-footed geese is sustainable. A comparatively small, but sustained, increase in shooting could lead to long term decline and a significant risk of the population falling to less than a quarter of its current size within 25 years. This may have important implications should measures to reduce greylag shooting be introduced, since there may be a knock-on effect of increasing the number of pink-footed geese shot as an alternative quarry species.
- 2 Improving the monitoring of goose shooting levels in the UK is a vital part of the assessment of the health of the pink-footed goose population, and efforts to develop robust estimation methods should be made a priority.
- 3 Simulations indicate that significant pink-footed goose population declines are unlikely to result from the currently proposed hydro-power schemes in Iceland. However, this situation should be closely monitored, since further energy generating schemes are planned in Iceland, and this may lead to considerably more habitat degradation, and consequently a much greater risk of decline.

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Figure 1 Icelandic pink-footed goose shooting bag (1995–2002) on the left y-axis, (upper) blue line and the proportion of juvenile pink-footed geese in the bag (1995–2000) estimated from wing surveys on the right y-axis, (lower) green line. Based on Frederiksen *et al.*, 2004.

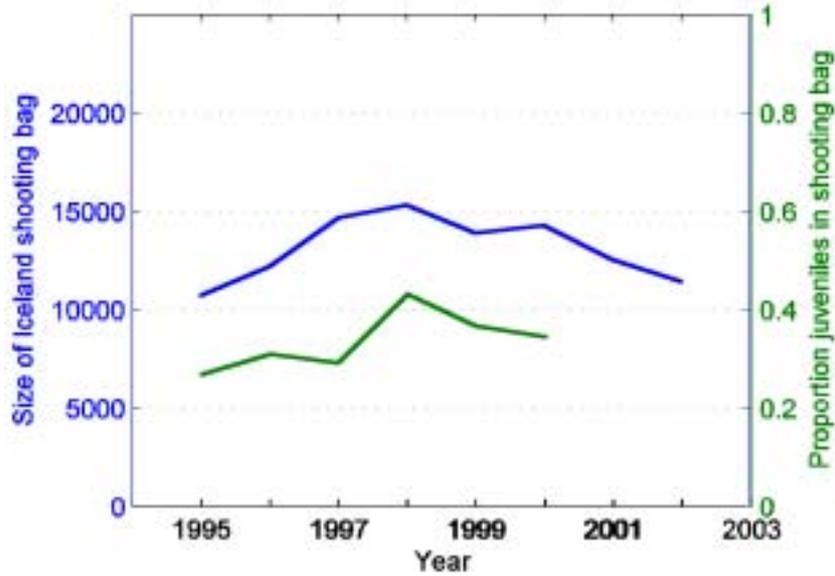


Figure 2 Icelandic breeding pink-footed goose population size, 1950–2002, derived from coordinated autumn counts conducted in the UK. Counts have been conducted in November since 1950 (blue line) and additionally in October since 1990 (red line). The October counts illustrate that the November census may underestimate the true population size in years when significant onward movement southward begins earlier in the autumn.

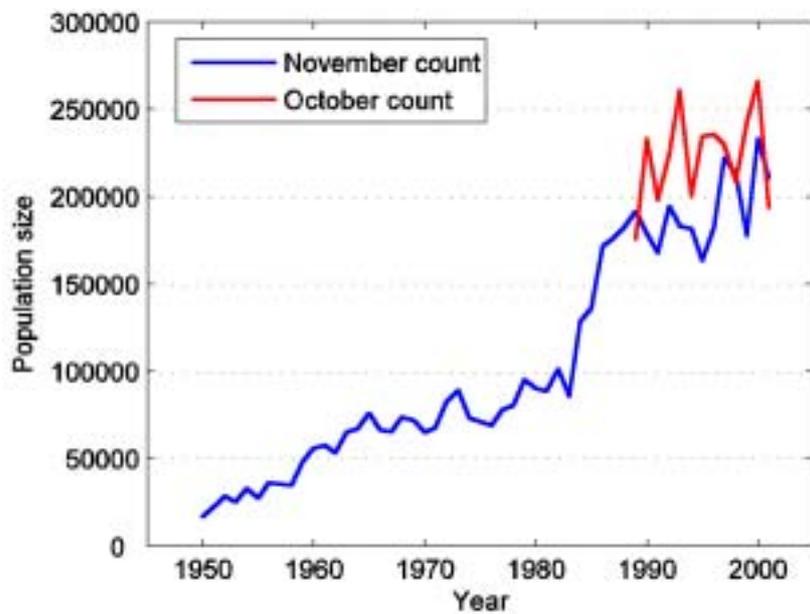


Figure 3 Pink-footed goose population projection over 100 years starting from the 1950 census. The solid red line is the median population size, the dashed and dotted blue lines respectively the 50% and 95% confidence intervals. The solid black line is the observed population, 1950–2002. The model predicts an equilibrium median population size of around 220,000.

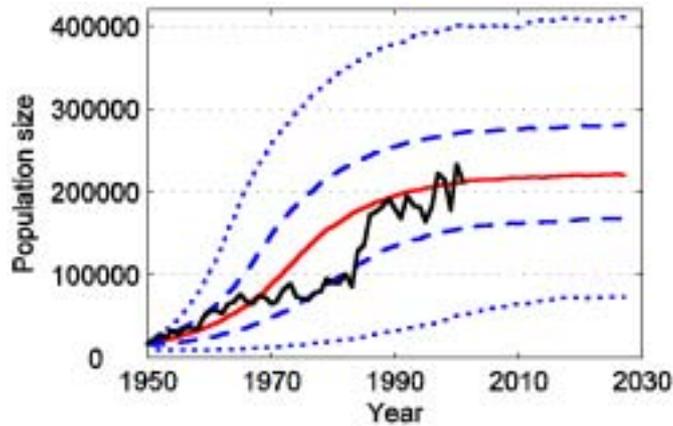


Figure 4 Pink-footed goose population projection over 40 years starting from the 1988 census. The solid red line is the median population size, the dashed and dotted blue lines respectively the 50% and 95% confidence intervals. The black lines are the observed population counts for the period 1988–2002; the solid line is the November count and the dotted line the October count. The model predicts a median equilibrium population of approximately 220,000.

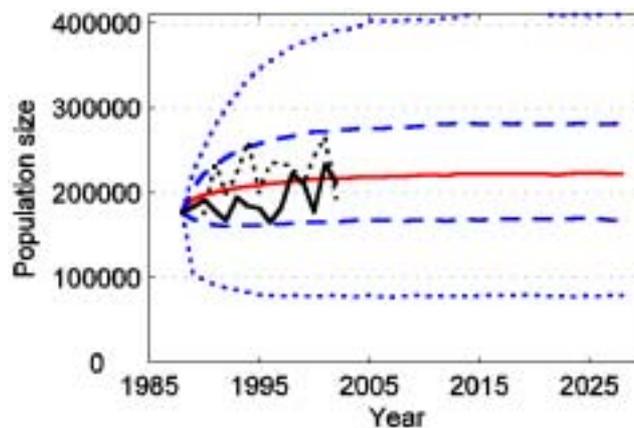


Figure 5 Plots indicating the relative sensitivity to change of the different demographic parameters in the Icelandic pink-footed goose population model. The graphs indicate the probability of the population declining below critical levels (ie quasi-extinction at: 50,000, solid black line; 25,000, dashed red line; 10,000, dotted blue line) within 25 years as a result of equivalent proportional change to the mean juvenile survival rate, adult survival rate and brood size.

The value of each rate was perturbed in turn across the range -50 to +10% of its mean value and the subsequent proportion of 10,000 simulations which decline below each of the population thresholds recorded. This proportion provides a measure of the quasi-extinction probability (error bars have been omitted due to their small size). The most sensitive rate in terms of quasi-extinction risk is mean adult survival (middle panel). The standard deviations for the demographic rates were also perturbed across the same range, but are not shown here. The risk of quasi-extinction is extremely insensitive to change in the standard deviation of juvenile survival and brood size, and only changes by a few percent with change in the standard deviation of adult survival.

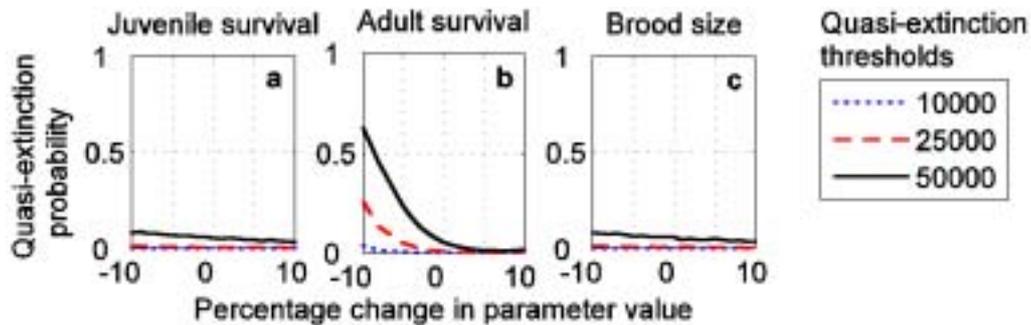


Figure 6 Quasi-extinction probabilities within 25 years for the Icelandic pink-footed goose population obtained with change in the size of the current shooting bag. The existing combined shooting bag for Iceland and the UK (estimated to be approx. 38,000/yr) is represented at 0 on the x-axis. Positive values on the x-axis represent an increase in the number shot, negative values a decrease.

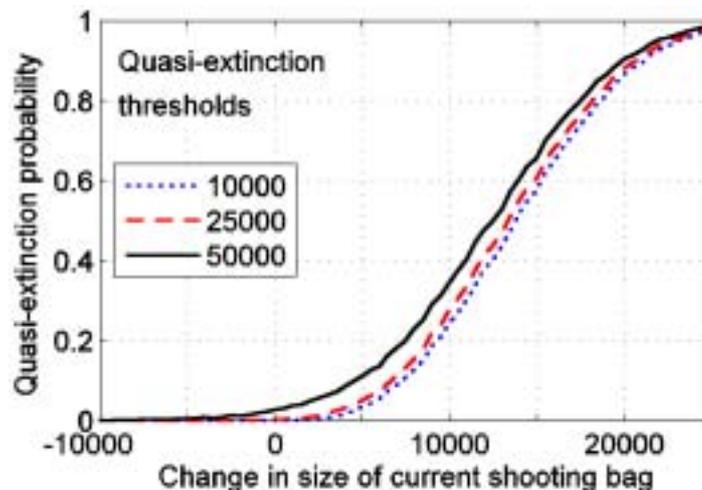


Figure 7 Plots of the probability of quasi-extinction within 100 years for the Icelandic pink-footed goose in response to changing frequency and severity of catastrophic mortality events. The annual probability of a catastrophe occurring (y-axis, lower-left) varies between an average of once in every 10 years (0.1) to once in every 1000 years (0.001). The occurrence of a catastrophe in any particular year of a population simulation is determined by a random 'coin-toss' process. The proportion of the population removed by a catastrophe (x-axis, lower right) varies between 0–0.9 (ie 0–90% of the population dies). Quasi-extinction probabilities (z-axis, vertical) are derived from the proportion of simulations (out of 1000) which fall below population thresholds of 10,000 and 50,000 individuals within 100 years. For example, the risk of the population falling below 10,000 individuals within 100 years (Figure 7a) when catastrophes occur on average once every 10 years ('annual probability of catastrophe' = 0.1) is negligible when less than 30% of the population is killed ('catastrophic mortality \leq 0.3), but rises rapidly as a greater proportion of the population is removed. However, the likelihood of the population being reduced below 50,000 (Figure 7b) is almost certain ('quasi-extinction probability' = 1) when catastrophes occur on average once every 10 years and 50% or more of the population is removed.

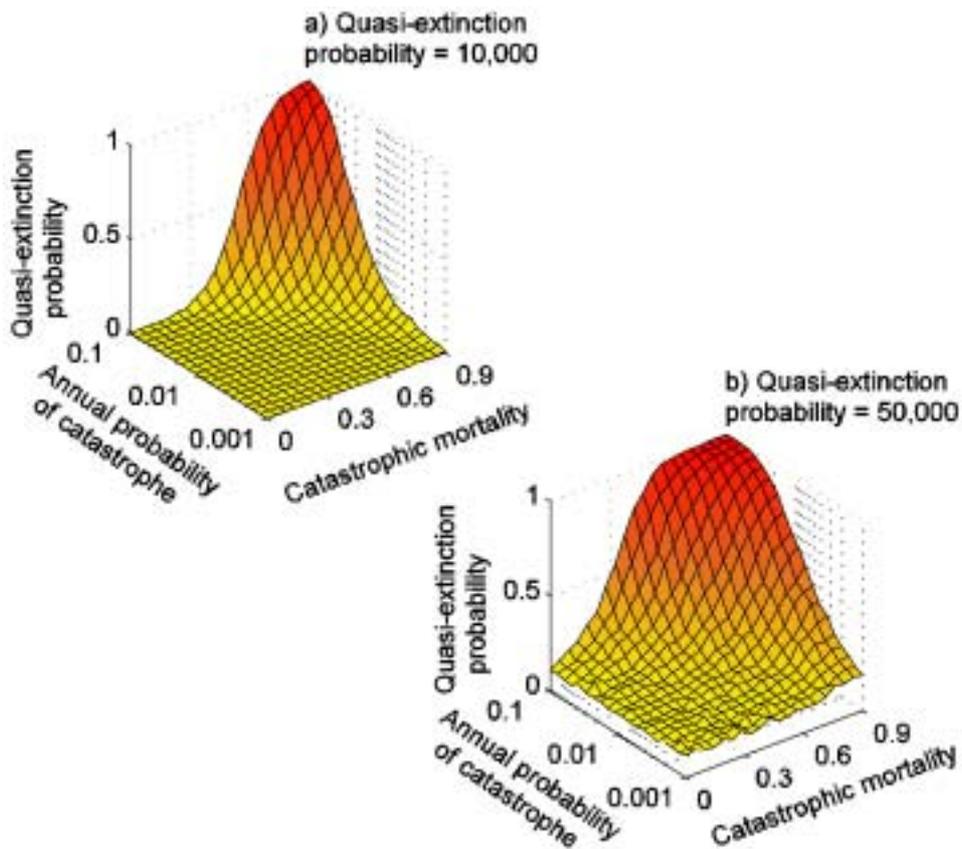


Figure 8 Predicted quasi-extinction probabilities resulting from increasing levels of breeding habitat loss.

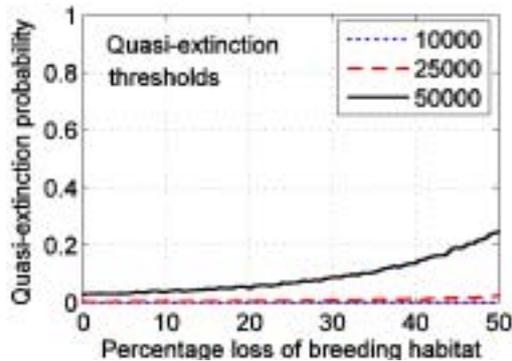


Figure 9 Predicted stochastic growth rate over 25 years resulting from increasing levels of breeding habitat loss. The solid red line indicates the average stochastic growth rate and the dotted blue lines are the upper and lower 95% confidence intervals. Over 50% of simulated populations decline when habitat loss exceeds 4%.

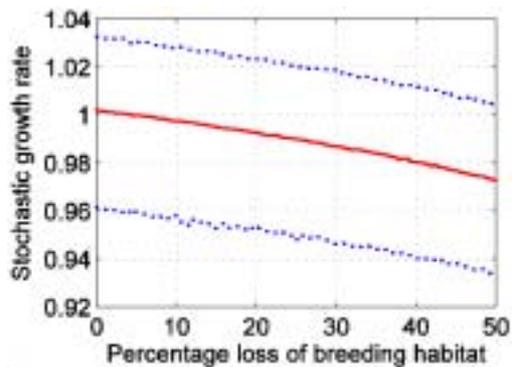
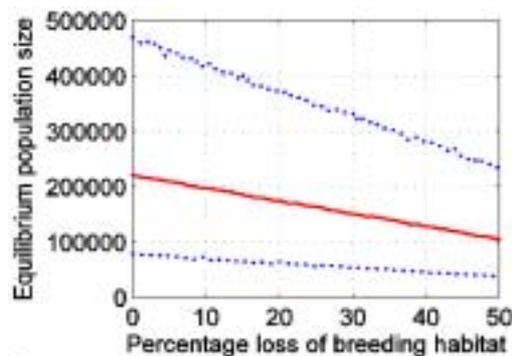


Figure 10 The predicted population size in 25 years resulting from increasing levels of breeding habitat loss. The solid red line is the predicted median population size, the dotted blue lines the upper and lower 95% confidence intervals.



N.B. In all the above cases (Figures 8–10) breeding habitat loss was simulated by reducing the population threshold parameter of the density-dependent proportion of breeding birds. The percentage habitat loss is relative to the estimate of the current breeding population in Iceland.

APPENDIX 1

Calculation of demographic data and age class sizes for the Icelandic breeding population of pink-footed geese using the annual total population count (N), proportion of juveniles (j) and mean brood size (bs) data. In all of the following equations subscript 't' is used to denote the current year, 't-1' the previous year.

Number of juveniles:

$$J_t = j_t * N_t$$

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

$$S_t = \frac{N_t - J_t}{N_{t-1}}$$

Number of birds in their second year:

$$N2_t = J_{t-1} * S_t$$

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:

$$PB_t = \frac{J_t / bs_t}{0.5 * N3_t}$$

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

Threshold density-dependence:

(Parameters: Nlim = threshold population size of breeding age birds;
MaxPB = maximum proportion of breeders)

If $N3_{t-1} < Nlim$

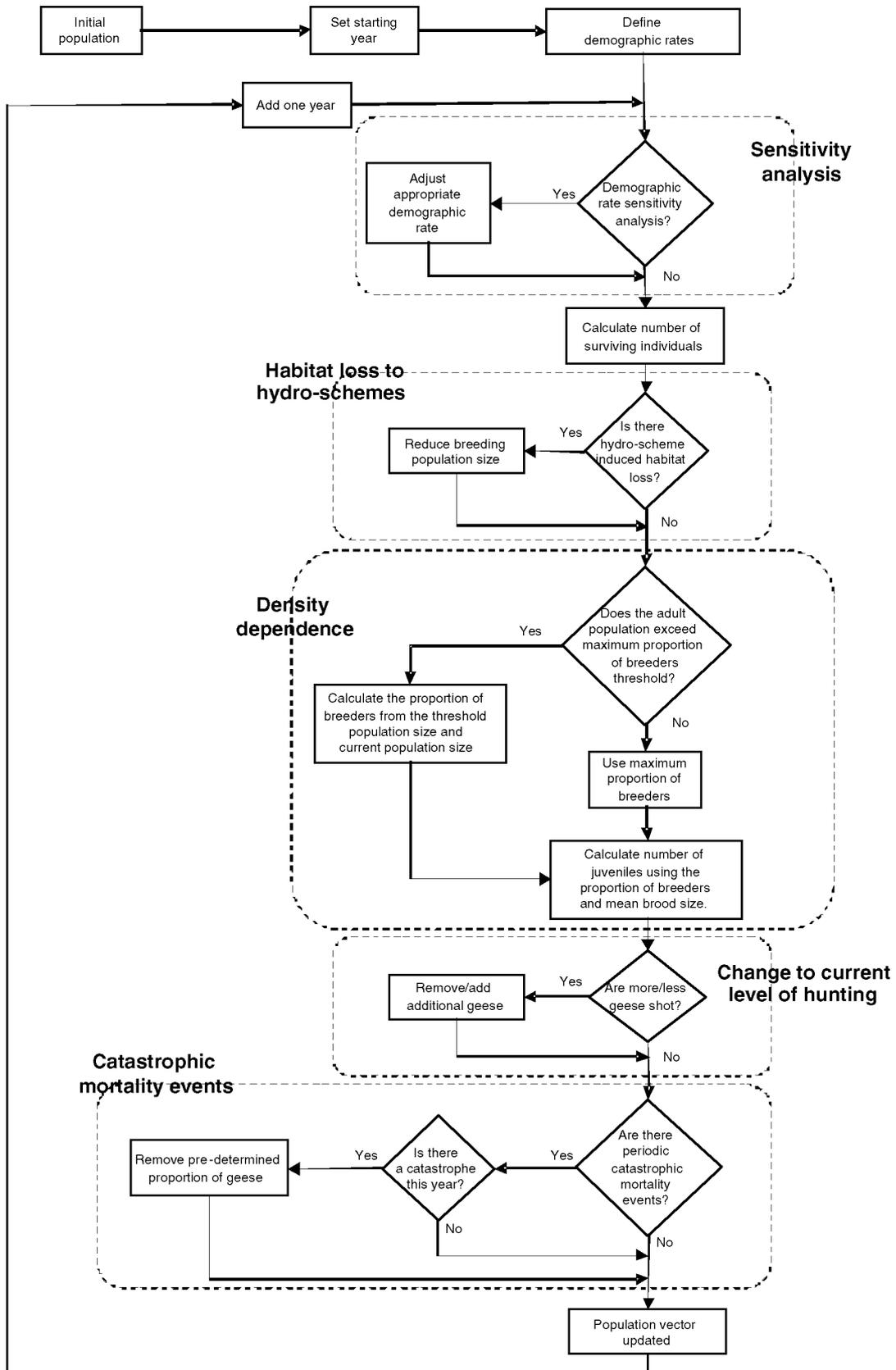
$$DDpropB_t = MaxPB$$

If $N3_{t-1} > Nlim$

$$DDpropB_t = MaxPB * \frac{Nlim}{N3_{t-1}}$$

The parameters for the threshold model were identified in two stages. First the values for the MaxPB and Nlim were estimated from the proportion of breeding birds and number of breeding age birds in the previous year using the pre-1984 data (best fit was established using a least squares methodology). Subsequently a second, higher, Nlim was found which provided the best fit to the existing MaxPB value when applied to the post-1987 data. This second Nlim value was used in conjunction with the MaxPB in the population simulations.

APPENDIX 2 – Flow chart describing the density dependent, stochastic population model for the pink-footed goose



2 STATUS AND POPULATION VIABILITY OF THE GREENLAND WHITE-FRONTED GOOSE IN SCOTLAND

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2.1 Introduction

This report summarises the analysis of census and productivity data collected for the population of Greenland white-fronted geese (*Anser albifrons flavirostris*) which winters along the north and west coasts of Scotland. Trends in the population counts and derived demographic rates are described, along with the outputs from population viability models developed using the demographic rates. Factors which may influence the future growth of the population are discussed. Several competing hypotheses have been put forward to explain the recent downward trend in the global population, these include shooting on the staging grounds in Iceland and competition for breeding space from a growing population of Canada geese (Tony Fox, *pers. comm.*).

Ruttledge & Ogilvie (1979) presented the historical information available for the Greenland white-fronted goose and estimated that, while in the 1950s the population numbered between 17,500–23,000, by the late 1970s it had fallen to 14,300–16,600. A coordinated count network was established in 1982 by the Greenland White-fronted Goose Study (GWGS), and this group has continued to collect annual count and age ratio data from all known flocks within the UK (Fox, 2003). Analysis of the data collected by the GWGS is presented here, along with predictions of the future population size and potential risks to the population derived from models developed using these data. The main conclusion of a previous assessment of the population's viability (Pettifor *et al.*, 1999) indicated that the Scottish sub-population was experiencing a period of slow growth (c. 7% per annum) but the long-term viability of the population would be compromised by a relatively modest reduction (>2%) in survival.

2.2 Methods and results

The population data have been collected synchronously at up to 30 sites in Scotland since 1982 (last available census date: spring 2003). The measures collected at these sites are: the total number of geese, the proportion of the total made up of juveniles and the mean brood size. The juvenile proportion and mean brood size have not been collected in all years at some of the sites, and the data from these were therefore amalgamated for analysis, reducing the number of sites in the analyses to 23. The data were also combined to provide estimated values for the total Scottish population, with the juvenile proportion and mean brood size measures first weighted by flock population size. The raw demographic information was used to derive three further demographic parameters:

- 1 the annual survival rate (the proportion of the population surviving from one year to the next),
- 2 the productivity rate (the number of young produced per breeding age adult on arrival in Scotland),
- 3 the proportion breeding (the proportion of breeding age birds returning to Scotland with young).

See Appendix 2 for the derivation of these parameters.

2.2.1 Analysis of population count data

Numbers in Scotland as a whole have increased from the estimated low point of the late 1970s. From 7141 geese recorded in Scotland over the 1982/83 winter, the Scottish population increased to a peak of 21,164 in 1998/9 before subsequently declining to 17,563 in 2002/3 (Figure 1). This compares to the global trend (including the Irish counts, collected by the National Parks and Wildlife Service), with a total population of 16,541 in 1982/3, a peak of 35,573 in 1998/9 and a decline to 26,454 in 2001/2 (the most recent total population count available; Figure 2). The best-fitting, quadratic regression lines to the log transformed data are provided in Figure 3. In order to determine if there is any evidence for a decline in the population growth rate as the population has increased, tests for the presence of density-dependence in the population time series were conducted using the randomisation test of Pollard *et al.* (1987) and the boot-strap test of Dennis & Taper (1994). Both tests yield significant p-values (Pollard *et al.*: $p = 0.033$; Dennis & Taper: $p = 0.039$), thus the count data suggests that the Scottish population of white-fronted geese is currently regulated by density-dependence.

Approximately one third of the local Scottish winter flocks (accounting for 25% of the total population size) have increased linearly since 1983. Another third (accounting for slightly less than 70% of the Scottish total), initially increased, before peaking (between 1987–1998) and have since declined. The remaining third of the winter flocks (accounting for approximately 5% of the Scottish total) display no significant temporal trends. Amongst the flocks which have increased in size, the individual rates of increase have not been the same, leading to changes in the distribution of white-fronted geese in Scotland. For example, the percentage of the Scottish population wintering on Islay increased between 1982–2003 from 48–60%, while the percentages at Machrihanish and Rhunahaorine (on the neighbouring Kintyre peninsula) have barely changed, remaining at around 6–8% of the Scottish total (see Appendix 1, Table 3 for further details). However, it should be noted that while the numbers on Islay peaked in the 1998/99 winter and have since declined, there is no evidence for a peak in the numbers on Kintyre (Figure 1c). The cause of this difference is not yet clear, but does not appear to be due to differences in the productivity associated with each winter flock (paired t-test: $t=0.84$, $p=0.4$). There is no clear geographical pattern to these different trends, with all three categories spread throughout Scotland, nor does there appear to be a connection between the type of growth observed for any particular flock and the presence of Local Goose Management Schemes (LGMS). Among the flocks found within LGMS areas, two have increased linearly (Tiree, Kintyre), three have peaked (Islay, Coll, Orkney) and one has shown no significant trend (Uists).

2.2.2 Analysis of demographic data

The mean annual demographic rates (and their standard deviations) derived using the Scottish population data between 1982–2003 are provided in Table 1, together with the same rates calculated using the run of years available at the time of the previous PVA (1982–1994; Pettifor *et al.*, 1999). These are presented with those years of data collected since (1995–2003), in order to highlight where changes have occurred (see Appendix 2 for calculation methodology). Comparing the previous and current estimates (columns 1 and 2 in Table 1), the only parameter which has changed significantly is the proportion breeding (2 sample t-test, $t = 2.72$, $p = 0.014$). Declines in both the proportion of juveniles and the overall productivity approach significance at the 5% level (prop juveniles: $t = 1.94$, $p = 0.067$; productivity: $t = 1.89$, $p = 0.074$). Thus it appears that adult survival has not changed, and birds which breed are still producing similar numbers of young. However, the proportion of the population which breeds in any particular season has declined, thus reducing the proportion of juveniles seen in Scotland and the overall productivity.

Table 1 Demographic parameters derived from the Scottish population count, proportion of juveniles and brood size estimates for the periods 1982–94, 1995–2003 and all years 1982–2003. The rates as derived for the previous PVA exercise (Pettifor *et al.*, 1999) are included for comparison with the more recent estimates. The survival rate is a combined estimate for all birds older than c.6 months, calculated as the number of adults in the current year divided by the total population in the previous year; productivity is the ratio of juveniles to breeding age adults; mean brood size is the estimated family size in a sample of Scottish flocks; proportion of juveniles is the percentage of juveniles in a sample of Scottish flocks; proportion breeders is the minimum number of adults required to have bred (in order to account for the estimated number of juveniles) divided by the total adult population. See Appendix 2 for further details.

	Previous estimate (1982–1994)	Current estimate (1995–2003)	Overall estimate (1982–2003)
Parameter	Mean (St. dev)	Mean (St. dev)	Mean (St. dev)
Survival	0.898 (0.059)	0.895 (0.086)	0.897 (0.069)
Productivity	0.198 (0.079)	0.131 (0.078)	0.172 (0.083)
Mean brood size	3.293 (0.301)	3.342 (0.357)	3.342 (0.357)
Proportion juveniles	0.162 (0.054)	0.112 (0.061)	0.143 (0.061)
Proportion breeders	0.143 (0.050)	0.083 (0.043)	0.120 (0.044)

Density-dependence in the demographic rates was investigated by testing for relationships between the reproductive parameters in Table 1 and population density (for all years: 1982–2003). There is strong evidence that the proportion breeding, as observed on the wintering grounds, is negatively related to the population size in the previous year (linear regression of proportion breeders vs. breeding age birds: $F=9.76$, $p=0.006$). An improved fit to the data was obtained using a threshold model, developed to explain this relationship in more mechanistic biological terms. This model has two parameters; a maximum proportion of breeding birds (0.159) which is achieved when the number of breeding age birds is below a threshold size (8180). Above this number of adults the proportion breeding declines at a constant rate with increasing population size (see Appendix 2 for further details).

Clearly it would be useful to know if the decline in the proportion of breeding birds has been shared equally among all the regional sub-populations, however ageing of flocks (necessary to determine the proportion of juveniles and mean brood sizes) has only been undertaken in every year at one site (Islay), with the remaining sites being sampled between 1–19 times over the 21 year data span. Consequently the only reasonable sub-division is to split the data into two: Islay and the ‘rest of Scotland’. Analysis of the two resulting datasets suggests there may be different regulatory mechanisms operating within the two sub-groups. On Islay the apparent survival rate has declined with increasing local population density while the reproductive parameters show no detectable trends, whereas the opposite pattern is seen in the rest of Scotland data, with reproduction falling but no trend in survival. This contrast may be a reflection of different conditions experienced by each sub-population on either the breeding or the wintering grounds. For example, the two sub-groups could be at different stages in relation to their respective wintering ground carrying capacities, with the consequence that different demographic rates are currently more sensitive to population density. Unfortunately we have insufficient data with which to determine the causes of these results at present, and we cannot rule out the possibility that the apparent relationships may be artefacts of differential movement rates between the sites.

2.3 Population model

A model to simulate the Scottish Greenland white-fronted goose population was developed using the data derived from the above analyses. In each year of a simulated population the survival rate and mean brood size are drawn at random from probability distributions defined by the observed data. The proportion of the population which breeds each year is calculated using the density-dependent threshold model described above (section 2.2; see Appendix 3 for a flow chart of the model structure). The population model was used to investigate the risk of population decline below specific thresholds (quasi-extinction) within the short to medium term, as a result of changes in conditions which may affect the population. The term quasi-extinction probability as used here refers to the likelihood that the population will fall below a specific size within a particular period of time (eg the chance that the population will fall below 10,000 in the next 25 years), expressed as a proportional (or percentage) probability.

2.3.1 Baseline model outputs

The model predicts a median equilibrium Scottish population size of just under 20,000 (Figure 4), assuming the current conditions and demographic rates are maintained (ie there is no change in the number shot in Iceland, nor is there any loss of available habitat in either Greenland or Scotland). However, each individual population trajectory varies considerably over time, with the result that approximately 1% of simulated populations fall below 10,000 within the next 25 years and 5% fall below 10,000 in the next 100 years. Thus, even though the summary population plot suggests that the population will, on average, be maintained around its current size, there is still a chance that it will fall significantly. The most sensitive demographic rate in terms of its influence on the likelihood of population decline is adult survival (Figure 5), which is typical of long-lived, slow breeding species. If mean adult survival is reduced by 5% the model predicts that within 25 years there is a 50% probability of the population falling below 10,000 individuals. By contrast the same 5% reduction in either the mean juvenile survival rate or the mean productivity rate yields a less than 3% chance of the population falling below 10,000.

2.3.2 Risk analysis

2.3.2.1 Additional shooting

Accurate reporting of shooting bags in Iceland since 1995 indicates that an average of just over 3,000 Greenland white-fronted geese are shot annually in Iceland (source: Icelandic Institute of Natural History), of which one third on average are juvenile birds. It is estimated that approximately 100–200 geese are also shot in Greenland each year (Fox & Stroud, 2002). This level of shooting is implicitly included in the model structure, and changes to this are modelled simply as an increase or decrease in the size of shooting bag. Model predictions of the probability that the population will decline below key thresholds (1,000, 5,000, 10,000) in response to changes to this level of shooting mortality are shown in Figure 6. To simulate the different levels of shooting mortality, the appropriate number of geese are either removed (representing an increase in shooting) or added (representing a reduction in shooting) during the post-breeding period each year. The bag consists of both juveniles and adults, with the juvenile proportion of the bag set at 0.33. If the current level of shooting is maintained, the probability of the population falling below 10,000 within 25 years is less than 1%. As the additional number shot each year increases, the probability of population decline rises. For example, the risk of decline below 10,000 increases to 13% if 500 extra birds are shot each year, and exceeds 50% if more than 800 extra birds are shot. In making these predictions we are

assuming that the extra shooting mortality occurs in addition to the underlying mortality rate, rather than replacing other 'natural' causes. There is some justification for this assumption as analysis of survival rates for the Irish population collected before and after the shooting moratorium there indicated that shooting loss was additive, rather than compensatory (Fox *et al.*, 1998).

2.3.2.2 Catastrophic mortality

The risk analysis thus far has assumed that patterns of variability in the future will remain the same as observed over the last 25 years. Over longer periods, it is likely that there will be occasional "catastrophic" events, causing mortality well above the range of values observed in the relatively short span of data available to us (for example, severe storms in the north Atlantic during migration). The sensitivity of the population to occasional large increases in mortality was therefore investigated by recording the quasi-extinction probability resulting from the removal of a proportion of the population at random intervals (Figure 7). At the beginning of each simulation the average annual frequency of catastrophes (from 1 in 1000 years to 1 in 10 years) and the proportion of the population to be removed by each event are selected (between 10–90%). The likelihood of the population falling below 1,000 individuals within 100 years is extremely small, unless catastrophes are either moderate but frequent (removing more than 40% of the population once every 10 years on average), or infrequent but severe (90% removal one year in 500). However, if catastrophes occur on average at least once in 100 years then the probability of the population falling below 10,000 (within 100 years) rises rapidly to substantial levels as the percentage of the population removed increases above around 30%.

2.3.2.3 Canada goose population expansion

Over the last 30 years the status of a population of Canada geese on the west coast of Greenland has changed from that of 'rare breeders' prior to 1980, to 'locally common breeders' by the early 1990's. In 1999 an aerial survey of the region estimated there to be a breeding population of at least 2500 pairs (Malecki *et al.*, 2000). This same survey revealed that, while the populations of Canada and Greenland white-fronted geese overlapped at the broad scale, at a local level there was a high degree of separation. Canada geese are believed to be behaviourally dominant over white-fronted geese (Malecki *et al.*, 2000), which has led to concern about the possible effects on white-fronted goose productivity should the number of Canada geese continue to increase. In addition, it is estimated that 80% of the observed Canada geese were using a region more generally associated with birds from the Scottish portion of the white-fronted goose population (Fox *et al.*, 1983), although there has been no recent reassessment of this geographical relationship.

We explored the potential consequences of an increase in the Greenland breeding population of Canada geese and the associated loss of breeding territories for Greenland white-fronted geese using the model. In doing this it is assumed that Canada geese are dominant over white-fronted geese, and that each additional pair of Canada geese in the population displaces one pair of white-fronted geese, who are thus prevented from breeding. Although the Greenland breeding population of Canada goose has clearly increased over the last 25 years, there is insufficient information with which to describe the pattern of increase in detail. We therefore simulated three different forms of population growth: asymptotic, linear and exponential. The model predicts that any growth in the Canada goose population, irrespective of the type of slope (asymptotic, linear or exponential) causes the white-fronted goose population to decline on average, with a consequent increase in the likelihood of quasi-extinction (Figure 8). For example, if the Canada goose

population doubles over the next 25 years, following a simple linear growth (Figure 8b), the model predicts a 28% probability that the white-front population will be reduced below 10,000 (Table 2). If the Canada goose population trebles in size to 15,000 (following the same linear growth, over the same time period) the model predicts a 35% probability that the white-front population will decline below 5,000 individuals. The projected white-front quasi-extinction risk over 25 years obtained if the Canada goose population grows linearly to a range of final sizes is shown in Figure 9. Thus, it can be seen that if the number of Canada geese breeding on Greenland increases by even quite modest amounts the model predicts significant declines in the white-front population.

Table 2 Quasi-extinction probabilities resulting from increase in the Canada goose population to either 10,000 or 15,000 by 2028. Three possible Canada goose population growth types are listed (linear, asymptotic and exponential) and the white-fronted goose population thresholds are at 1000, 5000 and 10000 individuals. If the Canada goose population increases to 15,000 by 2028 either linearly or asymptotically the model predicts there is a greater than 95% probability of the Greenland white-front population falling below 10,000. See Figure 8 for examples of population plots for both species when the Canada goose population increases to a final size of 10,000 and Figure 9 for an illustration of how the quasi-extinction probability changes with increasing Canada goose population.

		Predicted Canada goose population size in 2028					
		10,000			15,000		
GWF Quasi-extinction threshold		Linear	Asymptotic	Exponential	Linear	Asymptotic	Exponential
1000	Extinction probability	0	0	0	0	0.03	0
5000		0.0001	0.007	0	0.35	0.99	0
10000		0.28	0.77	0.02	0.96	1.0	0.15

2.4 Conclusions

2.4.1 Implications of PVA results for Scottish Greenland white-fronted goose population

- 1 The baseline model predicts an equilibrium Scottish population size of around 20,000, with a low risk of decline below 10,000 within 25 years, assuming the conditions experienced over the last 20 years are maintained.
- 2 The recent stabilisation and slight decline in the population appears to be attributable to a reduction in the proportion of birds breeding successfully, rather than any changes in the mean brood size or adult survival rate.
- 3 The most sensitive demographic rate is adult survival. The probability of significant population decline is greatly enhanced by even modest increases in the shooting bag (eg 800 extra adults shot/yr yields a 50% probability of population decline below 10,000 in 25 years).
- 4 Expansion of the Greenland breeding population of Canada geese, and subsequent competition for territories with white-fronts may severely reduce the latter's overall productivity, leading to a high risk of significant population decline.

2.4.2 Advice

- 1 An assessment of the current status and growth rate of the Canada goose population on Greenland, together with investigations of the nature of interactions between the species on the breeding grounds should be made a priority.
- 2 The sensitivity of the population to changes in the adult survival rate indicates that additional shooting should be avoided, since a comparatively small increase in shooting loss may have a significant impact on the likelihood of population decline.
- 3 It was not possible to determine if the apparent differences between Scottish sub-populations with regard to density-dependent regulation of population processes is real or an artefact of unequal movement between sites. We therefore suggest that increased efforts are made to ring and re-sight colour marked individuals in Scotland in order to clarify this issue.
- 4 In addition a greater geographical spread in the recording of juvenile proportions and mean brood sizes would improve the estimation of breeding performance.
- 5 In the light of the above recommendations it is imperative that population monitoring is maintained at least at its current level in order that any further population changes are detected at the earliest possible time.

2.5 References

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Figure 1 Greenland white-fronted goose population plots, 1982–2002/3. The Irish population peaked earliest (early 1990s) while the Scottish and total lines peaked in 1999.

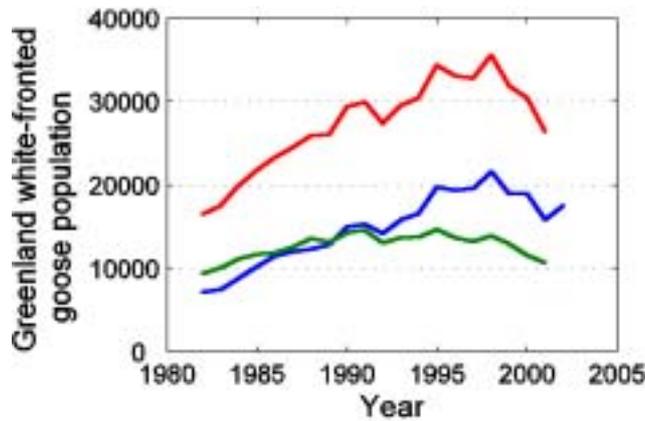
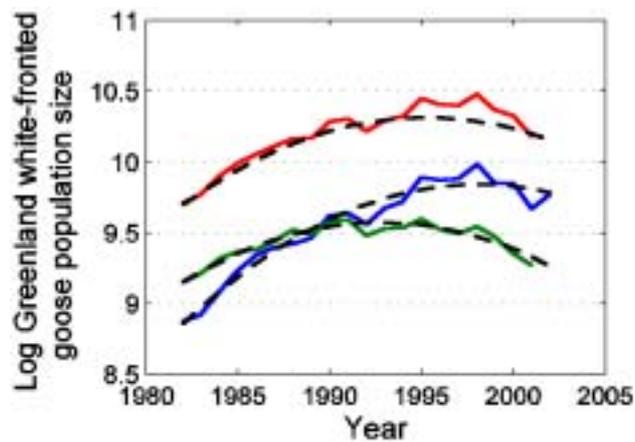


Figure 2 Log population plots of Greenland white-fronted goose population, 1982–2003. The best-fit lines are quadratic regressions:

Total population: $\text{Log}_e(N) = -0.0035\text{yr}^2 + 0.1\text{yr} + 9.6$; $R^2 = 0.94$; $F = 132.8$; $p < 0.001$;

Scottish population: $\text{Log}_e(N) = -0.0038\text{yr}^2 + 0.13\text{yr} + 8.73$; $R^2 = 0.95$; $F = 190.1$; $p < 0.001$;

Irish sub-population: $\text{Log}_e(N) = 0.0036\text{yr}^2 + 0.085\text{yr} + 9.07$; $R^2 = 0.89$; $F = 83.4$; $p < 0.001$.



NB: in Figures 1 and 2, the upper (red) line is the total population, the middle (blue) line is the Scottish sub-population and the lower (green) line is the Irish sub-population.

Figure 3 Log plots of selected Scottish flocks, 1982–2003. Islay flock – blue line, best-fit polynomial regression, Kintyre flocks – red (Rhunahaorine) and green (Machrihanish), best fit linear regressions. It can be seen that the Islay population peaked in 1998/99 and has since declined, while the Kintyre populations appear to be still increasing. The missing counts from 2000 were due to the foot and mouth outbreak preventing full coverage.

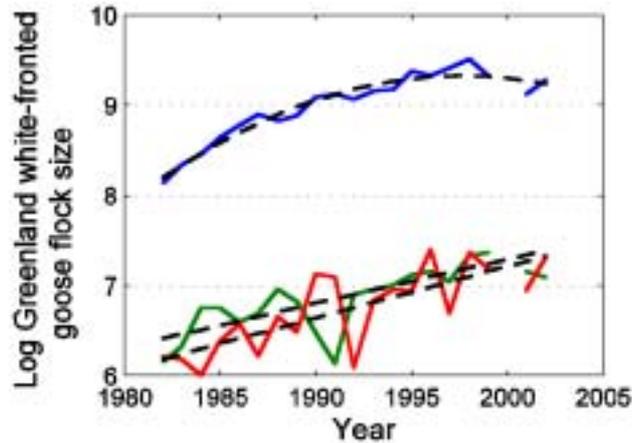


Figure 4 Scottish Greenland white-fronted goose population projected until 2028. The solid red line is the median population size, the dashed and dotted blue lines respectively the 50% and 95% confidence intervals. The black line is the observed population count. The model predicts a median Scottish equilibrium population size of approximately 19,700.

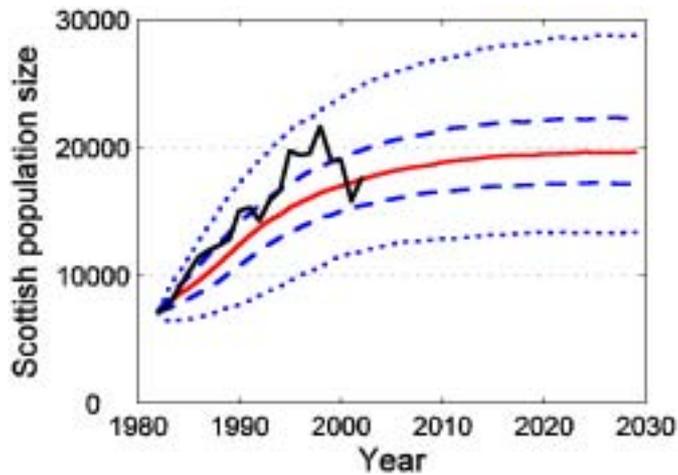


Figure 5 Plots indicating the relative sensitivity to change of the different demographic parameters in the Greenland white-fronted goose population model. The graphs indicate the probability of the population declining below critical levels (ie quasi-extinction at: 10,000, solid black line; 5,000, dashed red line; 1,000, dotted blue line) within 25 years as a result of equivalent proportional change to the mean juvenile survival rate, adult survival rate and mean brood size. [It should be noted that the actual survival rate value used for juveniles and adults is the same, as we do not have independent estimates of annual survival for each age class. However simulations have revealed that this does not have a significant effect on the results of this analysis].

The value of each rate was perturbed in turn by +/- 10% of its mean value and the subsequent proportion of 10,000 simulations which decline below each of the population thresholds recorded. This proportion provides a measure of the quasi-extinction probability (error bars have been omitted due to their small size). The most sensitive rate in terms of quasi-extinction risk is mean adult survival (middle plot). The standard deviations for the demographic rates were also perturbed across the same range, but are not shown here. The risk of quasi-extinction is extremely insensitive to change in the standard deviation of juvenile survival and brood size, and only changes by a few percent with change in the standard deviation of adult survival.

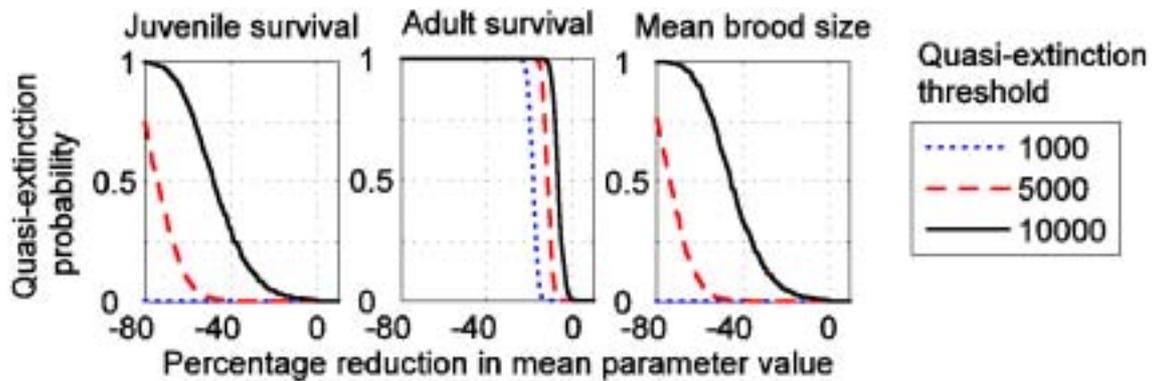


Figure 6 Quasi-extinction probabilities within 25 years for the Scottish Greenland white-fronted goose population obtained with changing levels of shooting pressure. When the size of the shooting bag equals 0, the quasi-extinction probabilities are those predicted under the current level of shooting mortality (of approximately 3,000/yr.). Negative values for the shooting bag represents a reduction in the bag size, positive values an increase in bag size. The probability of decline below 10,000 within 25 years is greater than 50% when the additional number of geese shot per year exceeds 800.

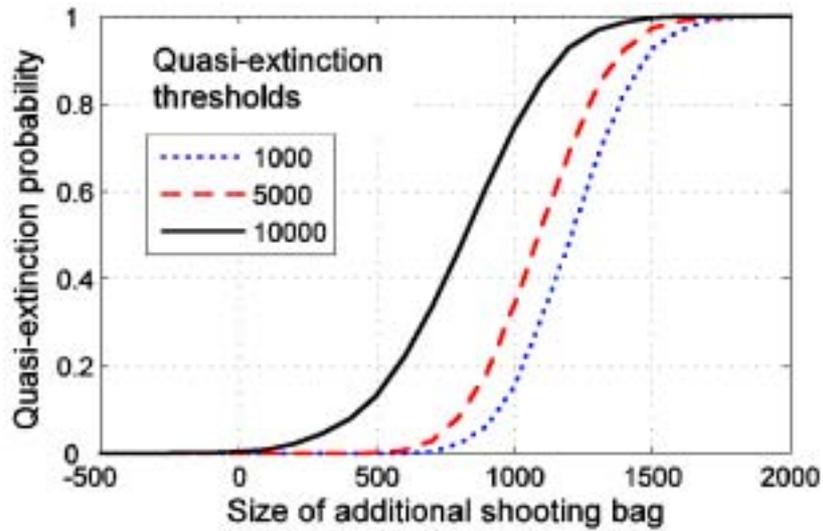


Figure 7 Plots of the probability of quasi-extinction within 100 years for the Scottish population of Greenland white-fronted geese resulting from catastrophic mortality events. The annual probability of a catastrophe occurring (y-axis, lower-left) varies between an average of once in every 10 years (0.1) to once in every 1000 years (0.001). The occurrence of a catastrophe in any particular year of a population simulation is determined by a random 'coin-toss' process. The proportion of the population removed by a catastrophe (x-axis, lower right) varies between 0–0.9 (ie 0–90% of the population dies). Quasi-extinction probabilities (z-axis, vertical) are derived from the proportion of simulations (out of 1000) which fall below population thresholds of 1,000 and 10,000 individuals within 100 years. For example, the risk of the population falling below 1000 individuals within 100 years (a) when catastrophes occur on average once every 10 years ('annual probability of catastrophe' = 0.1) is negligible when less than 30% of the population is killed ('catastrophic mortality <= 0.3), but rises rapidly as a greater proportion of the population is removed. However, the likelihood of the population being reduced below 10,000 (b) is almost certain ('quasi-extinction probability' = 1) when 50% or more of the population is removed on average once every 10 years.

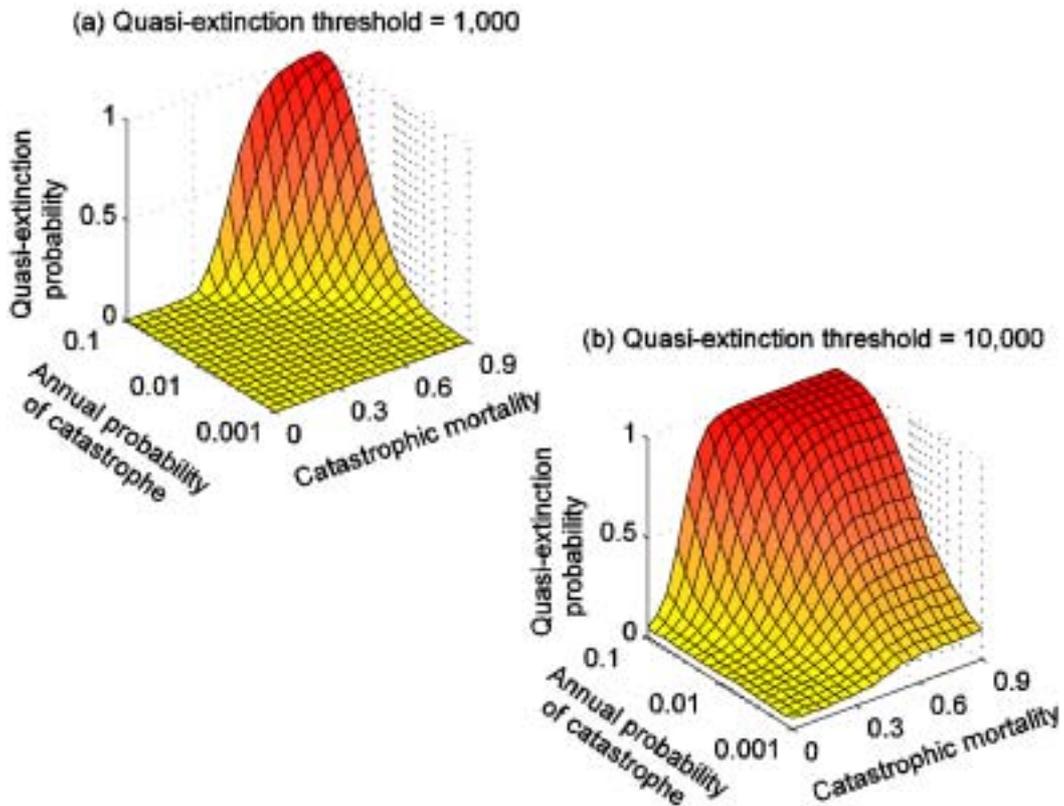


Figure 8 Projected change in the Greenland white-fronted goose population in the presence of four different projected Canada goose populations. In each graph the Canada goose population (black dash-dot line) begins at 5000 in 1999 (based on the Greenland Canada goose census carried out in that year) and either remains at that level (8a), or increases to 10,000 over 25 years following one of three trajectories: (8b) linear, (8c) asymptotic and (8d) exponential. The predicted Greenland white-front population size derived from 1000 simulations is also shown (median population size: solid red line; 95% confidence intervals: dotted blue lines and 50% confidence intervals: dashed blue lines). As the Canada goose population increases the number of breeding territories available for Greenland white-fronts decreases, under the simplifying assumption that each additional pair of Canada geese prevents one pair of white-fronts from breeding. Thus the overall white-front productivity is reduced leading to a reduction in size of the white-front population.

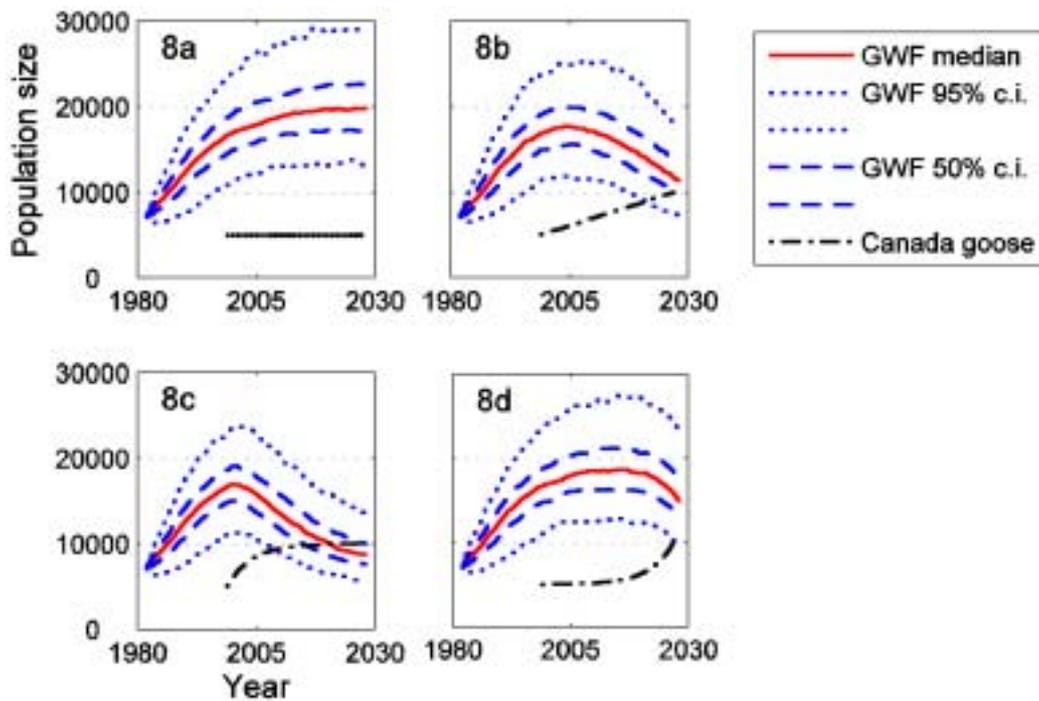
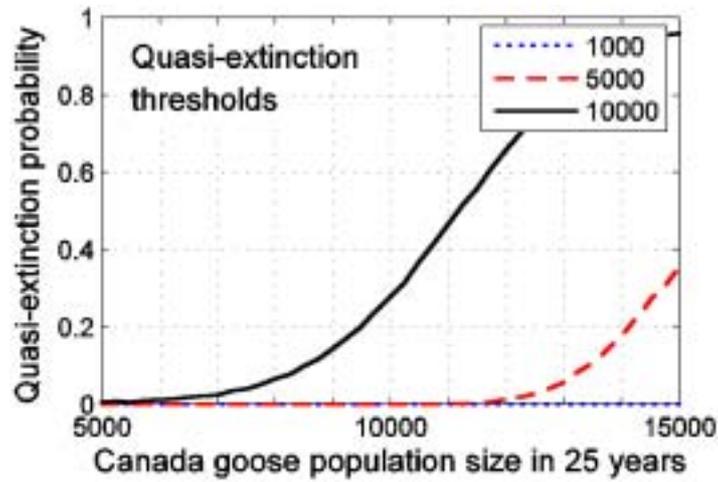


Figure 9 Probability of Greenland white-fronted goose quasi-extinction resulting from growth of the Canada goose population to different sizes over 25 years, obtained using the linear Canada goose growth model. The probability that the white-front population will decline below 10,000 in 25 years if the Canada goose population doubles (to 10,000) is 28%, with the risk rising to 96% if the Canada goose population increases to 15,000.



APPENDIX 1 – Regional Greenland white-fronted goose population count data

Table 3 Change in numbers of 23 Scottish Greenland white-fronted goose populations, 1982/83-2002/03 and the relative proportions of the total Scottish population size. Table 3a lists the populations which have increased linearly in size, Table 3b those which increased to a peak and have subsequently declined and Table 3c those which show no significant trend over the 21 years of data. The left half of each table provides the population sizes in 1982/3 and 2002/3 while the right half provides an average over five years from the beginning (1982/83–1986/87) and end (1998/99–2002/03) of the period. In each case the actual population numbers are given, along with the proportion of the Scottish total which this represents. For both sets of values the change in size, expressed as a percentage is provided. The best-fitting trend for each population was determined using polynomial, least squares regression applied across the complete time series.

(Note: the coefficients, F statistics and probabilities are not included in the Tables)

3a Regional populations which have increased with linear best-fit trends (all statistically significant at $p < 0.05$).

Population	Regional population size (single year)						Regional population size (5 year average)					
	Actual numbers			Proportion of total			Actual numbers			Proportion of total		
	1982	2003	% change	1982	2003	% change	1982-6	1998-02	% change	1982-6	1998-02	% change
Caithness	387	398	3	0.054	0.022	-59	318	421	32	0.035	0.023	-36
Lewis	27	24	-11	0.004	0.001	-65	16	27	75	0.002	0.001	-16
Tiree	433	1040	140	0.061	0.058	-4	505	1199	137	0.056	0.064	15
Benderloch	182	413	127	0.025	0.023	-9	132	340	158	0.015	0.018	25
Rhunahaorine	475	1200	153	0.067	0.067	1	695	1399	101	0.077	0.075	-3
Machrihanish	500	1501	200	0.070	0.084	20	539	1360	153	0.060	0.073	22
Bute	110	186	69	0.015	0.010	-32	131	194	49	0.015	0.010	-28
Total	2114	4762	125	0.296	0.266	-11	2335	4941	111	0.259	0.264	2

3b Regional populations which have increased and subsequently declined, with quadratic and cubic best-fit trends (all statistically significant at $p < 0.05$).

Population	Regional population size (single year)						Regional population size (5 year average)					
	Actual numbers			Proportion of total			Actual numbers			Proportion of total		
	1982	2003	% change	1982	2003	% change	1982-6	1998-02	% change	1982-6	1998-02	% change
Orkney	80	61	-24	0.011	0.003	-70	100	114	14	0.011	0.006	-45
Skye	33	51	55	0.005	0.003	-38	76	43	-43	0.008	0.002	-73
Muck	20	32	60	0.003	0.002	-36	33	32	-4	0.004	0.002	-53
Coll	230	605	163	0.032	0.034	5	278	862	210	0.031	0.046	49
Colonsay	58	156	169	0.008	0.009	7	70	126	80	0.008	0.007	-13
Islay	3441	10677	210	0.482	0.597	24	4902	11150	127	0.543	0.596	10
Keills	90	289	221	0.013	0.016	28	80	294	267	0.009	0.016	77
Lomond	66	124	88	0.009	0.007	-25	134	163	22	0.015	0.009	-41
Dyfi	73	126	73	0.010	0.007	-31	86	116	34	0.010	0.006	-35
Total	4091	12121	196	0.573	0.678	18	5760	12900	123	0.639	0.690	8

3c Regional Populations with no significant growth trends.

Population	Regional population size (single year)						Regional population size (5 year average)					
	Actual numbers			Proportion of total			Actual numbers			Proportion of total		
	1982	2003	% change	1982	2003	% change	1982-6	1998-02	% change	1982-6	1998-02	% change
Uists	75	160	113	0.011	0.009	-15	75	102	35	0.008	0.005	-35
Shiel	45	35	-22	0.006	0.002	-69	28	39	43	0.003	0.002	-31
Mull	97	33	-66	0.014	0.002	-86	66	50	-25	0.007	0.003	-64
Jura	79	94	19	0.011	0.005	-52	94	73	-22	0.010	0.004	-63
Moine Mhor	35	29	-17	0.005	0.002	-67	15	31	108	0.002	0.002	1
Stranraer	300	369	23	0.042	0.021	-51	397	263	-34	0.044	0.014	-68
Loch Ken	305	240	-21	0.043	0.013	-69	250	264	6	0.028	0.014	-49
Total	936	960	2	0.131	0.054	-0.55	925	822	-11	0.103	0.044	-57

APPENDIX 2

Calculation of demographic data and age class sizes for Greenland white-fronted geese using the annual population count (N), proportion of juveniles (j) 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: $J_t = j_t * N_t$

Crude annual survival rate (from year t-1 to year t): $S_t = \frac{N_t - J_t}{N_{t-1}}$

Number of birds in their second year: $N2_t = J_{t-1} * S_t$

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: $PB_t = \frac{J_t / bs_t}{0.5 * N3_t}$

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

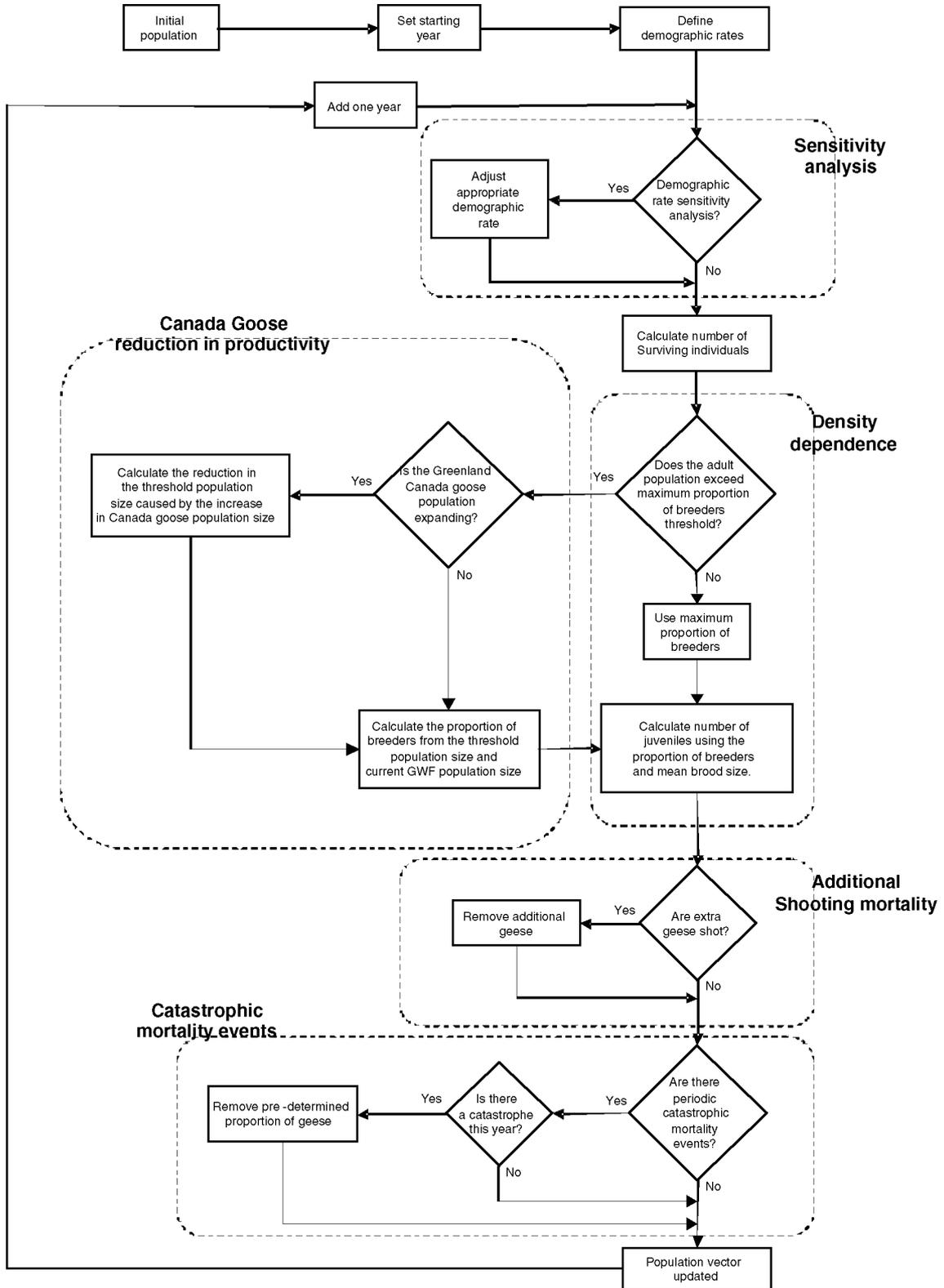
Threshold density-dependence:

(Parameters: Nlim = threshold population size of breeding age birds;
MaxPB = maximum proportion of breeders)

If $N3_{t-1} < Nlim$ $DDpropB_t = MaxPB$

If $N3_{t-1} > Nlim$ $DDpropB_t = MaxPB * \frac{Nlim}{N3_{t-1}}$

APPENDIX 3 – Flow chart describing the density-dependent, stochastic population model for the Greenland white-fronted goose



3 STATUS AND POPULATION VIABILITY OF THE ICELANDIC BREEDING GREYLAG GOOSE IN SCOTLAND

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3.1 Introduction

This report summarises analyses of data for the Icelandic breeding greylag goose *Anser anser* population which over-winters in Scotland and northern England. The data available for this population comprise counts made in Scotland each autumn since 1960, records of the size of the Icelandic shooting bag collected since 1995 and independently derived survival rate estimates for the period 1996–2000 (Frederiksen *et al.*, 2004). Trends in the population counts, and demographic data derived from the counts are discussed. Population models were developed using both the count data, and also the independent estimates for survival and the Icelandic shooting bag estimates. Using these models a range of possible scenarios are explored. This migratory population is distinct from the two resident populations of greylag goose in the UK; the remnant native population which is confined to north and west Scotland (estimated summer 2003 population, 14,000; Swann, 2004) and the re-introduced population, which is more widely distributed in England and Scotland (estimated population, 25,500 in 2001; Pollitt *et al.*, 2003).

3.2 Methods and results

The Icelandic breeding population of greylag geese spends the early part of each winter in north and east Scotland, with large concentrations of geese found during this period at relatively few roost sites. Estimation of the total population size has been undertaken synchronously each year during this period since the 1950s (Mitchell & Sigfusson, 1999). As the winter progresses, the birds disperse more widely within Scotland and northern England. In addition to the population size estimates, since the 1960s the percentage of juveniles and average brood size have been recorded for a sample of flocks, from which population wide estimates are calculated. Using these data three further demographic parameters have been derived:

- 1 the annual (crude) survival rate (the proportion of the population surviving from one year to the next),
- 2 the productivity rate (the number of young produced per breeding age adult on arrival in Scotland),
- 3 the proportion breeding (the proportion of breeding age birds returning to Scotland with young).

See Appendix 1 for the derivation of these parameters.

In 1995 the Icelandic Institute of Natural History (IINH) and WWT initiated research into the dynamics of the Icelandic breeding populations of the greylag goose and the pink-footed goose, with a particular emphasis on improving understanding of the impact of shooting on the two populations. Between 1996–2000 over 1,200 greylag geese were fitted with individually identifiable colour rings in Iceland. Colour rings have also been fitted to a comparable number of geese caught in Scotland each winter since 1992. Combined analysis of the live re-sightings and dead recoveries of the ringed geese has provided adult and juvenile survival rate estimates which, unlike the crude survival rate described above, are independent of population counts (Frederiksen *et al.*, 2004).

Since 1995 renewal of shooting licences in Iceland has required hunters to submit a report of the number of each species they shot in the previous season. There is some evidence of a small amount of over-reporting in these data, but this is not thought to significantly reduce their accuracy (Frederiksen *et al.*, 2004). The shooting bag data collected in this way are made widely available at: <http://www.ust.is/Veidistjornun/Almennt/Veiditolur/>. The number of shot greylag geese reported to the scheme has varied by only a few thousand each year, with an average value of 35,270 (1995–2002; Figure 1). Between 1993–2000 the IINH collected goose and duck wings from hunters, analysis of which provides an estimate of the proportion of juveniles in the shooting bag of 40% (Frederiksen *et al.*, 2004). No equivalent reporting scheme currently exists for hunters in the UK. However, a pilot study based on independent surveys of both British Association for Shooting and Conservation (BASC) members and firearm licence holders in selected Scottish police force regions, provides a preliminary estimation that 15,000 greylag geese are shot in Scotland each year (Hart & Harradine, 2003). It should be noted that this figure does not include additional groups known to shoot geese in Scotland (eg visiting hunters from overseas), nor is it possible at this time to distinguish between the three greylag populations in the UK, so the Icelandic greylag goose proportion of this total is unknown. However, using the reporting probability for geese ringed in Iceland and shot in the UK, together with the Icelandic shooting bag data, Frederiksen (2002) estimated that, given similar shooting conditions to those in Iceland, 20,000–25,000 Icelandic greylag geese are shot in Scotland each winter.

3.2.1 Analysis of population count data

One of the most significant results of the research initiated jointly by IINH and WWT, was the discovery that the different sets of data for the greylag population (population counts, age ratios, shooting bags and survival estimates) do not correspond: the bag statistics imply a population size which is approximately twice the recent autumn estimates, with a much greater proportion of juveniles than that reported (Frederiksen *et al.*, 2004). While all of the parameter estimates have associated errors which together may account for this discrepancy, it is suggested that the survival rates (derived from the ringing, re-sighting and dead recoveries) and the Icelandic shooting figures are the least prone to bias (Frederiksen, 2001). Since the extent to which resident and migratory birds congregate in mixed flocks in Scotland is also unknown, the autumn population counts and proportion of juveniles estimated in Scotland need to be treated with a high degree of caution. However, there are currently no alternative methods available for estimating the population size. Therefore, in the absence of alternative sources of data for all but the last 10 years we have analysed the whole population time series. In doing this we make the assumption that while there is a high probability that the values are inaccurate, they still provide an index of the true population, and trends within the data reflect similar trends in the actual population. The counts indicate the population grew from 30,000 in 1960 to a peak of 115,000 in 1990 and has since declined to less than 70,000 in 2002, (Figure 2). Tests for the presence of density-dependence in the population time series were conducted using the randomisation test of Pollard *et al.* (1987) and the boot-strap test of Dennis & Taper (1994). The test by Pollard *et al.* returned a non-significant p-value of 0.067, while Dennis & Taper's test yielded a significant p-value of 0.031. Thus there is some suggestion that the greylag population has been regulated by density-dependence. However, since a considerable number of birds are shot each year both in Iceland and Scotland, we cannot rule out the alternative explanation that this result may be an artefact of heavy shooting mortality. The following section details further tests for density-dependence in order to clarify this issue.

3.2.2 Analysis of demographic data

While the demographic parameters derived from the count, percentage juvenile and mean brood size estimates should be treated with caution, analysis of the data for trends is still of value in highlighting areas warranting further investigation. Table 1 provides the derived demographic parameter estimates for the greylag population. None of the rates has changed significantly since the previous PVA was developed for this population (Rowcliffe *et al.*, 2000), although this may partly be due to the relatively few years of additional data since that analysis. Investigation of changes in the demographic rates in relation to the current and previous year's population density and environmental conditions was conducted using Generalised Linear Models (GLMs) and Robust Regression. In contrast to standard (ordinary least squares) linear regression, where outlying data points can disproportionately influence the results obtained, Robust Regression methods weight data points according to their proximity to the fitted regression line: points which lie further from the fitted trend consequently have a reduced influence. While GLMs enable interactions between population density and environmental variables to be tested, they are sensitive to the presence of outliers in the data. Conversely, Robust Regression minimises sensitivity to outliers, but cannot handle interactions between parameters. The two methods therefore complement one another. In order to control for environmental effects, weather variables recorded at a weather station located within the breeding distribution (Hamraendar, 22W, 65N) were also used in the analysis. The variables investigated were: mean monthly temperatures (April–July) and the North Atlantic Oscillation (NAO) index for the main migration months (April and October).

Table 1 Icelandic greylag goose demographic parameters derived from the population counts, proportion of juveniles and mean brood size estimates made in Scotland each autumn since 1960. The previous rates represent those available for the previous PVA exercise (Rowcliffe *et al.*, 2000) and are included for comparison with the more recent estimates. The survival rate is a combined estimate for all birds older than c.6 months, calculated as the number of adults in the current year divided by the total population in the previous year; productivity is the ratio of juveniles to breeding age adults; mean brood size is the estimated family size in a sample of Scottish flocks; proportion of juveniles is the percentage of juveniles in a sample of Scottish flocks; proportion breeders is the minimum number of adults required to have bred (in order to account for the estimated number of juveniles) divided by the total adult population. See Appendix 2 for further details.

	Previous estimate (1966–1997)	Current estimate (1998–2002)	Overall estimate (1966–2002)
Parameter	Mean (St. dev)	Mean (St. dev)	Mean (St. dev)
Survival	0.85 (0.17)	0.79 (0.11)	0.84 (0.16)
Productivity	0.27 (0.13)	0.26 (0.05)	0.27 (0.12)
Mean brood size	2.22 (0.34)	2.74 (0.15)	2.3 (0.37)
Proportion juveniles	0.18 (0.07)	0.18 (0.03)	0.18 (0.06)
Proportion breeders	0.23 (0.09)	0.2 (0.04)	0.23 (0.08)

Due to limitations in availability for some of these datasets, and potentially unreliable demographic estimates from the earlier years (due to small sample sizes) the tests were run using data restricted to 1966–2002. No significant interactions between population density and environmental variables were revealed by GLMs,

and the results of Robust Regression are therefore reported here. The only variable which was significantly related to population density was the crude survival rate ($\log_e(N_{t+1})$, $t = -3.36$, $p = 0.002$, negative relationship). The proportion of juveniles, mean brood size and productivity were all positively related to the mean June temperature in Iceland, but not to any population density estimate, while the proportion of breeders was not significantly related to any variable tested. The lack of any detectable relationship between the population's size and reproductive output suggests the population may currently be limited by shooting to a level below the carrying capacity of the breeding range. Since the survival estimates are also strongly affected by the level of shooting mortality, this may account for the apparent density-dependent decline in this rate.

3.3 Population model

Three models were developed for the Icelandic greylag population, each based on a different set of survival and productivity estimates. The first (model 1) uses rates derived from the count, percentage juveniles and mean brood size data collected in Scotland since 1966 (parameters as listed in Table 1). The second (model 2) uses rates calculated in the same way. However, since Frederiksen *et al.* (2004) estimated that the proportion of juveniles in Scottish flocks in the autumn is actually 73% higher than that recorded (caused by misidentification of juveniles in the autumn), the juvenile proportion in each year was multiplied by 1.73 prior to rate calculation. The third (model 3) uses the adult and juvenile survival rates derived from the ring re-sightings and recoveries (Frederiksen *et al.*, 2004) and a productivity rate calculated from these survival rates and an estimate of the combined total shooting bag (ie the Icelandic shooting bag plus Frederiksen's (2002) estimate of the Icelandic greylag shooting bag in the UK; see Appendix 1 for details). It should be noted that this UK shooting bag estimate assumes equivalent shooting conditions in Iceland and the UK (Frederiksen, 2002). Nonetheless, model 3 is based on the least biased data currently available (Frederiksen, 2001). All three models are density-independent since there is currently no compelling evidence for the presence of density-dependent regulation of population growth.

Using these three models, we investigated the risk of population decline below specific thresholds (quasi-extinction) within the short to medium term, resulting from changes in conditions which may affect the population. The term quasi-extinction probability as used here refers to the likelihood that the population will fall below a specific size within a particular period of time (eg the chance that the population will fall below 25,000 in the next 25 years), expressed as a proportional (or percentage) probability.

3.3.1 Baseline model outputs

Using the untransformed count data (model 1) the population is predicted on average to increase at a slow rate (approx, 1.6% per year, Figure 3), reaching a median population size of approximately 180,000 by 2027. In contrast, the models based on the transformed juvenile count data (model 2, Figure 4) and the independent survival rates and shooting bag data (model 3, Figure 5), produce population projections which on average decline, by respectively 1.8% and 3.5% per year (with corresponding median population size estimates of 55,000 and 30,000 by 2027). Models 2 and 3 are in closer agreement with the observed population counts than model 1: since 1992 the population has declined on average by 4.5% per year. As previously noted these counts probably underestimate the true population size, at least in recent years, and while the apparent decline observed in the population could be caused by an increasing proportion of the population being missed during censuses, a previous investigation found little support for

this premise (Rowcliffe *et al.*, 2000). Therefore, if the Scottish counts are considered to be an index of true population trends, the more pessimistic outputs of models 2 and 3 provide a better fit to the data than that from model 1.

For all three models the most sensitive demographic rate in terms of its influence on the likelihood of population decline is adult survival (Figure 6), with the sensitivity to quasi-extinction increasing from models 1 to 3, reflecting the difference in the population predictions (Figures 3, 4, 5). In addition the sensitivity to change in the juvenile survival and productivity rates also increases from models 1–3, due to differences between the models in terms of the relative contribution which these parameters make to the population growth rate. The probability that the population will decline below 25,000 individuals within the next 25 years if there is a 5% reduction, no change or a 5% increase in average adult survival is provided in Table 2. If current conditions are maintained then the probability that the population will fall below 25,000 in the next 25 years varies between 14% (model 1) and 58% (model 3).

Table 2 Probability that the greylag goose population will fall below 25,000 individuals within 25 years, with average adult survival maintained at its current level (middle row) or changed by +/-5%.

Percentage change to adult survival rate	Model number		
	1	2	3
-5	0.46	0.75	0.97
0	0.14	0.43	0.58
+5	0.03	0.16	0.07

3.3.2 Risk analysis

3.3.2.1 Changes to the current level of shooting

The probability that the population will decline below key thresholds (5,000, 10,000, 25,000) in response to changes to the current level of shooting mortality, obtained using all three models are provided in Table 3, and Figure 7a–c. Between 1995–2002, an average of 35,000 greylag geese were shot each year in Iceland, and it is estimated that 20,000–25,000 Icelandic geese have been shot annually in recent years in Scotland (Frederiksen, 2002) thus overall, approximately 55,000–60,000 geese are shot annually. This level of shooting is implicitly included in the model structure, and changes to this are modelled simply as an increase or decrease in the size of shooting bag. To simulate the different levels of shooting mortality, the appropriate number of geese is either removed (representing an increase in shooting) or added (representing a reduction in shooting) during the post-breeding period each year. The bag consists of both juveniles and adults, with the juvenile proportion of the bag set at 0.4, corresponding to the reported proportion of juveniles in the Iceland bag (Frederiksen and Sigfússon, unpubl. report). In terms of the quasi-extinction probability, if the current level of shooting is maintained, the probability of the population falling below 25,000 within 25 years varies between 0.14 (model 1) and 0.58 (model 3). If 5,000 less birds are shot then the probability of decline below 25,000 is reduced to between 0–0.004 for all models, whereas if 5,000 more birds are shot the probability of decline below 25,000 is almost certain (0.95–1). As well as changes in the quasi-extinction risk, we can also consider how the stochastic growth rate changes with change to the current shooting level. Under current conditions the average stochastic growth rates are

1.016, 0.982 and 0.965 for models 1,2 and 3 respectively. If an additional 1,700 birds are shot/yr the average stochastic growth rate is predicted to be less than 1 (ie population decline on average) for all models, and only becomes greater than 1 for all models if the shooting bag is reduced by at least 2,100 birds/yr (Figure 8). However, in order for 95% of the population simulations obtained using models 2 and 3 (the more pessimistic models) to have a growth rate of 1 or more (ie only 5% of simulated populations decline over 25 years) then the current shooting bag needs to be reduced by 4,900 and 6,100 respectively (Figure 9).

Table 3 Quasi-extinction probabilities for Iceland greylag geese in response to different levels of shooting mortality. The probability of the population declining below specific levels (10,000, 25,000) within 25 years resulting from change to the current annual shooting mortality (ie current shooting bag +/-5,000) are shown for all three models. When the additional number shot/yr equals zero, shooting mortality is maintained at its current level (c. 55,000–60,000). Negative additional shooting represents a reduction in the current level and positive values indicate an increase above the current level.

		Quasi-extinction probability					
		Model 1		Model 2		Model 3	
Quasi-extinction threshold		10000	25000	10000	25000	10000	25000
Additional Number shot/year	-5000	0	0	0	0.004	0	0
	-2500	0	0.012	0	0.07	0	0.001
	0	0.01	0.14	0.1	0.43	0.03	0.58
	2500	0.46	0.61	0.78	0.87	0.98	0.99
	5000	0.93	0.95	0.98	0.99	1	1

3.3.2.2 Catastrophic mortality

The aim of catastrophic event simulations is to determine the sensitivity of the population to extreme events which can give rise to rates of survival or reproduction which are outside the range encountered during the period of data collection. Over long periods, it is likely that there will be occasional “catastrophic” events, causing mortality well above the range of values observed (caused for example by severe storms in the north Atlantic during migration). The sensitivity of the population to occasional large increases in mortality was therefore investigated by recording the quasi-extinction probability over 100 years resulting from the removal of a proportion of the population at random intervals (Figure 10). At the beginning of each simulation the average annual frequency of catastrophes (from 1 in 1,000 years to 1 in 10 years) and the proportion of the population to be removed by each event are selected (between 0–90%). Since the quasi-extinction probabilities for models 2 and 3 are relatively high, even in the absence of simulated catastrophes, only model 1 was used for this analysis. The sensitivity of the population to change in the frequency and severity of catastrophes is unlikely to differ greatly between the three models, although the actual quasi-extinction probabilities obtained for model 3 will be much greater than those for model 1. Thus these results should be viewed as an indicator of the pattern of quasi-extinction which would be seen using all three models. The likelihood of the population falling below 10,000 individuals within 100 years is negligible, until catastrophes are either moderate but frequent (removing more than 10% of the population once every 10 years on average), or infrequent but severe (greater than 50% removal, one year in 100). Even in the

absence of catastrophes the risk of the population declining below 25,000 within 100 years is around 25%. This figure rises rapidly with even comparatively small losses (10–20% of the population) on a regular basis (once in 10 years); a loss of 30% of the population on average once every 10 years results in a risk of population decline below 50,000 in 100 years of almost 90%.

3.3.2.3 Loss of breeding habitat

The impact of breeding habitat loss on the viability of the greylag goose population was investigated using all three models in order to determine the potential consequences of proposed hydro-power schemes in the Icelandic Highlands. It is not expected that the developments would affect breeding directly (eg through flooding of nest sites), since the greylag population predominantly breeds in coastal areas. However, modified river flow downstream of hydro developments may lead to a decline in the suitability of some current breeding areas for nesting and moulting (Anon, 2003). Since the severity of such habitat modification is very hard to predict, simulated loss of between 0–25% of the current breeding habitat was undertaken. This provides both an indication of the sensitivity of the population to habitat loss and will also permit population predictions to be made when more information regarding the proposed developments becomes available. At the beginning of each simulation a percentage (0–25%) of the initial population is split off into a ‘non-breeding’ sub-group. While members of this group remain alive their numbers are added to the total population size, however they do not breed and so make no contribution to population growth. This represents an extreme interpretation of the possible impacts of breeding habitat loss, since it is likely that in response to such loss at least a portion of the affected birds would breed elsewhere. However, this approach was taken since we have no information with which to estimate how many displaced birds could be accommodated elsewhere. The change in the probability that the population will fall below 25,000 in 25 years obtained using each model is provided in Table 4 and Figures 11–13. The risk of quasi-extinction increases in each case as the percentage of loss increases. No attempt was made to model changes in survival which may also result from hydro-scheme induced habitat changes, as we currently have no means with which to predict such effects.

Table 4 Comparison of the probability that the greylag goose population will fall below 25,000 individuals within 25 years, with increasing loss of breeding habitat. See Figures 11–13 for more detail.

Quasi-extinction probabilities (25 years)			
	Model number		
Percentage loss of breeding territory	1	2	3
0	0.14	0.43	0.58
10	0.18	0.49	0.68
25	0.24	0.6	0.81

3.4 Conclusions

3.4.1 Implications of PVA results for Icelandic greylag goose population

- 1 There is currently a great deal of uncertainty in the Icelandic greylag population estimates. This is due to a combination of the difficulty of accurately counting and ageing flocks in Scotland, reliably distinguishing the migratory population from the resident ones, and very limited data on the numbers shot in the UK.
- 2 Three alternative models, based on different evaluations of the data, have been used to predict future population growth. We do not currently have the means to determine which of these provides the most robust population predictions. However, model 3 provides the best fit to the observed recent population trend, and while recent research work indicates these population counts may be underestimates, there is no evidence to suggest that the downward trend in the counts is incorrect.
- 3 In the light of the uncertainty in the population data, it is sensible to apply a precautionary principle to the interpretation of model outputs. Therefore, the following summary predictions are those derived from models 2 and 3, both of which predict continued population decline on average. While model 3 is more pessimistic in terms of the predicted average annual decline, the wider confidence intervals associated with model 2 mean predictions based on this model are more cautious.
- 4 Under model 3, and assuming maintenance of current conditions, the Icelandic breeding greylag population is predicted to decline by approximately 3.5% per year, with a 58% probability that the population will fall below 25,000 within 25 years.
- 5 While the quasi-extinction probability is most sensitive to adult survival, reduction of either juvenile survival or productivity also leads to an elevated risk of significant population decline.
- 6 Using an estimate of the UK shooting bag based on the assumption of equivalent reporting of shot, ringed geese in the UK and Iceland, the current number of Icelandic greylag geese shot each year appears to be unsustainable. A reduction in the size of the overall shooting bag, of approximately 5,000 less geese shot/yr, reduces the predicted probability of decline below 25,000 within 25 years to zero (model 2). Conversely, an increase in the level of shooting by the same amount makes the likelihood of decline below 25,000 in 25 years almost certain (all models).
- 7 In order to obtain an average population growth rate of 1 or more (ie avoiding population decline on average) using model 3, a minimum reduction in the shooting bag of 2,100 is required. In order for 95% of simulated population projections to have a growth rate of 1 or more using model 2, a minimum reduction in the shooting bag of 6,100 is required.
- 8 The probability of quasi-extinction increases with increasing breeding habitat loss. While this analysis is intended to provide guidelines for the consequences of proposed hydro-power schemes in Iceland, it must be stressed that this analysis is based on very limited data, and these results should therefore be treated with caution.
- 9 Since the population is already at significant risk of decline due to heavy shooting mortality and the potential loss of breeding habitat it is, not surprisingly, also highly vulnerable to occasional catastrophic mortality events. This is only likely to be reduced if action is taken to decrease the other current threats to the population.

3.4.2 Advice

- 1 A comprehensive list of recommendations with regards to both data collection and population management was provided by Frederiksen (2001). The following points include many of those raised in that report, and for which action is still required.
- 2 There is an urgent need to improve the monitoring of the Icelandic greylag population throughout its range. Particular consideration should be given to extending the geographical area sampled in the UK, using a stratified approach, and to the development of methods to distinguish the resident greylag populations from the migratory one. Concerted efforts are also required to improve the UK shooting bag estimates.
- 3 If the estimate of the Icelandic greylag goose shooting bag in the UK is accurate, the observed decline in this population appears likely to continue while the number shot each year remains at its current level. A relatively small reduction in the level of shooting is predicted to be sufficient to safeguard the population at its current size. However, until the means to accurately assess the size of the UK shooting bag have been put in place it is difficult to recommend an appropriate upper limit on the annual number shot.
- 4 The extent to which the hydro-electricity generating schemes currently being developed in Iceland may affect greylag goose breeding areas is poorly understood and the longer term ramifications of the possible habitat degradation which may result is very hard to discern. This situation should be closely monitored, with further modelling undertaken when better data become available.

3.5 References

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Figure 1 Icelandic greylag goose shooting bag in Iceland (1995–2002) on the left y-axis, and the proportion of juvenile greylag geese in the bag in Iceland (1995–2000) estimated from wing surveys on the right y-axis, dashed green line. Based on Frederiksen *et al.*, 2004.

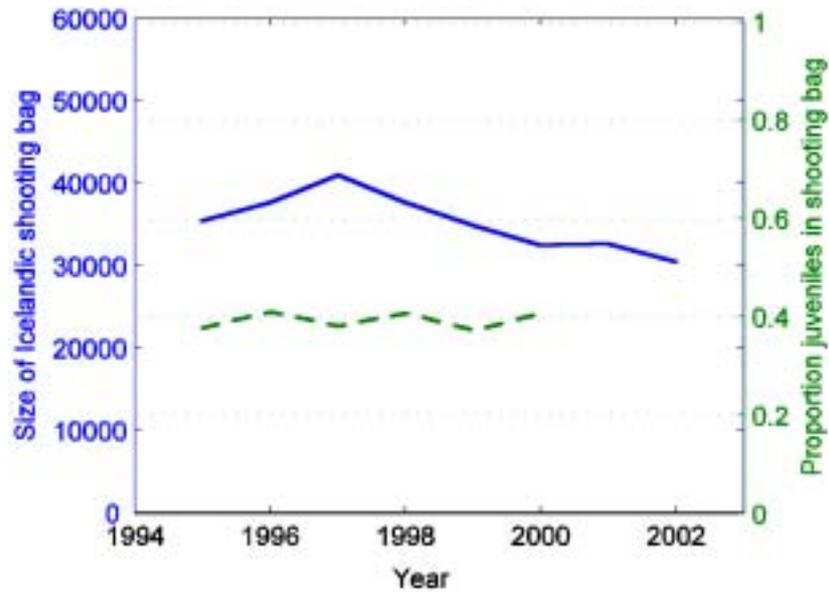


Figure 2 Icelandic greylag goose population size, 1960-2002, derived from coordinated autumn counts conducted in Scotland (blue line) with the best-fit cubic polynomial line (black line; population = $-2.1 \cdot \text{year}^3 + 1.2 \cdot 10^4 \cdot \text{year}^2 - 2.4 \cdot 10^7 \cdot \text{year} + 1.6 \cdot 10^{10}$, $F=51.8$, $p<0.001$)

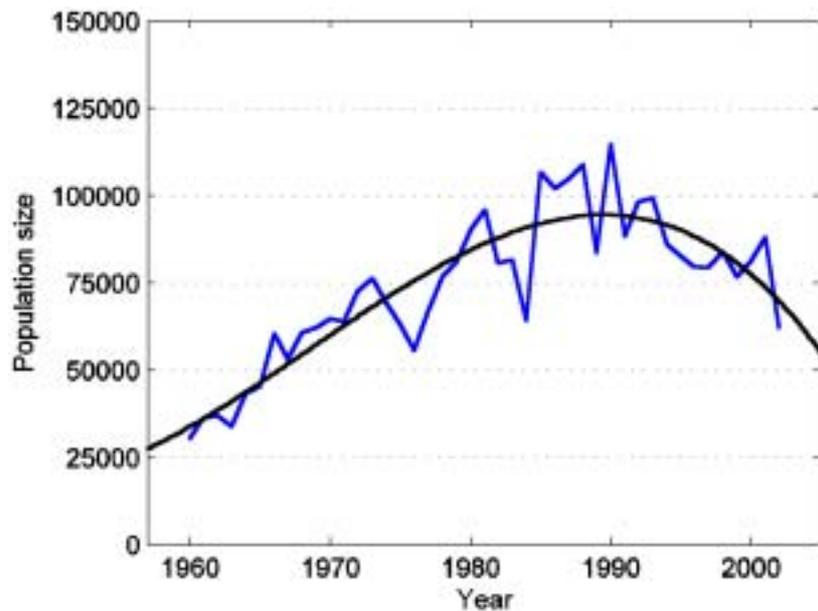


Figure 3 Icelandic greylag goose population projection using model 1 (untransformed Scottish count data). The stochastic growth rate is 1.016, indicating a projected average population increase of 1.6% per year.

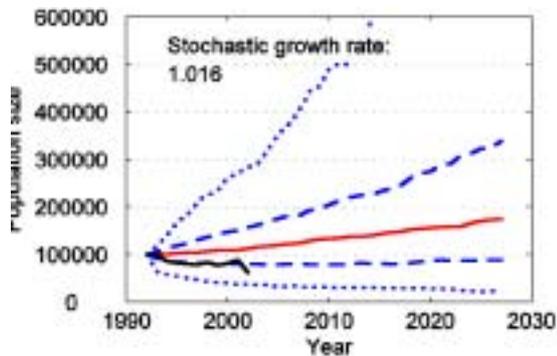


Figure 4 Icelandic greylag goose population projection using model 2 (Scottish count data, with the proportion of juveniles multiplied by 1.73). The stochastic growth rate is 0.982, indicating a projected average population decrease of 1.8% per year.

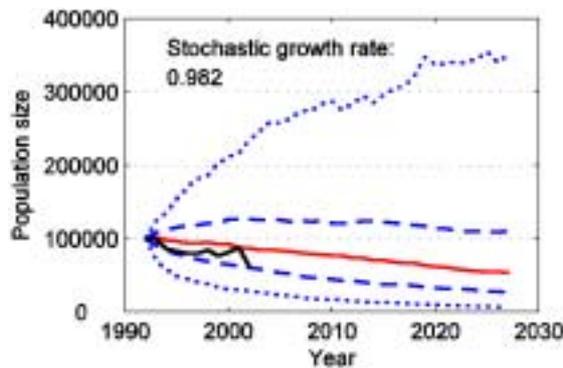
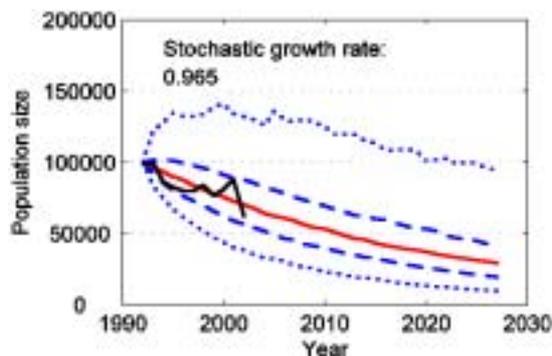


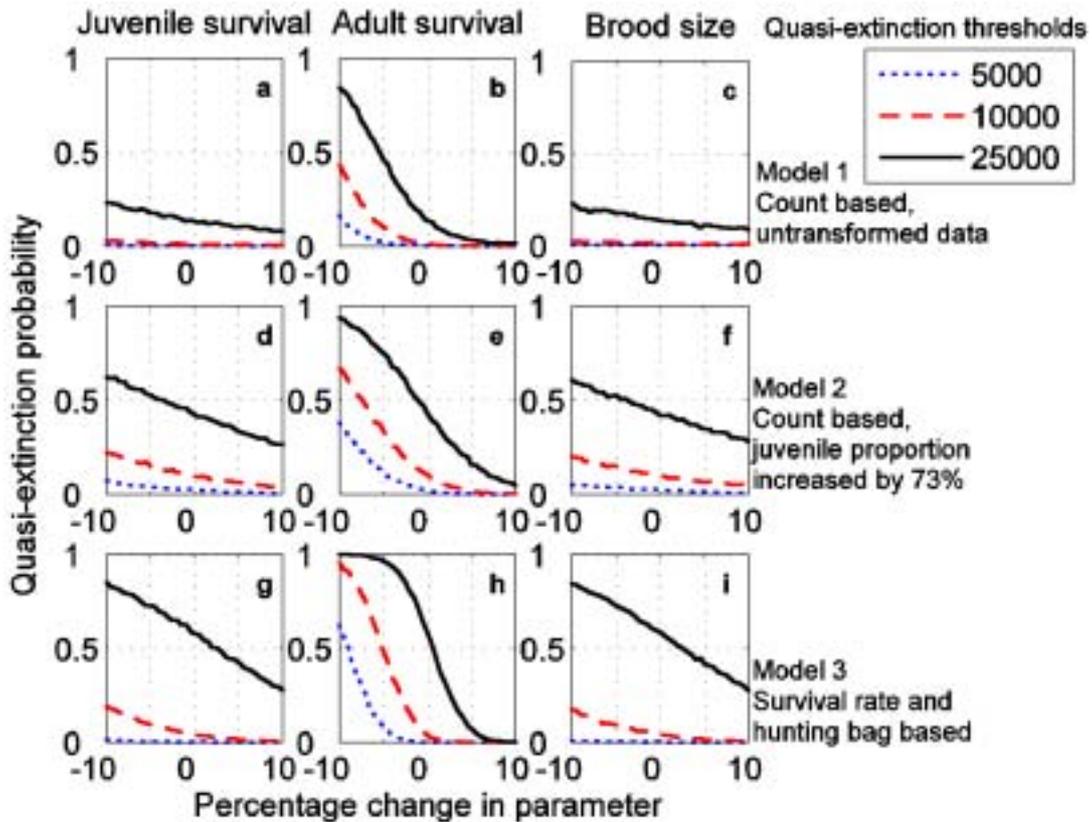
Figure 5 Icelandic greylag goose population projection using model 3 (using independent survival rates and shooting bag derived productivity estimate). The stochastic growth rate is 0.965, indicating a projected average population decrease of 3.5% per year.



N.B. In all cases the solid red line is the median population size, the dashed and dotted blue lines the 50% and 95% confidence intervals respectively and the solid black line is the observed population, 1992–2002.

Figure 6 Plots indicating the probability of the Icelandic greylag goose population declining below critical levels (ie quasi-extinction at: 25,000 = solid black line; 10,000 = dashed red line; 5,000 = dotted blue line) within 25 years as a result of proportional change to the mean rates of juvenile survival, adult survival and mean brood size. The upper panels (subplots a-c) are derived using model 1 (count based parameters, untransformed), the middle panels (subplots d-f) are derived from model 2 (count based parameters, with the juvenile proportion first increased by 73%) and the lower panels (subplots g-i) are derived from model 3 (survival from analysis of ringed geese, productivity estimated using shooting bag and survival rates).

To estimate the quasi-extinction risk the mean value of each rate is perturbed in turn across the range +/- 10% of its baseline value and the quasi-extinction probability calculated as the proportion of 1000 simulations which decline below each of the thresholds (error bars have been omitted due to their small size). For all 3 models the rate with the greatest influence on quasi-extinction probability is mean adult survival (middle column). The standard deviations for the demographic rates were also perturbed across the same range (not shown). For all models the risk of quasi-extinction was almost completely insensitive to change in the standard deviation of juvenile survival and productivity, and only changed by a few percent with change in the standard deviation of adult survival.



Figures 7a–c Quasi-extinction probabilities within 25 years for the Icelandic greylag goose population with changing levels of shooting, obtained for all 3 models. When the size of the shooting bag equals 0, the quasi-extinction probabilities are those predicted under the current level of shooting mortality (representing a combined Iceland-UK bag of c. 55,000/yr.). Negative values for the shooting bag represent a reduction in the bag size, positive values an increase in bag size. In all cases birds are added (-ve) or removed (+ve) post-breeding, mimicking autumn/winter goose shooting. The proportion of juveniles in the bag is 0.4, corresponding to the proportion of young birds reported in the Iceland shooting bag.

Figure 7a Model 1

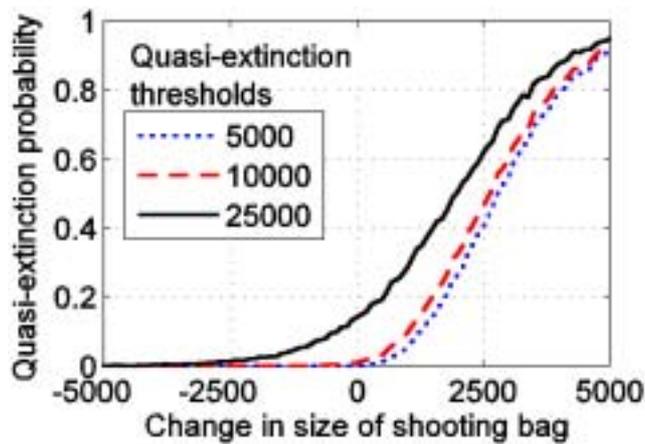


Figure 7b Model 2

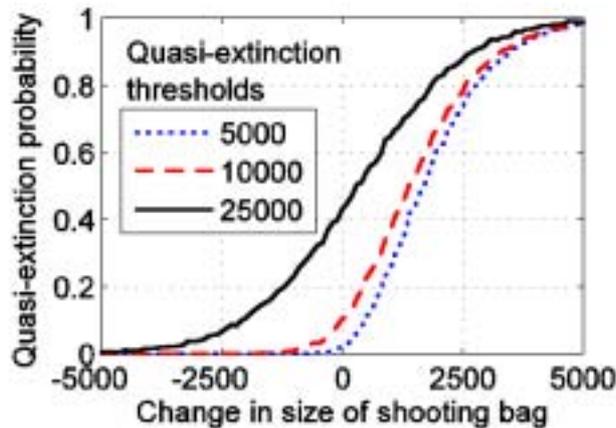


Figure 7c Model 3

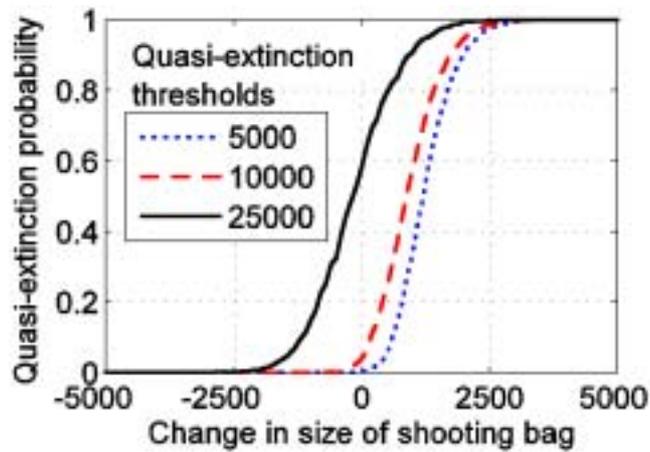


Figure 8 Change in the Icelandic greylag goose population average stochastic growth rate predicted using all 3 models over 25 years with change to the current size of the shooting bag. The minimum change in the size of the shooting bag needed in order to obtain an average growth rate of 1 or more for model 3 (the most pessimistic model) is a reduction of 2100/yr (Figure 9 provides more detail for this relationship for model 3). If an additional 1700 are shot per year then even the most optimistic model (model 1) has an average growth rate less than 1.

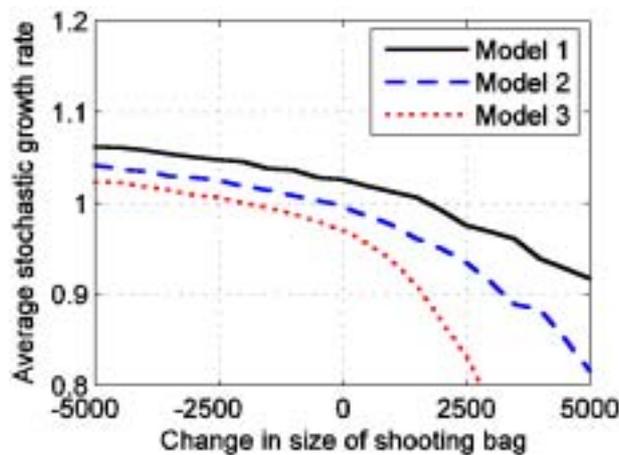


Figure 9 Change in the Icelandic greylag goose population average stochastic growth rate predicted using model 2 (Figure 9a) and model 3 (Figure 9b). The plots show the average stochastic growth rate (dotted red line) and 95% confidence intervals (dashed blue lines) obtained when the current size of the annual shooting bag is reduced by 4000 to 7000 (Figure 9a, model 2) and by 2000 to 6000 (Figure 9b, model 3). In order for the lower 95% confidence interval of the stochastic growth rate to exceed 1 (ie for 95% of simulations to have a growth rate, measured over 25 years, of 1 or more) the reduction in the annual shooting bag needed using model 2 is 6,100 birds and with model 3 is 4,900.

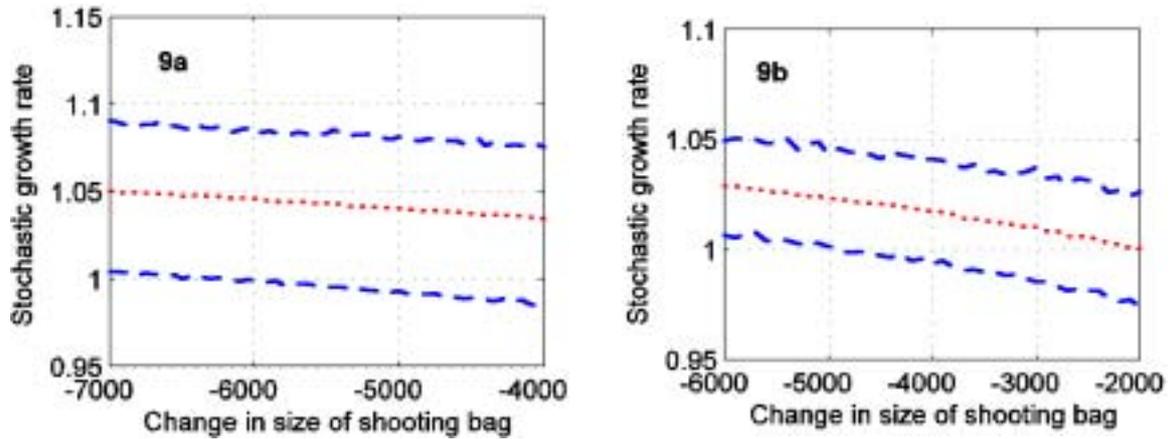
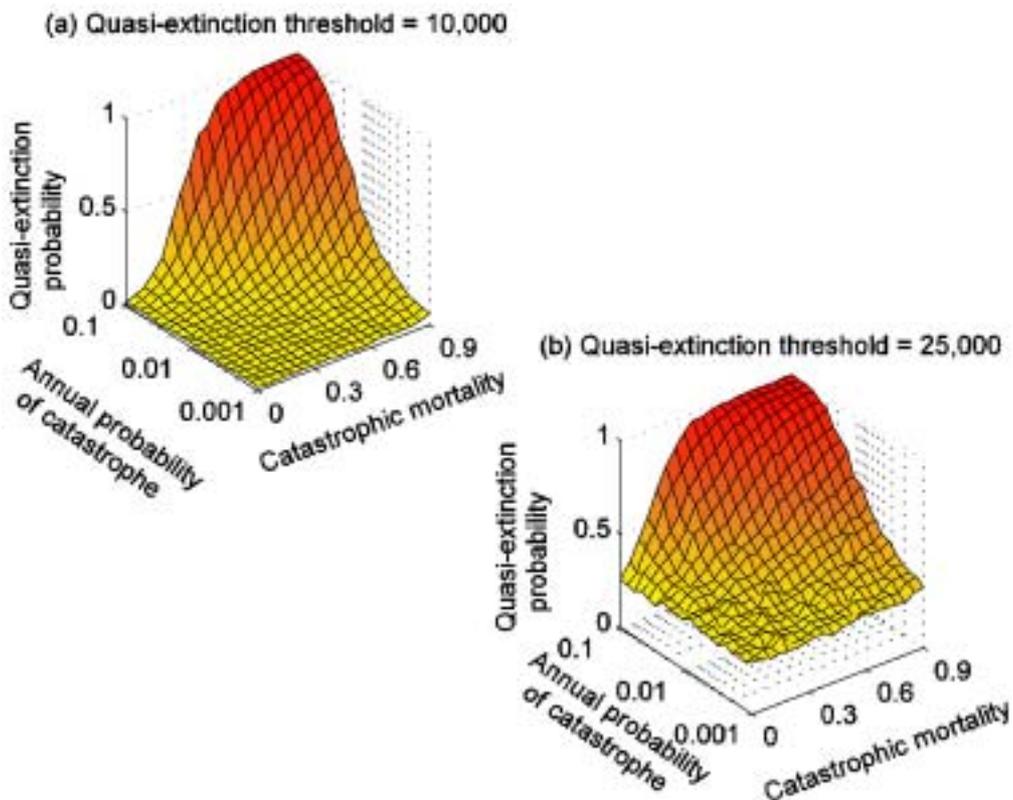


Figure 10 Plots of the probability of quasi-extinction within 100 years for the Icelandic greylag goose (model 1) in response to changing frequency and severity of catastrophic mortality events. The annual probability of a catastrophe occurring (y-axis, lower-left) varies between an average of once in every 10 years (0.1) to once in every 1000 years (0.001). The occurrence of a catastrophe in any particular year of a population simulation is determined by a random 'coin-toss' process. The proportion of the population removed by a catastrophe (x-axis, lower right) varies between 0–0.9 (ie 0–90% of the population dies). Quasi-extinction probabilities (z-axis, vertical) are derived from the proportion of simulations (out of 1000) which fall below population thresholds of 10,000 and 50,000 individuals within 100 years. For example, the risk of the population falling below 10,000 individuals within 100 years (Figure 10a) when catastrophes occur on average once every 10 years ('annual probability of catastrophe' = 0.1) is negligible when less than 50% of the population is killed ('catastrophic mortality < 0.5) on average less than once in 100 years ('annual probability of catastrophe' = 0.01), but rises rapidly if either a greater proportion of the population is removed or the frequency of catastrophes increases. Even in the absence of catastrophes, the risk of decline below 25,000 in 100 years is around 25% (Figure 10b), rising towards 100% ('quasi-extinction probability' = 1) when catastrophes occur on average once every 10 years and 30% or more of the population is removed



Figures 11–13 Predicted change in quasi-extinction probabilities for the Icelandic greylag goose population obtained using each model resulting from a reduction in the current breeding habitat. To simulate habitat loss a percentage of the adult population (in the range 0–25%) is prevented from breeding for the duration of each population simulation.

Figure 11 Model 1

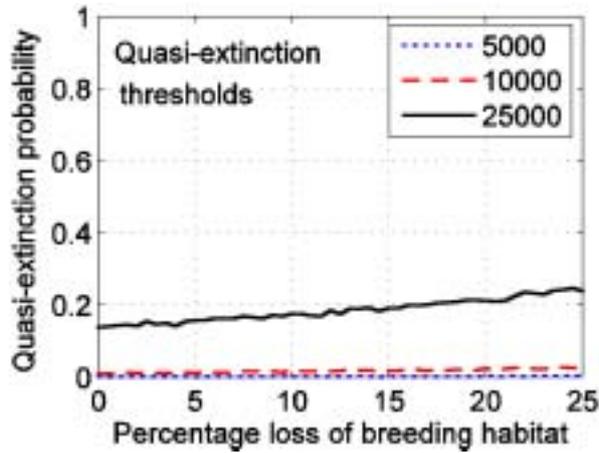


Figure 12 Model 2

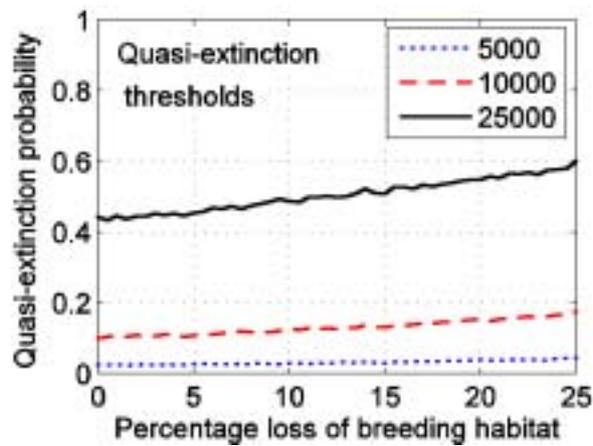
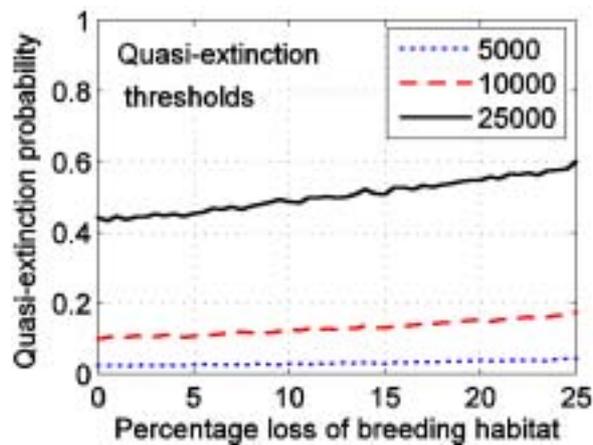


Figure 13 Model 3



APPENDIX 1

Calculation of demographic data and age class sizes for the Icelandic greylag goose population using the annual total population count (N), proportion of juveniles (j) and mean brood size (bs) data. In all of the following equations subscript 't' is used to denote the current year, 't-1' the previous year.

Number of juveniles: $J_t = j_t * N_t$

Crude annual survival rate (from year t-1 to year t): $S_t = \frac{N_t - J_t}{N_{t-1}}$

Number of birds in their second year: $N2_t = J_{t-1} * S_t$

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: $PB_t = \frac{J_t * bs_t}{0.5 * N3_t}$

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

Mean number of adults (post-breeding, pre-shooting): $Na' = \frac{Ht * (1 - pHj)}{1 - Sj}$

Mean number of juveniles (post-breeding, pre-shooting): $Nj' = \frac{Ht * pHj}{1 - Sj}$

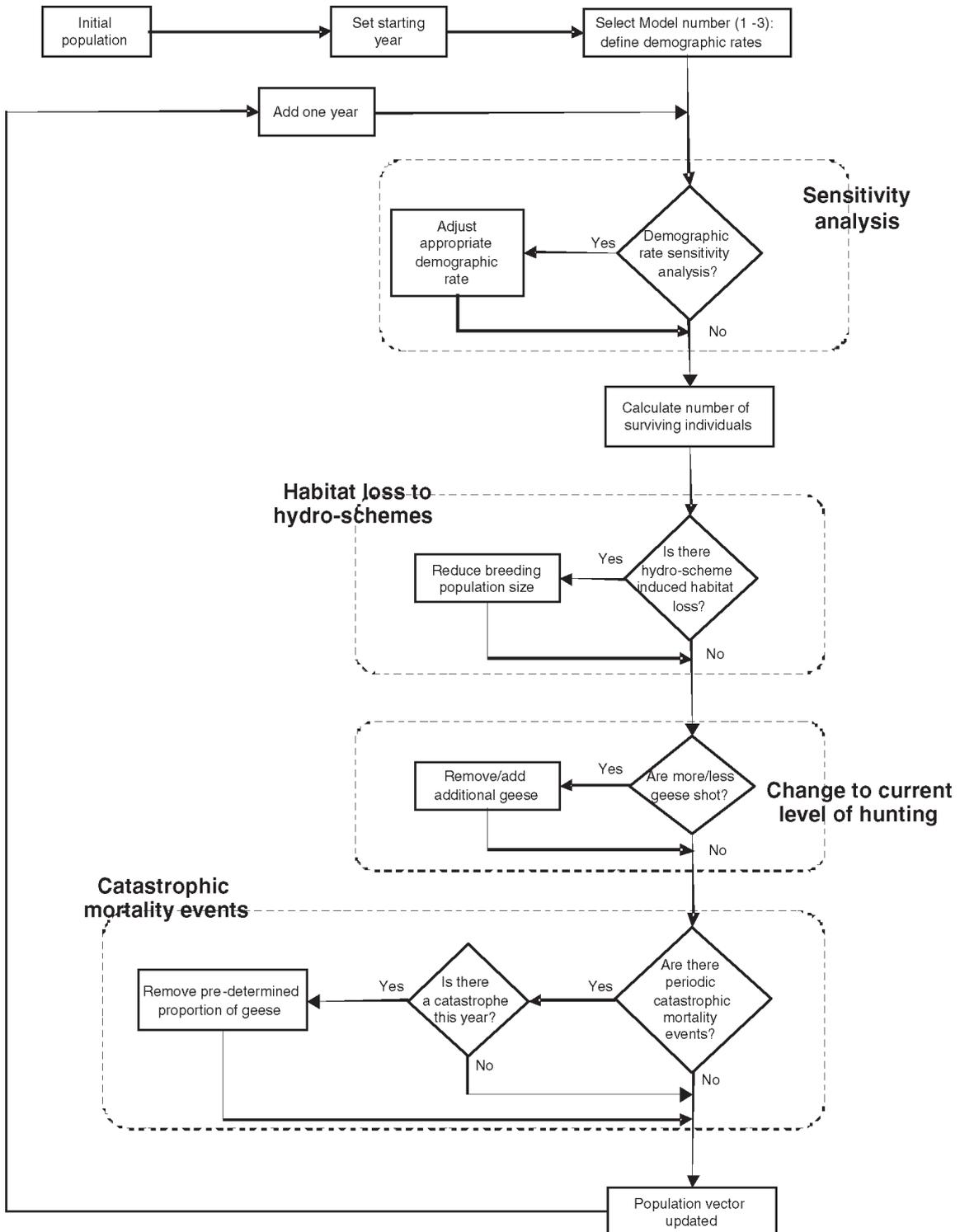
(Na' is the mean no. of adults, Nj' is the equivalent no. of juveniles, Ht is the mean total shooting bag (for Iceland and Scotland), pHj is the mean juvenile proportion in the bag, Sa is the mean adult survival rate (from summer to summer) and Sj is the equivalent mean juvenile rate). Shooting is assumed to be the only source of mortality in the population.

Mean number of two year old birds: $N2' = Nj' * Sj$

Mean number of three years and older birds: $N3' = Na' * N2'$

Mean productivity derived from survival and shooting:
bag estimates: $P = \frac{Nj'}{N3'}$

APPENDIX 2 – Flow chart describing the density dependent, stochastic population model for the Icelandic greylag goose



4 STATUS AND POPULATION VIABILITY OF THE GREENLAND BARNACLE GOOSE IN SCOTLAND, WITH PARTICULAR REFERENCE TO THE ISLAY SUB-POPULATION

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4.1 Introduction

This report summarises analysis of available data for the Greenland-breeding barnacle goose *Branta leucopsis* population which winters in Scotland. The data comprise total Scottish counts obtained by aerial survey (undertaken at approximately five year intervals) and more detailed annual information from Islay, the main wintering haunt. Analysis of the Islay sub-population data is discussed, along with the outputs from population models developed using the Islay data. These outputs include predictions of the population size to be expected if conditions remain unchanged, and also those resulting from changes in mortality. The bulk of the analyses and population modelling presented here relate to the Islay sub-population, the status of which has a considerable bearing on the total population. However, it is worth noting that the conditions experienced on Islay may not be the same as those encountered by the remainder of the Scottish population.

4.2 Methods and results

The Greenland-breeding population of barnacle geese winters along the northern and western coasts of Scotland and Ireland, predominantly on offshore islands. Due to the remote location of many of these sites, estimating the total population size is only practical from a combination of air and ground surveys. Between 1959–2003 11 full surveys have been conducted, at approximately five-year intervals. Since the early 1970s the largest single population has been on Islay, which currently holds an estimated 77% of the Scottish population (and 65% of the global population). Between two and six ground counts have been conducted each winter on Islay (on behalf of WWT and SNH) since the mid 1950s. In addition, since the 1960s an estimate of the proportion of juveniles and the mean brood size have also been made each autumn. Most of the analysis and modelling presented here is based on the Islay population due to the limited nature of the data for the rest of the Scottish population. In some previous reports the adopted annual population estimates for Islay have been based on the maximum count recorded on Islay in each winter, irrespective of the month in which that figure was recorded. It is now known that there is a considerable degree of within-winter movement between sites (Percival, 1991), thus these counts may confound years of elevated passage migration through Islay with higher population estimates. In this report, to minimise the influence of seasonal movement rates on the population estimates, the November count was selected as the annual estimate of population size. November was chosen since it yields the highest winter count in more years than any other month, and also provides the longest unbroken run of counts. Prior to 1965 there was little consistency in the timing of the ground counts on Islay, so for the reasons discussed above this analysis only uses data collected since 1965.

The raw demographic data obtained from the total flock counts on Islay were used to derive three further demographic parameters:

- 1 the annual (crude) survival rate (the proportion of the population surviving from one year to the next),
- 2 the productivity rate (the number of young produced per breeding age adult on arrival in Scotland),
- 3 the proportion breeding (the proportion of breeding age birds returning to Scotland with young).

See Appendix 1 for the derivation of these parameters.

Since the early 1980s over 3,000 individuals have been caught (mainly on Islay) and fitted with unique colour leg rings. Re-sighting observations of these birds on Islay between 1984–2003 (provided courtesy of Steve Percival) have been analysed here to produce independent estimates of survival.

4.2.1 Analysis of population count data

The global population of the Greenland barnacle goose has grown from just over 8,000 in 1959 to over 56,000 in 2003 (Figure 1). Since the 1970s the average annual growth rate for the total population has been 2.8%. In the late 1960s the Islay population rapidly increased in size to almost 15,000, and since then the estimated annual growth rate here has been slightly higher than elsewhere; 3%, compared to equivalent annual rates of increase for Ireland and the rest of Scotland of 2.7% and 2.4% respectively. The population size recorded by aerial survey or annual ground count for the other main Scottish regional haunts since the 1980s is shown in Figure 2. The considerable variation between years in some of these data, particularly for the Outer Hebrides, is most likely a consequence of the inherent 'snapshot' nature of surveying mobile populations from the air (Ogilvie *et al.*, 1999). It can be seen from Figure 2 that the Orkney and Coll and Tiree populations have increased significantly in the last 10 years, and together now account for almost 10% of the total population. Analysis of the Islay population counts in a previous PVA report (Pettifor *et al.*, 1999) using the randomisation test of Pollard *et al.* (1987) provided evidence that, over the period 1966–1987, the growth rate of the Islay sub-population had exhibited a density-dependent reduction. This test was repeated using the Islay population counts over the period 1966–2003, together with another test for density-dependence in population time series developed more recently (Dennis & Taper, 1994). Neither test returned a significant result, therefore, on the basis of count data alone, there is currently no evidence for density-dependent regulation. Further tests for the presence of density-dependence in the demographic rates of the Islay population are described in the following section.

4.2.2 Analysis of demographic data

The mean annual demographic rates (and their standard deviations) derived using data from the Islay population between 1966–2003 are provided in Table 1, together with the rates calculated using the data available for the previous PVA (1966–1994; Pettifor *et al.*, 1999) and those for the years collected since (1995–2003), in order to highlight where changes have occurred. There have been significant declines in the proportion of breeding birds (2 sample t-test, $t=2.62$, $p=0.013$) and productivity (2 sample t-test, $t=2.13$, $p=0.039$) since 1995. The decline in the proportion of juveniles is almost significant at the 5% level (2 sample t-test, $t=1.99$, $p=0.054$).

Table 1 Greenland barnacle goose demographic parameters derived from the Islay population count, proportion of juveniles and mean brood size estimates for the periods 1966–94, 1995–2003 and all years 1966–2003. The previous rates represent those available for the previous PVA exercise (Pettifor *et al.*, 1999) and are included for comparison with the more recent estimates. The survival rate is a combined estimate for all birds older than c.6 months, calculated as the number of adults in the current year divided by the total population in the previous year; productivity is the ratio of juveniles to breeding age adults; mean brood size is the family size estimated from a sample of flocks; proportion of juveniles is the percentage of juveniles in a sample of flocks; proportion breeders is the minimum number of adults required to have bred (in order to account for the estimated number of juveniles) divided by the total adult population. See Appendix 2 for further details.

	Previous estimate (1966–1994)	Current estimate (1995–2003)	Overall estimate (1966–2003)
Parameter	Mean (St. dev)	Mean (St. dev)	Mean (St. dev)
Survival	0.899 (0.184)	0.944 (0.06)	0.925 (0.161)
Productivity	0.171 (0.085)	0.109 (0.032)	0.157 (0.067)
Mean brood size	1.994 (0.34)	2.05 (0.223)	1.995 (0.318)
Proportion juveniles	0.126 (0.052)	0.09 (0.026)	0.118 (0.049)
Proportion breeders	0.168 (0.07)	0.106 (0.023)	0.153 (0.067)

Investigation of changes in the demographic rates in relation to the current and previous year's population density and environmental conditions was conducted using Generalised Linear Models (GLMs) and Robust Regression. As a first step GLMs were used in order to check for the presence of significant interactions between the population density and environmental variables. As no interactions were identified, Robust Regression methods were used for the remaining analyses since this approach is less sensitive to the presence of outliers in the data. The climate covariates used were the average monthly temperatures for May–August, recorded at Danmarkshavn, Greenland (at the northern end of the breeding range) and the North Atlantic Oscillation (NAO) indices for May and September. Of these, only the average May temperature had any significant explanatory power. The proportion of breeding birds, proportion of juveniles and the productivity have all decreased significantly with increasing population size in the previous year, and are higher in years with milder May temperatures. The mean brood size and the crude survival rate have both increased with increasing population size, but show no response to the environmental variables tested (the full list of significant results is provided in Table 2).

Table 2 Significant results of statistical analysis of the Greenland barnacle goose demographic data from the Islay population. Explanatory variables were: $\log(N_t)$ – concurrent natural log of total population size; $\log(N_{t-1})$ – natural log of total population size in the previous year; May temperature – the average temperature for May each year recorded at Danmarkshavn, North-east Greenland (76.8N, 18.7W). North Atlantic Oscillation (NAO) indices for the migration months of May and September were also tested but did not return any significant results. In all instances Generalised Linear Models (GLM) were used first to check for the presence of significant interaction terms. None were identified so the remaining model refinement was performed using a Robust Regression routine, which is less sensitive to outliers in the data. All tests were conducted using Matlab (MathWorks, Inc.).

Demographic rate (transformation)	Explanatory variables	t	p	Parameter estimate	Standard error
Mean brood Size (natural log)	Constant	-1.88	0.068	-1.33	0.7
	Log (N_t)	2.87	0.007	0.203	0.071
Proportion breeders (square root)	Constant	5.48	<0.001	1.647	0.3
	Log (N_{t-1})	-3.57	0.001	-0.111	0.031
	May temperature	2.96	0.005	0.024	0.008
Proportion juveniles (square root)	Constant	3.64	0.001	1.101	0.302
	Log (N_{t-1})	-2.06	0.047	-0.064	0.031
	May temperature	2.29	0.028	0.019	0.008
Productivity (square root)	Constant	3.58	0.001	1.419	0.396
	Log (N_{t-1})	-2.13	0.04	-0.087	0.041
	May temperature	2.40	0.022	0.026	0.011
Survival (crude est; square root)	Constant	1.14	0.261	0.295	0.258
	Log (N_t)	2.53	0.016	0.065	0.026

While the randomisation tests used with the population time series (Section 4.2.1) failed to find evidence for density-dependence, the significant declines in reproduction are an indication of the presence of population regulation. The reason for this apparent contradiction is not clear, and it is unlikely to be the result of any single cause. However, since population growth in long-lived, slow breeding species like geese tends to be most sensitive to changes in survival, it is possible that the small increase in the survival rate has been sufficient to offset the decline in reproduction.

4.2.3 Individual based survival estimation

Re-sighting observations of marked individuals were analysed (using U-CARE and MSURGE) to provide estimates of survival for the Islay population (for the years 1984–2003) which are independent of the population census data. Before estimating the survival rate, goodness-of-fit testing of the data indicated that the most appropriate model structure for recapture rates (more accurately re-sighting rates here) included terms for time, sex and also a dummy-age effect to account for a higher probability of re-sighting in the year immediately after marking. Starting with this re-capture structure, the best fitting model for adult survival was found to include terms for time and sex (but with no significant interaction). Thus survival varied between years and was on average 2% higher for females than males (Figure 3). The average adult survival rate for

all years and both sexes combined was 0.846 (s.d. 0.04). Similarly, juvenile survival (between an individual's 1st and 2nd winters) was time and sex dependent, with an equivalent combined average rate of 0.821 (s.d. 0.06), indicating there is no significant difference between adult survival and that of young birds once they have survived as far as the wintering grounds. These survival estimates are significantly lower than those derived from the population counts for the same period (Mann-Whitney test, $p < 0.001$). The most likely reason for this is that the estimation of survival from re-sighting data is based on the assumption of a closed population, which is highly unlikely to be the case for the Islay sub-population. Consequently, any permanent emigration of ringed individuals from Islay reduces the survival rate estimates. However, we can use the two different estimates of survival (derived from the count and re-sighting data) to make an assessment of the immigration and emigration rates, as described in the next section.

4.2.4 Rates of movement in and out of the Islay population

Previous work has assumed that the greater increase in size of the Islay population compared to others elsewhere has resulted from immigration exceeding emigration, rather than through enhanced productivity or survival (Bell, 1993). However, this conclusion was based on limited supporting evidence. In order to explore this question more closely, both demographic data and ringing and re-sighting data from other locations are needed. This would permit both movement rates and breeding success to be assessed for a greater section of the population and thus begin to answer some of these questions. While a limited amount of this type of data has been collected, time constraints have prevented analysis for this report. However, using the two different survival rate estimates for the Islay population (one derived from re-sightings and one based on population counts), along with other demographic data for Islay, we can make some tentative suggestions about the relative importance of demographic and movement rates for this population. Given annual estimates for the Islay population growth rate (λ ; 1.036), re-sightings based survival (S_m ; 0.846) and productivity (P ; 0.143), for the years 1984–2003, the following formula can be used to calculate the immigration rate (i) to Islay:

$$i = \frac{\lambda}{S_m(1+P)} - 1$$

Thus our estimate for the average rate of immigration to Islay between 1984–2002 is 0.071 (ie an average of 7.1% of the population growth each year was due to the addition of immigrant birds, rather than inherent productivity). The re-sightings based mortality rate of 0.154 (=1-survival) includes both true mortality and permanent emigration, thus the annual rate of emigration from Islay lies between 0 (no emigration, all 'apparent' mortality is 'real' mortality) and 0.154 (all 'apparent' mortality is emigration). If we know the emigration rate (e) we can use the following formula to calculate 'true' survival (S):

$$S = \frac{S_m}{(1-e)}$$

If we assume emigration and immigration are in balance (ie emigration=immigration=0.071), we obtain a 'true' survival rate of 0.91, which is not untypical for goose survival and is also close to the count based estimate of 0.92. This suggests that movements to and from Islay have been more or less balanced since 1984, and consequently the contrasting growth of the different sub-populations has owed more to differences in demographic rates between sub-populations. Further support for this hypothesis can be gained from a comparison of reproductive data for the Inishkea Islands off the west coast of Ireland (the only other

population for which reproductive data is available, courtesy of D. Cabot). For the period 1965–2002 the average crude survival rate (0.95) and mean brood size (1.87) are not significantly different from those on Islay. However, the average proportion of juveniles is significantly lower on the Inishkea Islands than on Islay (0.069, s.d. 0.04 compared to 0.119 s.d. 0.05; two sample t-test, $t = -4.83$, $p < 0.001$).

4.3 Population model

Simulation models of the Islay population of the Greenland barnacle goose were developed using the demographic rates estimated above. The models have three age classes; juveniles (0–1 year olds), second years (1–2 year olds) and adults (2+ years). The adult population size in each year of a simulation is obtained from the product of the previous year's second year and adult populations and the survival rate, the second year population is the product of the previous year's juvenile population and the survival rate and new first year birds are derived from the product of the mean brood size and the proportion of the adult population which breeds. The survival rate and mean brood size are drawn at random from appropriate probability distributions each year. Since it was not possible to confirm a connection between the population's density and growth rate, two forms of the model were developed. The first has no density-dependent regulation of demographic rates and represents a possible upper limit of population growth. In the second, the proportion of the adult population which breeds is dependent on the population size in the previous year. This relationship is defined using a threshold model, with parameters derived from the data. A maximum proportion of birds (0.19, ie equivalent to 19% of adults being accompanied by juveniles on Islay) breed when the total population is below a threshold size of 16,345. Above this, the proportion breeding declines at a constant rate with increasing population size. This model fits the data as well as a simple linear regression, but is preferred for biological reasons (see Appendix 1 for details).

Using the models, we investigated the risk of population decline below specific thresholds (quasi-extinction) within the short to medium term, resulting from changes in conditions which may affect the population. The term quasi-extinction probability as used here refers to the likelihood that the population will fall below a specific size within a particular period of time (eg the chance that the population will fall below 10,000 in the next 25 years), expressed as a proportional (or percentage) probability. See Appendix 2 for a flow chart of the model structure.

4.3.1 Baseline model outputs

In the absence of density-dependent regulation, simulations starting from the 1966 population count produce a close match between the median predicted population in 2003 and the observed population size in that year (Figure 4). Projecting the population using this density-independent model yields a median predicted Islay population size of 100,000 in 25 years (Figures 4 and 5). In contrast, if the proportion of breeders is regulated by density-dependence, the population is predicted to stabilise around a median size of just over 34,000 (Figures 6 and 7). Under baseline conditions (ie no change to the current parameter estimates), the probability of the population declining below 10,000 individuals within the next 25 years derived from either the density-dependent or independent simulations is less than 0.003. The most sensitive demographic rate in terms of its influence on the likelihood of population decline is adult survival (Figure 8), which is typical of long-lived, slow breeding species. This result is the same for both the density-dependent and density-independent simulations.

4.3.2 Risk analysis

4.3.2.1 Population response to changes in the level of shooting

Between 1995–2002 an average of 1,700 Greenland barnacle geese were shot annually on Iceland. In addition, approximately 500 have been shot on Islay under licence each winter since 2000. This combined shooting mortality is implicitly included in the model. To investigate the effects on the population of increases in the size of the shooting bag, simulations were conducted where additional geese were removed from the model during the post-breeding period each year. In each year of a simulation the proportion of each age class in this additional shooting bag matches their respective proportions in the population. The probability that the population will decline below key threshold sizes (1000, 5000, 10000) within 25 years in response to this additional shooting mortality, derived from both density-dependent and independent simulations are provided in Table 3, and Figures 9a and 9b. At intermediate additional shooting bag sizes (1000–2000) the density-independent risks of quasi-extinction are approximately half of the density-dependent ones. With density-dependence operating, removal of an additional 500 or more birds from the Islay sub-population is predicted to reduce the median equilibrium population below 30,000 (Figure 10c). Removal of 1500 extra individuals reduces the median population to less than 15,000 and increases the probability that the population will fall below 10,000 within 25 years to 40% (Figure 10d). In the absence of density-dependence there is no upper limit on population growth, therefore an average population growth rate of 1 can only be achieved by removing sufficient individuals to match the average annual increase. density-independent simulations indicated that removal of around 1550 individuals results in an average growth rate of 1, but this figure is associated with a 22% risk of decline below 10,000 in 25 years.

Table 3 Quasi-extinction probabilities for Greenland barnacle geese on Islay in response to additional shooting mortality (above the current estimate of approx. 2200), spread across all age classes. The probability of the population declining below specific levels (columns 1000, 5000, 10000) within 25 years under different levels of additional annual shooting mortality (rows 0, 500, 1500, 2500) are shown for both density-dependent and density-independent simulations.

		Quasi-extinction probability					
		Density-independent			Density-dependent		
Quasi-extinction threshold		1000	5000	10000	1000	5000	10000
Additional Number shot/year	0	0	0.0002	0.0015	0	0	0.004
	500	0.0003	0.0024	0.012	0.0001	0.003	0.025
	1500	0.11	0.15	0.21	0.19	0.27	0.42
	2500	0.57	0.62	0.67	0.9	0.94	0.97

4.3.2.2 Catastrophic mortality

The aim of catastrophic event simulations is to determine the sensitivity of the population to extreme events which can give rise to rates of survival or reproduction which are outside the range encountered during the period of data collection. Over long periods, it is likely that there will be occasional "catastrophic" events, causing mortality well above the range of values observed (caused for example by severe storms in the north Atlantic during migration). The sensitivity of the population to occasional large increases in mortality was therefore investigated by recording the quasi-extinction probability resulting from the removal of a proportion

of the population at random intervals (Figure 11). The density-dependent version of the model was used to produce the following quasi-extinction estimates, although very similar results are obtained using the density-independent version. At the beginning of each simulation the average annual frequency of catastrophes (from 1 in 1000 years to 1 in 10 years) and the proportion of the population to be removed by each event are selected (between 0–90%). The likelihood of the population falling below 1,000 individuals within 100 years is extremely small, unless catastrophes are either moderate but frequent (removing more than 30% of the population once every 10 years on average), or infrequent but severe (80% removal one year in 100). The risk of the population declining below 10,000 is obviously greater, and even small removals (10–20%) on a regular basis (once in 10 years) give rise to an elevated risk of population decline.

4.4 Conclusions

4.4.1 Implications of PVA results for the Greenland barnacle goose population

- 1 There is good evidence that the reproductive output of birds in this population has declined as the population size has increased, and therefore the density-dependent model is likely to be more realistic than the density-independent one. Nonetheless, there is little evidence to suggest that the Islay population has reached the island's carrying capacity. Thus it remains possible that density-mediated regulation of population growth is sufficiently weak at present that the density-independent model is more appropriate.
- 2 The greater population growth seen on Islay compared to the other sub-populations appears to have been a result of higher productivity amongst Islay birds, rather than differential rates of movement between wintering locations.
- 3 If breeding is being regulated by population density, as simulated in the density-dependent version of the model, then numbers on Islay are predicted to remain near the current level of approximately 35,000.
- 4 Geese are currently legal quarry in Iceland and are shot under licence in Scotland. If the numbers shot each year remain at current levels the predicted risk of population decline below 10,000 in 25 years is less than 0.3%.
- 5 In the presence of density-dependence, additional removal in Scotland of as few as 500 individuals annually may be sufficient to reduce the median equilibrium population on Islay to less than 30,000, increasing the risk of decline below 10,000 within 25 years to 2.5%.
- 6 In the absence of density-dependence, additional removal of 1550 individuals is required to obtain a median population at the current size. However, the absence of regulation means this is not a stable equilibrium, and the risk of decline below 10,000 within 25 years increases to approximately 22%.
- 7 The population does not appear to be particularly sensitive to catastrophic mortality events, requiring frequent, moderate to large losses before the risk of population decline below 10,000 becomes significant. This result is little affected by the presence or absence of density-dependence, although the density-independent simulations show a slightly greater probability of reduction below 1,000 individuals in response to moderate levels of catastrophic event, reflecting the greater variability inherent in density-independent simulations.

4.4.2 Advice

- 1 If the current level of shooting in Iceland and Scotland is maintained there does not appear to be a significant risk of population decline, and if density-dependence is operating as modelled, the Islay population is predicted to remain near its current size.
- 2 Almost all the detailed productivity data (ie age ratios and brood sizes) available for Greenland barnacle geese are collected on Islay. It is important to know how representative these estimates are for the whole population, otherwise it is difficult to predict the effects on the total population of changes in goose management on Islay. Annual collection of population counts, age ratios and mean brood sizes from other important wintering sites would greatly improve our understanding of their relative contributions to the population.
- 3 In addition to expanding the collection of population-based data, more widespread ringing and ring-reading would greatly improve our ability to estimate movement rates between Scottish sub-populations. Again, it is important that these rates are known, since the potential knock-on effects of any change in the management on Islay are closely linked to relative movement rates.

4.5 References

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Figure 1 Greenland barnacle goose population size, 1959–2003, derived from coordinated counts (a combination of aerial surveys and ground counts; dotted lines, circles indicate count years) conducted at approximately 5 yearly intervals, and the annual counts conducted on Islay (solid line).

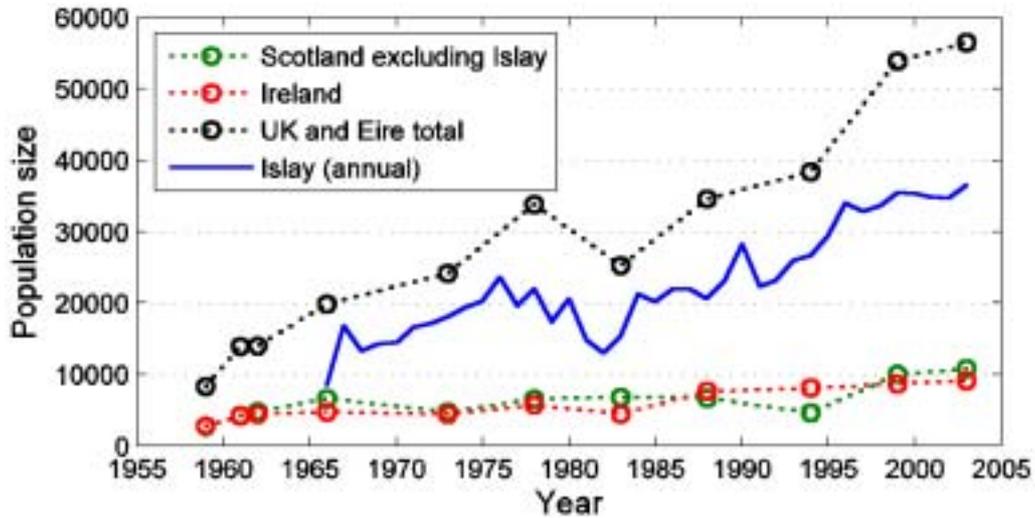


Figure 2 Greenland barnacle goose population trends at the main Scottish haunts, excluding Islay, since 1980. Data derived from a combination of aerial surveys and ground counts.

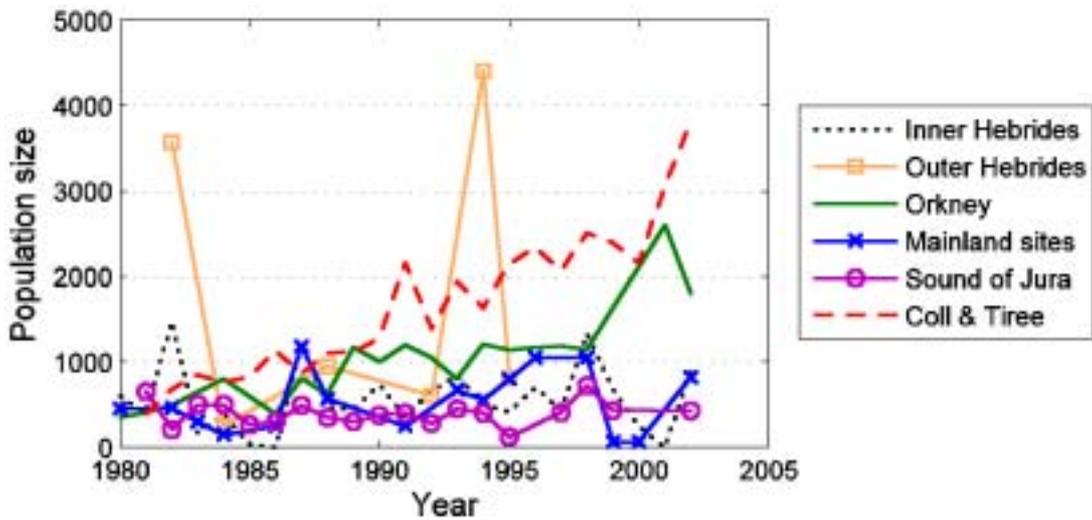


Figure 3 Adult survival rates for Greenland barnacle geese ringed on Islay. The survival estimates are for the transitions: 1984–5 to 2002–3. Error bars are not shown, but are smaller than the symbols used.

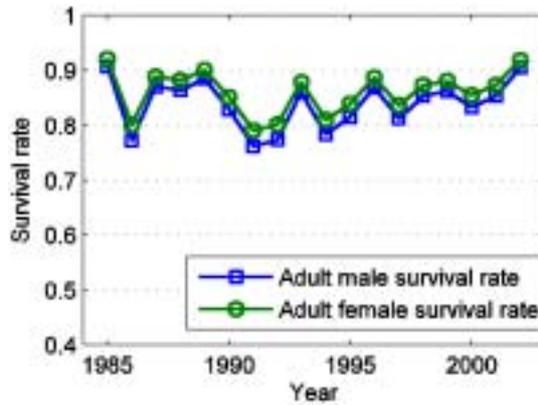


Figure 4 Density-independent projection of the Islay Greenland barnacle goose population, with population size plotted on a log scale. The starting point is the 1966 population estimate.

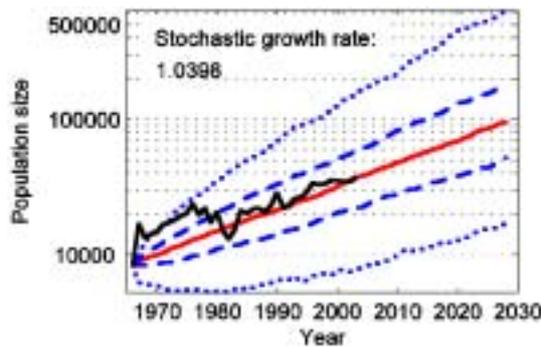
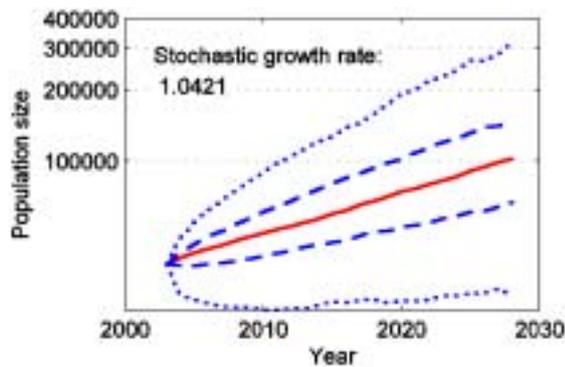


Figure 5 Density-independent projection of the Islay Greenland barnacle goose population, with population size plotted on a log scale. The starting point is the 2003 population estimate.



NB: In all cases the solid red line is the median population size, the dashed and dotted blue lines respectively the 50% and 95% confidence intervals and in the left hand plots the black line is the observed population between 1966–2003.

Figure 6 Density-dependent projection of the Islay Greenland barnacle goose, density-dependence operates through both the mean brood size and the proportion of breeders. The starting point is the 1966 population estimate.

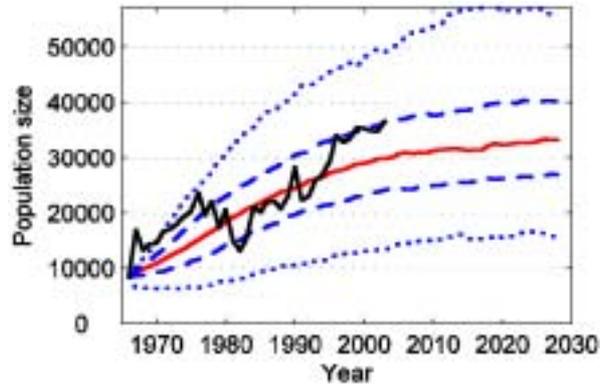


Figure 7 Density-dependent projection of the Islay Greenland barnacle goose, density-dependence operates through both the mean brood size and the proportion of breeders. The starting point is the 2003 population estimate.

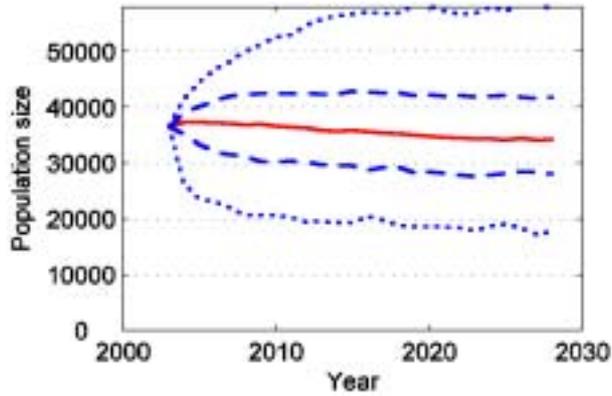
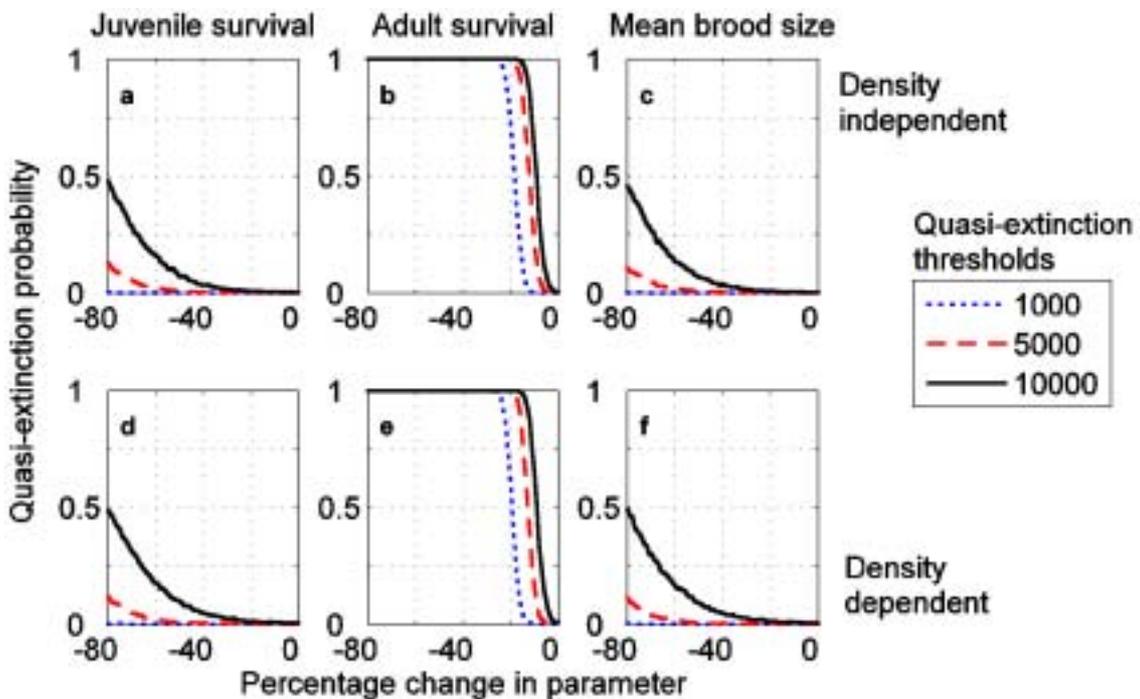


Figure 8 Plots indicating the probability of the Islay Greenland barnacle goose population declining below critical levels (ie quasi-extinction at: 10,000 = solid black line; 5,000 = dashed red line; 1,000 = dotted blue line) within 25 years as a result of proportional change to the mean rates of juvenile survival, adult survival and mean brood size. The upper panels (subplots a–c) are derived from density-independent simulations while the lower panels (subplots d–f) are derived from density-dependent simulations.

To estimate the quasi-extinction risk the mean value of each rate was reduced in turn by up to 80% of its overall baseline value estimated from all years of data (see Table 1 for baseline values) and the quasi-extinction probability calculated as the proportion of 1000 simulations which declined below each of the thresholds (error bars have been omitted due to their small size). The most sensitive rate with the greatest influence on quasi-extinction probability is mean adult survival (middle plots).



Figures 9a/b Greenland barnacle goose quasi-extinction probabilities within 25 years in response to additional shooting mortality obtained using: (a) density-dependent model and (b) density-independent model. Birds are removed post-breeding, mimicking autumn/winter goose shooting. The proportion of juveniles in the bag is 0.25, corresponding to the proportion of young birds reported in the Iceland shooting bag.

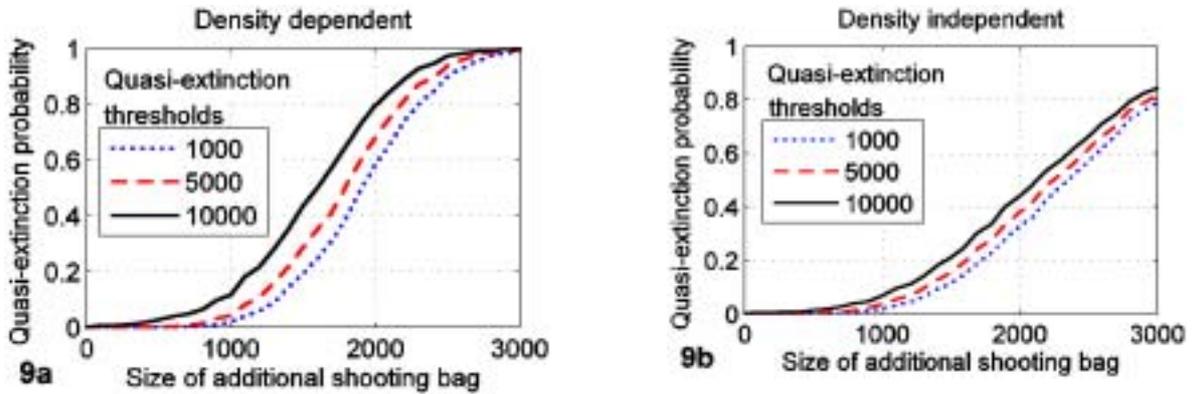


Figure 10a-d Projections of the Greenland barnacle goose Islay sub-population over 25 years under a range of different additional shooting mortalities in the presence of density-dependent regulation. The solid red lines indicate the median population size and the dashed and dotted blue lines, respectively the 50% and 95% confidence intervals. In each subplot the starting point is the 2003 population estimate and the size of the annual shooting bag is given in the top left corner.

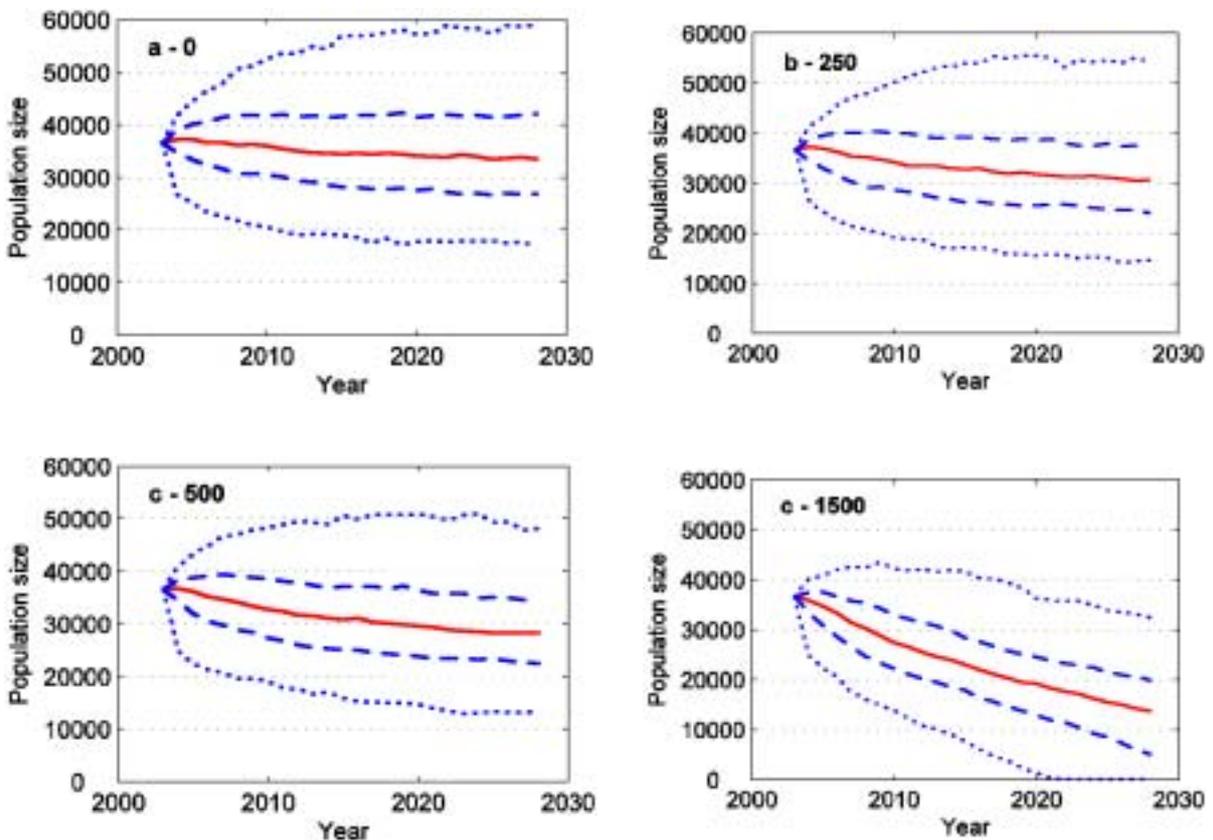
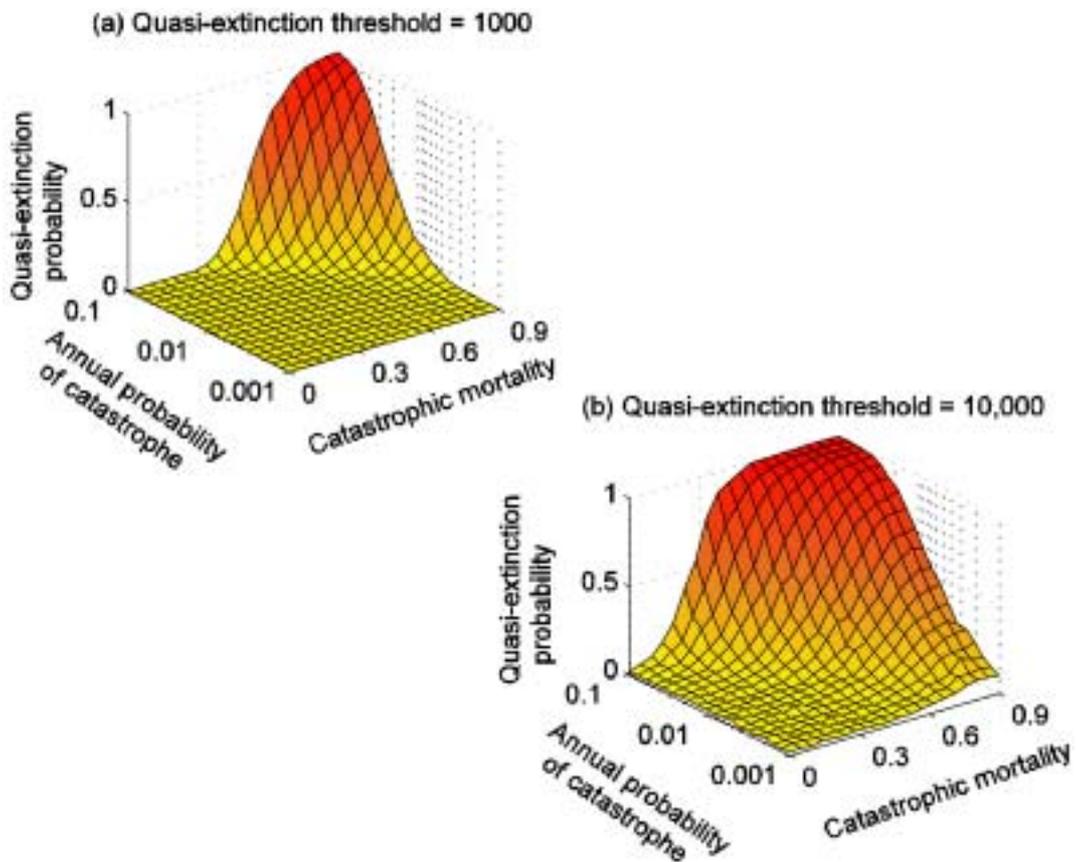


Figure 11 Plots of the probability of quasi-extinction within 100 years for the Islay Greenland barnacle goose resulting from catastrophic mortality events, derived using the density-dependent version of the model. The annual probability of a catastrophe occurring (y-axis, lower-left) varies between an average of once in every 10 years (0.1) to once in every 1000 years (0.001). The occurrence of a catastrophe in any particular year of a population simulation is determined by a random 'coin-toss' process. The proportion of the population removed by a catastrophe (x-axis, lower right) varies between 0–0.9 (ie 0–90% of the population dies). Quasi-extinction probabilities (z-axis, vertical) are derived from the proportion of simulations (out of 1000) which fall below population thresholds of 1,000 and 10,000 individuals within 100 years. For example, the risk of the population falling below 1000 individuals within 100 years (11a) when catastrophes occur on average once every 10 years ('annual probability of catastrophe' = 0.1) is negligible when less than 30% of the population is killed ('catastrophic mortality' \leq 0.3), but rises rapidly as a greater proportion of the population is removed. However, the likelihood of the population being reduced below 10,000 (11b) is almost certain ('quasi-extinction probability' = 1) when catastrophes occur on average once every 10 years and 50% or more of the population is removed.



APPENDIX 1

Calculation of demographic data and age class sizes for the Islay sub-population of Greenland barnacle goose using the annual population count (N), proportion of juveniles (j) and mean brood size (bs) data. In all of the following equations subscript 't' is used to denote the current year, 't-1' the previous year.

Number of juveniles:

$$J_t = j_t * N_t$$

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

$$S_t = \frac{N_t - J_t}{N_{t-1}}$$

Number of birds in their second year:

$$N2_t = J_{t-1} * S_t$$

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:

$$PB_t = \frac{J_t / bs_t}{0.5 * N3_t}$$

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

Threshold density-dependence:

(Parameters: Nlim = threshold population size of breeding age birds;
MaxPB = maximum proportion of breeders)

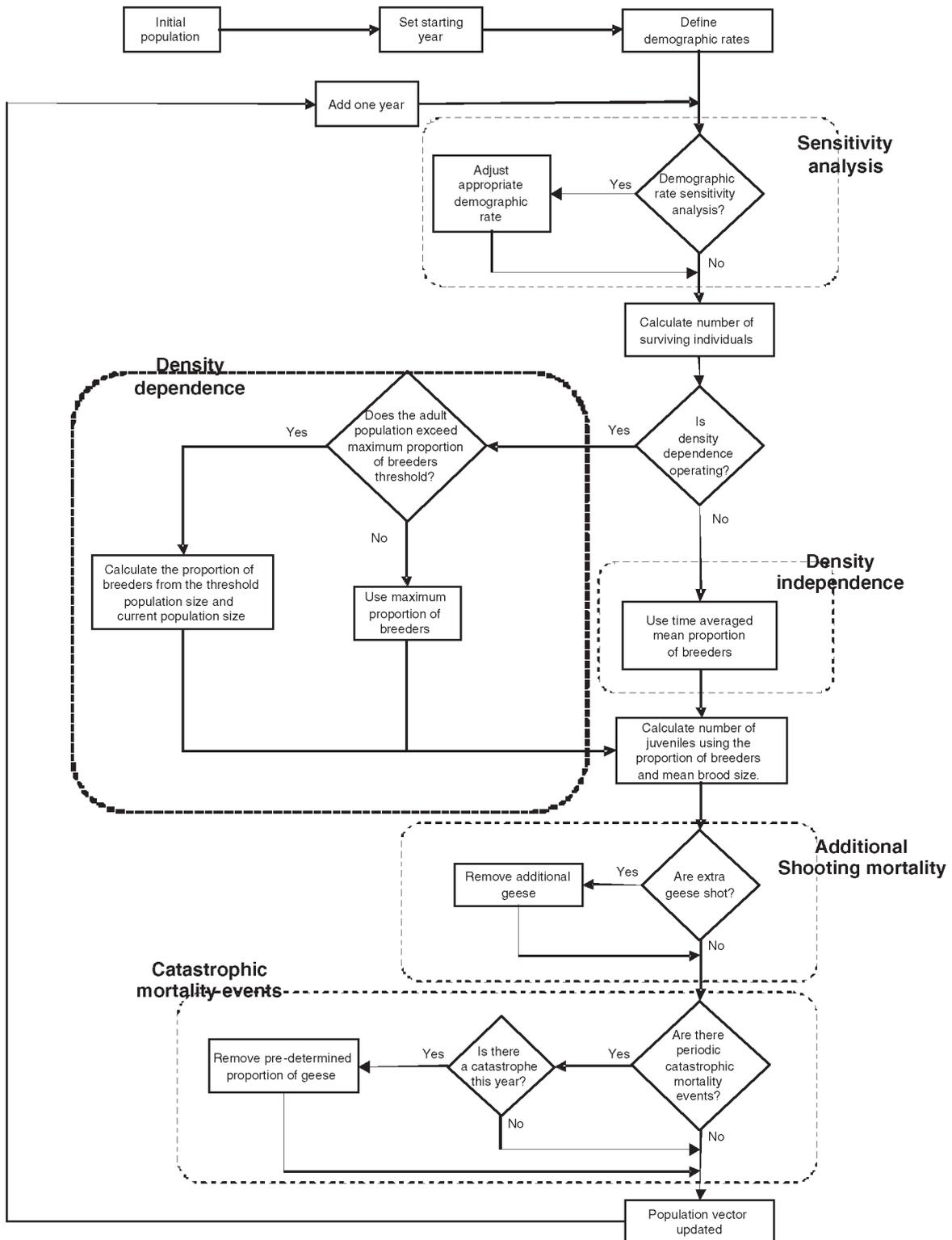
If $N3_{t-1} < Nlim$

$$DDpropB_t = MaxPB$$

If $N3_{t-1} > Nlim$

$$DDpropB_t = MaxPB * \frac{Nlim}{N3_{t-1}}$$

APPENDIX 2 – Flow chart describing the density dependent, stochastic population model for the Islay population of the Greenland barnacle goose



5 STATUS AND POPULATION VIABILITY OF THE SVALBARD BARNACLE GOOSE

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5.1 Introduction

This report summarises the analysis of census and productivity data collected for the Svalbard breeding population of barnacle geese *Branta leucopsis* which winters along both sides of the Solway Firth. The amount of data collected for this population, particularly since the early 1970s, has led to this being regarded as one of the best examples of a long term population study for any vertebrate population (Owen & Black, 1999). Trends in the population counts and demographic variables are discussed, together with the outputs from a population model developed from the data, which has been used to explore a range of possible scenarios.

5.2 Methods and results

Since 1958 the Wildfowl and Wetlands Trust (WWT) has conducted an annual count of the barnacle goose population on the Solway, and in addition estimated the proportion of juveniles present and the average brood size (the average family size). Up to and including winter 1998–99, co-ordinated total population counts were undertaken in mid-October, from which the total population size was determined (although occasional counts were also made in other months). In 1999–2000 and 2000–2001, one count was conducted each month from October–April inclusive, and the annual count was derived from these. Since the winter of 2001–02, more regular (twice-monthly) counting has been undertaken, and the annual population size estimated as the average of the top 10% of these counts. The raw demographic data obtained from the total flock counts were used to derive three further demographic parameters:

- 1 the annual survival rate (the proportion of the population surviving from one year to the next),
- 2 the productivity rate (the number of young produced per breeding age adult, estimated on arrival in Scotland),
- 3 the proportion breeding (the proportion of breeding age birds returning to Scotland with young).

See Appendix 1 for the derivation of these parameters.

There have been several major analyses of the dynamics of the population using these data (Owen & Norderhaug, 1977; Owen, 1984; Rowcliffe *et al.*, 1995; Pettifor *et al.*, 1998). In each case a prediction of the expected equilibrium population size was made, based on the observed trends. These predictions were: 8–12,000 geese (Owen & Norderhaug, 1977), 12,000 geese (Owen, 1984) and 10,500 geese (Rowcliffe *et al.*, 1995), all of which have considerably under-estimated the population's actual expansion (latest count, winter 2003/04: 27,250 geese). Population growth until the early 1990s was largely attributed to increasing levels of protection, with hunting banned initially on the wintering grounds in the

1950s and throughout the range by the mid 1970s (Owen, 1984). Hunting of this population is currently illegal throughout its range. In addition, the reserve areas on the Solway managed for the geese have been extended, thereby reducing the amount of disturbance they experience. As the population grew it was assumed that the breeding colonies on Svalbard would reach capacity, thereby limiting breeding, and that the population size would level off. However, while the established colonies do appear to have reached a limit in terms of their breeding capacity, what is now apparent is that in response to the subsequent crowding at these sites, new breeding colonies were founded, enabling the population to continue expanding (Black, 1998).

Since the 1960s almost 10,000 individuals in the population have had unique, colour-coded leg rings fitted, and re-sighting records of these marked individuals are available from 1972/73 to the present. This represents an extremely valuable ecological resource, in particular for estimating survival rates. Attempts to analyse this dataset in collaboration with J.D. Lebreton and co-workers at CNRS in Montpellier, using programs MARK and MSURGE proved more complicated than expected and have consequently been unsuccessful to date. Further efforts to resolve the problems encountered are on-going, unfortunately time constraints have prevented this analysis being completed and we are unable to present any results from this work here.

The reproductive success of marked individuals has also been recorded on the wintering grounds. These data are used here to compare the productivity of birds seen mainly within the reserves and Barnacle Goose Management Scheme (BGMS) areas with that for birds seen mainly on non-reserve and non-BGMS areas during the mid-winter period. Productivity was recorded as either the mean brood size or the mean proportion of juveniles across marked individuals and their families, taking the modal brood size recorded for an individual in a given winter where more than one sighting was made. The mid-winter location for each goose was determined by calculating whether it was seen most frequently in fields on (a) the reserves, (b) the management scheme areas, or (c) outside these areas, in the months of November to February inclusive. Geese that did not fall clearly into one of these categories (eg were seen equally on reserve and management scheme areas) were omitted from the analyses.

5.2.1 Analysis of population count data

The population of Svalbard barnacle geese has grown from a low point of 300 in 1948 to 27,250 in 2003–4 (Figure 1), and there is currently no indication that the population growth rate is beginning to slow (Figure 2). However, since previous analysis of the data found evidence of density-dependent declines in the demographic rates (Rowcliffe *et al.*, 1995), formal tests for density-dependence in population time series data were performed. Randomisation tests (Pollard *et al.*, 1987; Dennis & Taper, 1994) are more stringent than simple regressions tests for detecting density-dependence in population time series. Neither test returned a significant result; thus, from the population time series alone we have no evidence to suggest that the population as a whole has been regulated by density-dependence. Further tests for the presence of density-dependence in the demographic rates are described in the following section.

5.2.2 Analysis of demographic data

The mean annual demographic rates (and their standard deviations) derived using the population data between 1957–2003 are provided in Table 1, together with the same rates calculated using the run of years available at the time of the previous PVA (1957–1991; Rowcliffe *et al.*, 1995) and those for the years

collected since (1992–2003), in order to highlight where changes have occurred. Comparing the previous and current estimates (Table 1, columns 1 and 2), only the survival rate has increased, although not quite significantly (2 sample t-test, $t=-1.97$, $p=0.055$). Of the remaining rates the declines seen are all significant (productivity: $t=2.28$, $p=0.028$; mean brood size: $t=4.64$, $p<0.001$; proportion of juveniles: $t=2.36$, $p=0.023$) except for the proportion of breeding birds, although this is close to being significant at the 5% level ($t=1.99$, $p=0.053$). The changes in the reproductive rates can be attributed to both a decline in the mean values and a reduction in the annual variation, with the early years in particular being highly variable.

Table 1 Svalbard barnacle goose demographic parameters derived from the population count, proportion of juveniles and brood size estimates for the periods 1957–91, 1992–2003 and all years 1957–2003. The rates derived for the previous PVA exercise (Rowcliffe *et al.*, 1995) are included for comparison with the more recent estimates. The survival rate is a combined estimate for all birds older than c.6 months, calculated as the number of adults in the current year divided by the total population in the previous year; productivity is the ratio of juveniles to breeding age adults; mean brood size is the estimated family size from a sample of flocks; proportion of juveniles is the percentage of juveniles in a sample of flocks; proportion breeders is the minimum number of adults required to have bred (in order to account for the estimated number of juveniles) divided by the total adult population. See Appendix 2 for further details.

	Previous estimate (1957–1991)	Current estimate (1992–2003)	Overall estimate (1957–2003)
Parameter	Mean (St. dev)	Mean (St. dev)	Mean (St. dev)
Survival	0.870 (0.131)	0.950 (0.078)	0.891 (0.124)
Productivity	0.308 (0.244)	0.142 (0.090)	0.264 (0.226)
Mean brood size	2.248 (0.355)	1.745 (0.197)	2.117 (0.390)
Proportion juveniles	0.191 (0.119)	0.106 (0.060)	0.169 (0.113)
Proportion breeders	0.263 (0.169)	0.160 (0.096)	0.236 (0.159)

Investigation of changes in the demographic rates in relation to the current and previous year's population density and environmental conditions was conducted using both Generalised Linear Models (GLMs) and Robust Regression. In contrast to standard (ordinary least squares) linear regression, where outlying data points can disproportionately influence the results obtained, Robust Regression methods weight each data point according to its proximity to the fitted regression line, and consequently outlying points have a reduced influence. While GLMs enable interactions between population density and environmental variables to be tested, they are sensitive to the presence of outliers in the data. Conversely, Robust Regression minimises sensitivity to outliers, but cannot handle interactions between parameters. The two methods therefore compliment one another. In addition to population density, the following explanatory variables were used in order to control for the potentially confounding influence of environmental variation: Svalbard summer weather (average monthly temperatures for May to August, 1960–2001 and number of days in May and June with greater than 50% snow cover, 1976–1994, 2000–01, recorded at Svalbard airport, Longyearbyen) and North Atlantic Oscillation (NAO) index (for the main migration months, May and September, 1958–2001). Two different lengths of dataset were used, one of only 21 years (matching the snow cover records) and one of 42 years (matching the May temperature and NAO records). All the demographic rates (with the exception of survival) followed the same pattern, exhibiting significant relationships with:

- increasing population size (\log_e) in the previous year (negative relationship);
- increasing values of NAO index for May (representing years of enhanced westerly winds in the north Atlantic; negative relationship);
- the number of days on Svalbard in June with greater than 50% snow cover (negative relationship)
- the average temperature on Svalbard in May (positive relationship).

Thus it appears that as that population size has grown there has been a decline in reproduction, and that between year variation in reproduction is explained in part by the severity of weather conditions experienced during spring migration and the temperature and snow conditions on Svalbard during May and June. The only rate for which a significant interaction was obtained was mean brood size, with the negative effect of the previous year's population size on the mean brood size being more pronounced in years with a lower average May temperature ($t=-2.026$, $p=0.049$). The full results are listed in Appendix 2.

While the tests for density-dependence in the population time series failed to find evidence for density-dependence (section 2.1), the significant declines seen in all the reproductive parameters as the population size has increased are an indication of population regulation. The reason for this apparent contradiction is not clear, and it is unlikely to be the result of a single cause. However, since population growth in long-lived, slow breeding species like geese tends to be most sensitive to changes in survival, it is possible that the small increase in the survival rate has been sufficient to offset the concurrent decline in reproduction. In addition, while the number of breeding colonies on Svalbard has increased, the productivity at the newer sites has not matched that at the established ones (Prestrud *et al.*, 1989; Mitchell *et al.*, 1998). The number of breeding-age birds has therefore increased at a faster rate than the increase in overall production of young, leading to a decline in the average reproductive parameters.

5.2.3 Analysis of productivity in relation to local wintering area

Since 1994, a Barnacle Goose Management Scheme (BGMS) has operated on the Scottish side of the Solway, with the aim of minimising conflicts between agriculture and conservation. This scheme provides farmers with payments in return for managing their fields sympathetically for geese. Analysis of field use over the winter as a whole for the years immediately before and after the instigation of the scheme demonstrated an increase in the use of fields outside the nature reserves in the area after 1994 (Cope *et al.*, 2003). Looking at the relationship between the use of fields by geese and their designation (reserve, BGMS or non-BGMS) over the whole winter period reveals a temporal pattern in goose field preference (Figure 3). Goose numbers are highest on the reserves in the autumn, but between October and December numbers on the reserve and BGMS areas show opposite trends, with a shift away from the reserves onto the neighbouring BGMS fields, with peak numbers on the latter achieved in December. Subsequently, there is a similar shift of geese from the BGMS areas onto non-BGMS areas, which peaks in February. Finally there is an increase in numbers using the reserves again in March and April. It is likely that these shifts represent a response to grass depletion, with the return of geese to the reserves in the spring coinciding with fresh grass growth.

Behavioural dominance on the wintering grounds increases continuously with family size (Black & Owen, 1989), and we would therefore predict that both the mean brood size and the proportion of family groups will be higher in the areas with the best grazing. A comparison of the proportion of juveniles and mean brood size on the reserve and BGMS areas for the mid-winter period (November to February) supports this

prediction. Both measures of productivity are higher for birds observed primarily on BGMS areas than for those seen mainly on reserves in mid-winter, when reserve resources are heavily depleted (proportion juveniles: paired t-test, $t=-2.6$, $df=7$, $p=0.035$; mean brood size, paired t-test, $t=-5.81$, $df=12$, $p<0.001$). There was no evidence for individuals frequenting the BGMS in mid-winter having higher breeding success the following year than those on the reserve (mean brood size, paired t-test, $t=-0.901$, $df=11$, $p=0.387$) or those outside the BGMS area (mean brood size, paired t-test, $t=-0.544$, $df=4$, $p=0.615$).

5.3 Population model

Models to simulate the Svalbard barnacle goose population were developed using the data derived from the analyses of census data. The population size in each year of a simulation is calculated using demographic rates (survival and mean brood size) drawn at random from appropriate probability distributions, together with an estimate of the proportion of the adult population which breeds. Because the evidence for density-dependence in the population was equivocal, two versions of the model were developed. The first has no density-dependent regulation of demographic rates and represents a possible upper limit which may be achieved in terms of population growth. In the second, two determinants of reproductive output, the proportion of breeders and the mean brood size, depend on the population size in the previous year. The mean brood size declines with increasing population size in the previous year using coefficients obtained from the linear regression ($t=-4.323$, $p<0.001$; natural log mean brood size). The proportion of breeders each year is estimated using a threshold model, with parameters derived from the data. This model fits the data slightly less well than the linear regression, but is preferred for biological reasons. A maximum proportion of birds (0.35, ie equivalent to 35% of adults being accompanied by juveniles on the Solway) breed when the total population is below a threshold size of 4450. Above this, the proportion breeding declines at a constant rate with increasing population size, reflecting limited nest site availability (see Appendix 1 for details). This model was modified in order to accommodate the approximate fourfold increase in the number of colonies on Svalbard in the thirty years up to the mid 1980s (Prestrud *et al.*, 1989). During simulations the threshold population size (below which the maximum proportion of breeders is attained, set initially at 4450) increases, on average once every eight years (this time interval was chosen as an approximation of $30/4$). In each year of a simulation a random number is drawn in the range 0–1, if it is less than 0.125 then the threshold population size increases, emulating the establishment of a new colony. Each additional colony is smaller than the last, representing a gradual decrease in the availability of new areas for colonisation.

Using the model, we have investigated the risk of population decline below specific thresholds (quasi-extinction) within the short to medium term, resulting from changes in conditions which may affect the population. The term quasi-extinction probability as used here refers to the likelihood that the population will fall below a specific size within a particular period of time (eg the chance that the population will fall below 10,000 in the next 25 years), expressed as a proportional (or percentage) probability. See Appendix 3 for a flow chart of the model structure.

5.3.1 Baseline model outputs

In the absence of density-dependent regulation the predicted median population size in 25 years time (2029) is just over 63,000, with an average stochastic growth rate of 1.053 (Figure 4). The model in this form uses values for the mean brood size and proportion of breeders averaged across all years of data.

However, because of a few high estimates for these reproductive rates during the earliest years of study the observed population size in 2003 is higher than the median simulated population size. The effect of this on the predicted population size in 25 years' time can be seen by comparing the final population estimate in Figure 4 (median: 63,000) with that in Figure 5 (median: 110,000) which illustrates the result of projecting for 25 years starting from the population size in 2003.

With density-dependence operating through both the mean brood size and the proportion breeding, the population is predicted to continue growing but at a decreasing rate (Figure 6). The median population size achieved in 25 years' time is just under 29,000, with 95% confidence limits of just under 20,000 and just over 40,000. Unlike the output from the density-independent simulations (Figures 4 and 5), because the median predicted population size in 2003 is a close match for the actual population size in 2003, simulating the population until 2029 beginning from the 2003 census (Figure 7) yields a similar final population estimate to that beginning in 1958.

Under baseline conditions (ie no change to the current parameter estimates) the probability of the population declining below 10,000 individuals within the next 25 years derived from either the density-dependent or independent simulations is zero. The most sensitive demographic rate in terms of its influence on the likelihood of population decline is adult survival (Figure 8), which is typical of long-lived, slow breeding species. This result is matched in both the density-dependent and density-independent simulations, however the risk of quasi-extinction is greater under conditions of density-independence, reflecting the stabilising influence of mechanisms that regulate populations.

5.3.2 Risk analysis

5.3.2.1 Additional mortality

The probability that the population will decline below key thresholds (1000, 5000, 10000) in response to additional mortality, derived from both density-dependent and independent simulations are provided in Table 2, and for just density-dependent simulations in Figure 9. Additional mortality is simulated through the removal of a fixed number of individuals from the population each year, spread across all ages classes. Since it would be expected that juvenile birds are at greater risk from any additional sources of mortality the juvenile proportion of the removed birds is 30% higher than their proportion within the population. With density-dependence operating, loss of approximately 350 birds produces a stable median equilibrium population at its current size (c. 27,000). The loss of up to 1000 individuals results in only a small increase in the risk of the population declining below 10,000 within 25 years, with a median predicted population size of around 22,500 (Figure 10b). However, if more than 1000 are lost annually steady declines are seen in the population size (Figure 10c-d) with associated rapid rises in the risks of quasi-extinction (Figure 9). In the absence of density-dependence, a stable median equilibrium population size of 27,000 was only achieved when approximately 1,500 birds were removed. However, this level of annual loss from the population produced a substantially higher associated risk of population decline below 10,000 (25% compared with <0.1% for the density-dependent example).

Table 2 Quasi-extinction probabilities for Svalbard barnacle geese in response to elevated levels of loss from the population. The probability of the population declining below specific levels (1000, 5000, 10000) within 25 years in response to different levels of annual loss from the population (0, 1000, 2000, 3000) are shown for both density-dependent and independent simulations.

		Quasi-extinction probability					
		Density-independent			Density-dependent		
Quasi-extinction threshold		1000	5000	10000	1000	5000	10000
Additional loss/year	0	0	0	0	0	0	0
	1000	0.012	0.025	0.06	0.0002	0.001	0.01
	2000	0.42	0.48	0.55	0.36	0.48	0.66
	3000	0.88	0.89	0.92	0.99	0.99	0.99

The contrast between the density-dependent and density-independent models in terms of the size of population loss which produces the same equilibrium population size (respectively 350 and 1500), and the associated differences in the quasi-extinction probabilities (0% and 25% risk of decline below 10,000 in 25 years) are a consequence of fundamental differences between density-dependent and density-independent models. In the density-dependent case, the simulated population's growth is increasingly regulated as it approaches an upper size limit. Conversely, as the population declines below the limit, the degree of regulation eases with increasing distance from the limit and the consequent improvement in population growth permits population recovery back towards the upper limit. In contrast, a density-independent population model has no regulatory mechanisms limiting growth, therefore greater ultimate sizes can be achieved. However, such populations are also less able to recover from chance events which reduce the population size, such as sequential years of poor survival, since there is no compensating increase in reproduction. Thus, under such circumstances population extinction is more likely in the density-independent case. In order to achieve a stable median equilibrium size in the absence of density-dependent regulation it is therefore necessary to remove a considerable number of individuals, however while the median of a series of repeated simulations may be stable, this is achieved at the balance point between simulations which grow to extremely large sizes and those which go extinct; hence the elevated quasi-extinction probability.

5.3.2.2 Catastrophic mortality

The aim of catastrophic event simulations is to determine the sensitivity of the population to extreme events which can give rise to rates of survival or reproduction which are outside the range encountered during the period of data collection. Over long periods, it is likely that there will be occasional "catastrophic" events, causing mortality well above the range of values observed (caused for example by severe storms in the north Atlantic during migration). The sensitivity of the population to occasional large increases in mortality was therefore investigated by recording the quasi-extinction probability resulting from the removal of a proportion of the population at random intervals (Figure 11; the density-dependent version of the model was used to produce the following quasi-extinction estimates, although very similar results are obtained using the density-independent version). At the beginning of each simulation the average annual frequency of catastrophes (from 1 in 1000 years to 1 in 10 years) and the proportion of the population to be removed by each event are selected (between 10–90%). The likelihood of the population falling below 1,000 individuals within 100 years is extremely small, unless catastrophes are either moderate but frequent (removing more than 50% of the population once every 10 years on average), or infrequent but severe (90% removal one year in 100). The risk of the population declining below 10,000 is obviously greater, however even here the risk is small until at least 40% of the population is removed once in every 100 years on average.

5.4 Conclusions

5.4.1 Implications of PVA results for Svalbard barnacle goose population

- 1 There is currently no evidence to suggest the population has reached the carrying capacity of either the summer or winter range. However, there is evidence that reproductive output has declined with increasing population size.
- 2 If breeding is being regulated by population density, as simulated in the density-dependent version of the model, then further increases in population size may be relatively modest compared to those seen over the previous 15–20 years.
- 3 The population models assume the maintenance of the current breeding range, however if new breeding colonies continue to be established on Svalbard then the population may continue to grow. Preliminary results from work being undertaken as part of the FRAGILE (Fragility of Arctic Goose habitat: Impacts of land use, conservation and elevated temperatures) project suggest there is considerable scope for the breeding range on Svalbard to increase (M. O’Connell, *pers comm.*).
- 4 The most sensitive demographic rate is adult survival. Under conditions of density-dependence, additional loss of as few as 350 individuals annually produces a median equilibrium population at its current size of 27,000. The likelihood of long term population decline increases markedly if additional annual losses exceed 1000 or more.
- 5 In the absence of density-dependence, the modelled population is less stable. An annual loss of 1500 individuals produces a median equilibrium population number at the current size, however this also yields a 25% probability of population decline below 10,000 within 25 years.
- 6 The population does not appear to be particularly sensitive to catastrophic mortality events, requiring frequent, moderate to large losses before the risk of population decline below 10,000 becomes significant. This result is little affected by the presence or absence of density-dependence, although the density-independent simulations show a slightly greater probability of reduction below 1,000 individuals in response to moderate levels of catastrophic event, reflecting the greater variability inherent in density-independent simulations.

5.4.2 Advice

- 1 The movement of geese through the course of the winter from reserves to BGMS fields and then to non-BGMS fields, suggests that the capacity of the BGMS to accommodate the majority of the population through the winter has been exceeded. However, preliminary results have found no evidence to suggest that this is limiting population growth (eg through reduced productivity). Any decision to extend the BGMS should therefore be viewed as a farming issue, rather than a goose conservation one.
- 2 Simulated additional loss of comparatively few geese was sufficient to stabilise the population at its current level under the density-dependent model. Under the density-independent model, a greater loss was required in order to stabilise average population growth, however this leads to an elevated probability of significant population decline, caused by the wide margins of error associated with density-independent population projections. On this basis, assuming a goal of avoiding medium-term population decline, additional losses from the population exceeding approximately 350 geese annually should be avoided.

- 3 Under the current beneficial management scheme arrangements in winter it appears that the conditions on the breeding grounds have a greater influence on population growth. Management actions on the Solway employed to minimise conflict are therefore unlikely to influence patterns of population growth.
- 4 It is likely that the work being undertaken for the FRAGILE project will provide useful information regarding the future prospects for this population. A review of the results presented here should be made in the light of their conclusions, when they become available.

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Figure 1 Svalbard barnacle goose population 1957/8–2003/4.

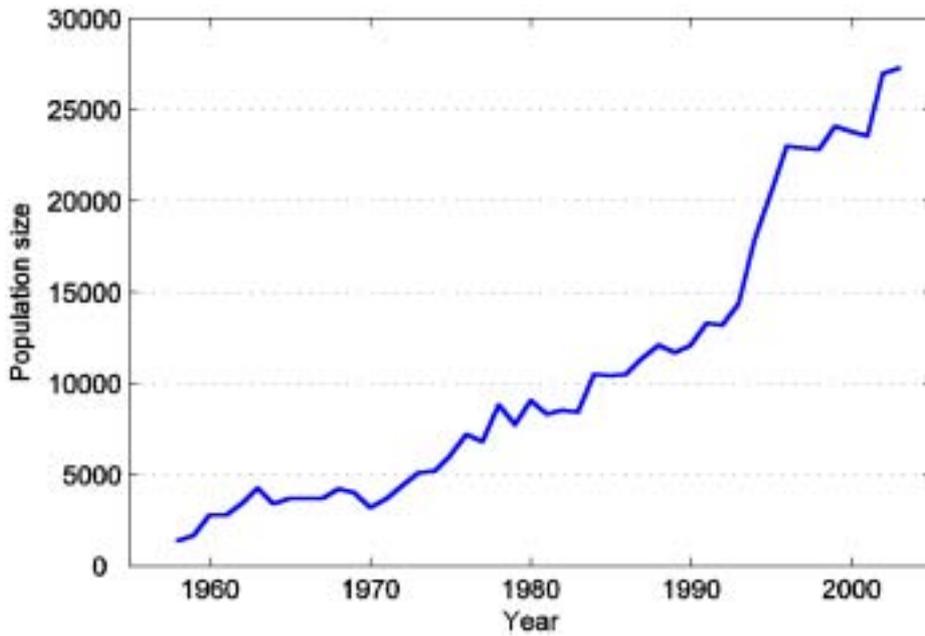


Figure 2 Plot of Svalbard barnacle goose (loge) population size 1957/8–2003/4 (blue line), with the best-fit linear regression (black line).

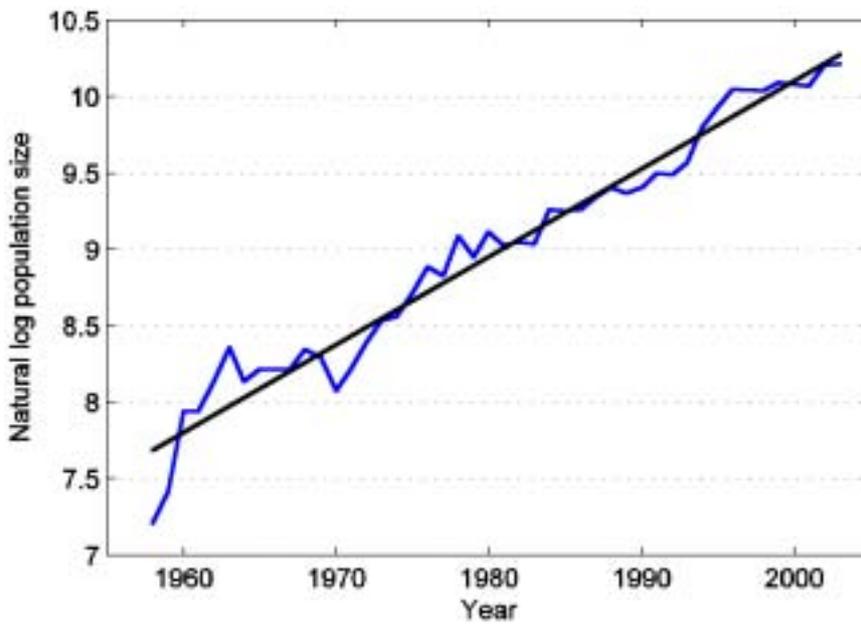


Figure 3 Relative goose numbers in reserve, Barnacle Goose Management Scheme (BGMS) and non-BGMS areas on the Scottish side of the Solway over the winter period. Values shown are the percentage of the total number of goose-days on each area per 2 week period, averaged for the years 1996–2002 (with standard error bars shown). Over the course of the winter, numbers are initially highest on the reserves, before a shift to the BGMS areas by mid-December. By the end of February the non-BGMS fields are most heavily used, before a rise in numbers on the reserves prior to spring migration.

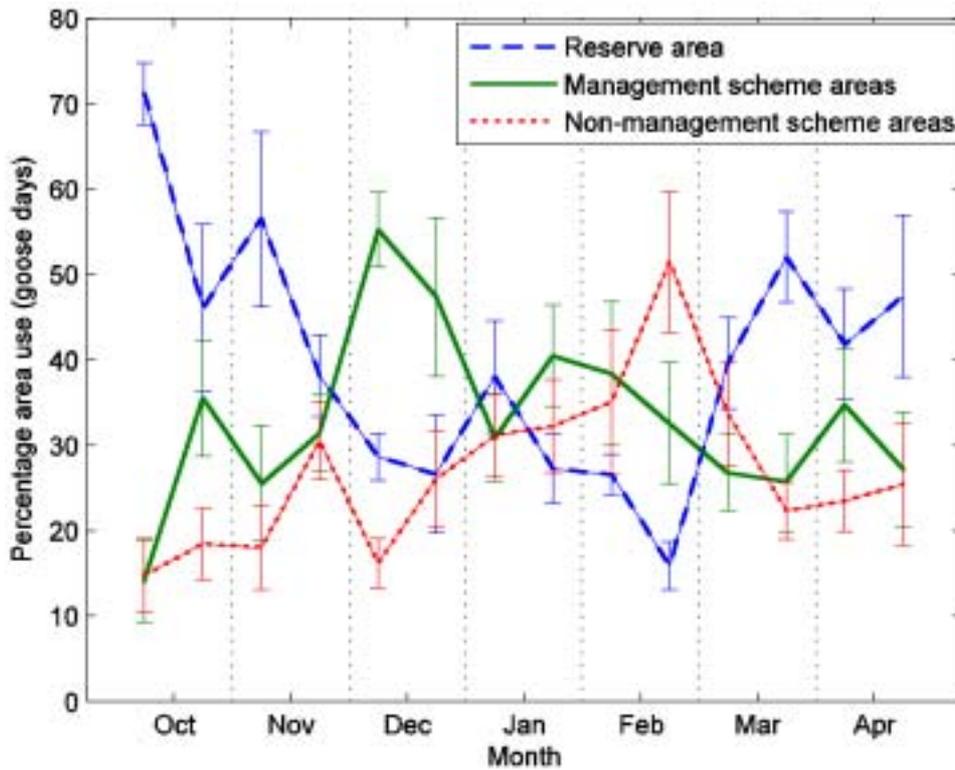


Figure 4 Density-independent projection of the Svalbard barnacle goose population, with population size plotted on a log scale. The starting point is the 1958 population estimate.

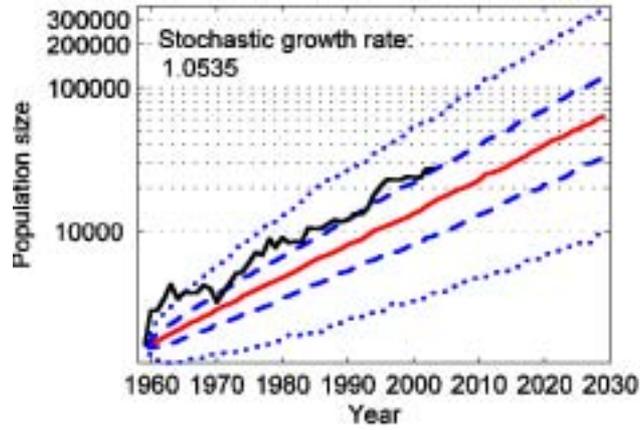


Figure 5 Density-independent projection of the Svalbard barnacle goose population, with population size plotted on a log scale. The starting point is the 2003 population estimate.

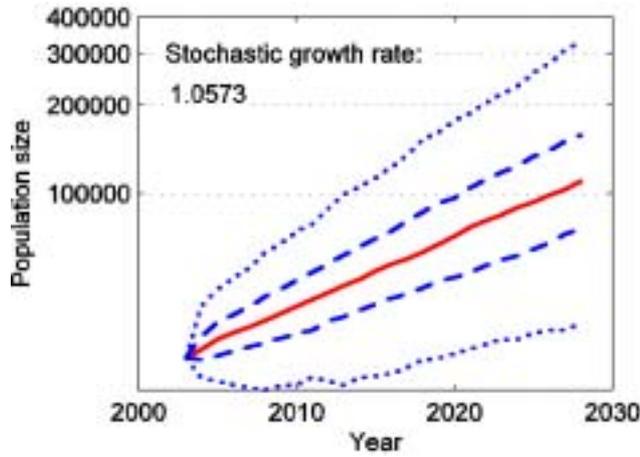


Figure 6 Density-dependent projection of the Svalbard barnacle goose population, density-dependence operates through both the mean brood size and the proportion of breeders. The starting point is the 1958 population estimate.

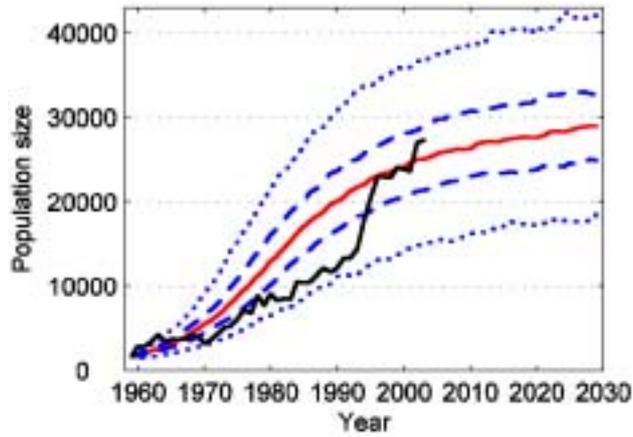
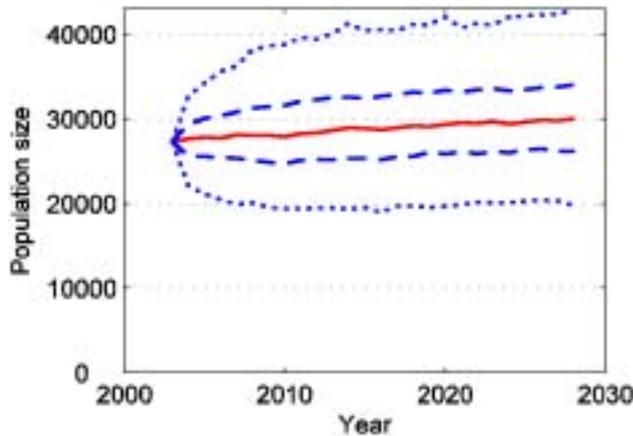


Figure 7 Density-dependent projection of the Svalbard barnacle goose population, density-dependence operates through both the mean brood size and the proportion of breeders. The starting point is the 2003 population estimate.



NB: In all case the solid red line is the median population size, the dashed and dotted blue lines respectively the 50% and 95% confidence intervals and in the left hand plots the black line is the observed population 1958–2003.

Figure 8 Plots indicating the probability of the Svalbard barnacle goose population declining below critical levels (ie quasi-extinction at: 10,000 = solid black line; 5,000 = dashed red line; 1,000 = dotted blue line) within 25 years as a result of proportional change to the mean rates of juvenile survival, adult survival and productivity (Note: the actual rate perturbed during simulations was the mean brood size). The upper panels (subplots a–c) are derived from density-independent simulations while the lower panels (subplots d–f) are derived from density-dependent simulations.

To estimate the quasi-extinction risk the mean value of each rate was perturbed in turn by +/- 10% of its overall baseline value estimated from all years of data (see Table 1 for baseline values) and the quasi-extinction probability calculated as the proportion of 1000 simulations which declined below each of the thresholds (error bars have been omitted due to their small size). The rate with the greatest influence on quasi-extinction probability is mean adult survival (middle plots; b & e). Density-dependent regulation acts to reduce the likelihood of decline, thus the quasi-extinction probabilities are lower in panel (e) than in panel (b).

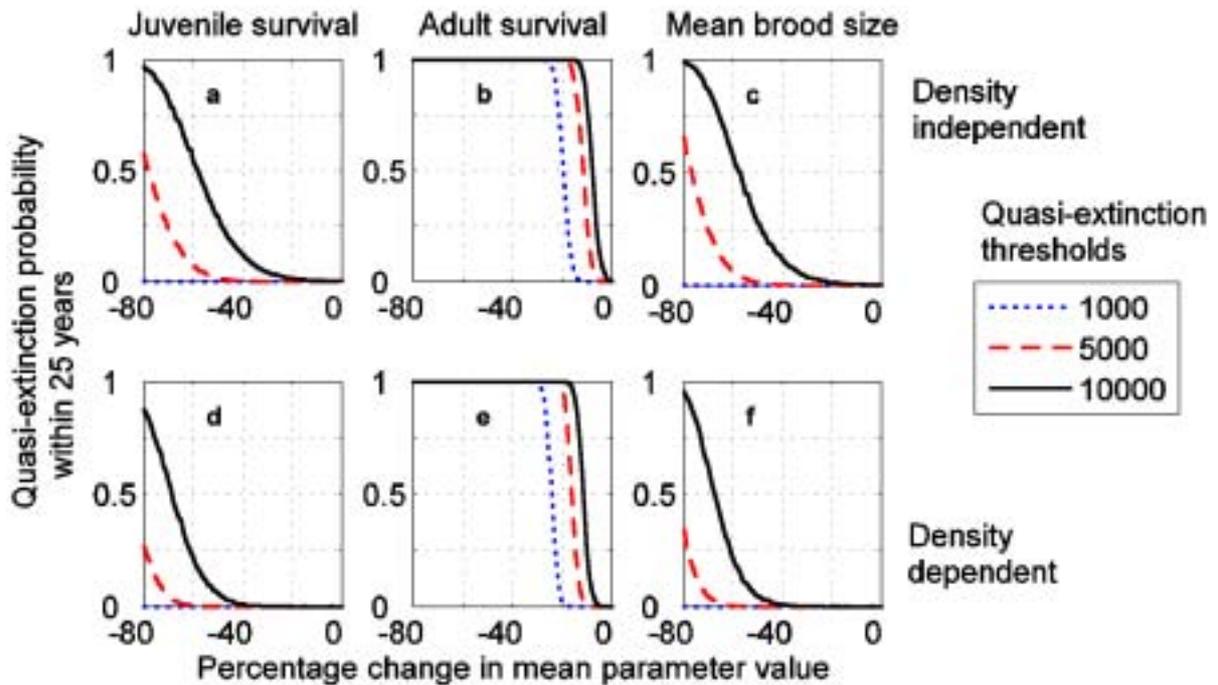


Figure 9 Svalbard barnacle goose quasi-extinction probabilities within 25 years resulting from increasing levels of loss of individuals from the population in the presence of density-dependent regulation.

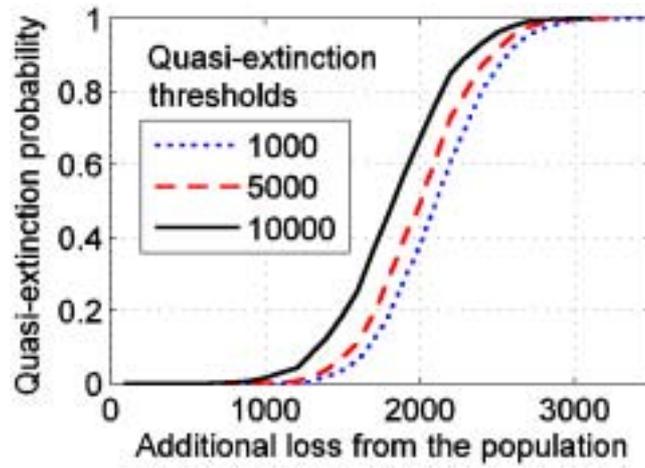


Figure 10a–e Projections of the Svalbard barnacle goose population over 25 years obtained from a selection of different annual losses from the population (simulated using the density-dependent model). The solid red lines indicate the median population size and the dashed and dotted blue lines, respectively the 50% and 95% confidence intervals. In each subplot the starting point is the 2003 population estimate and the number lost annually from the population is given in the top left corner.

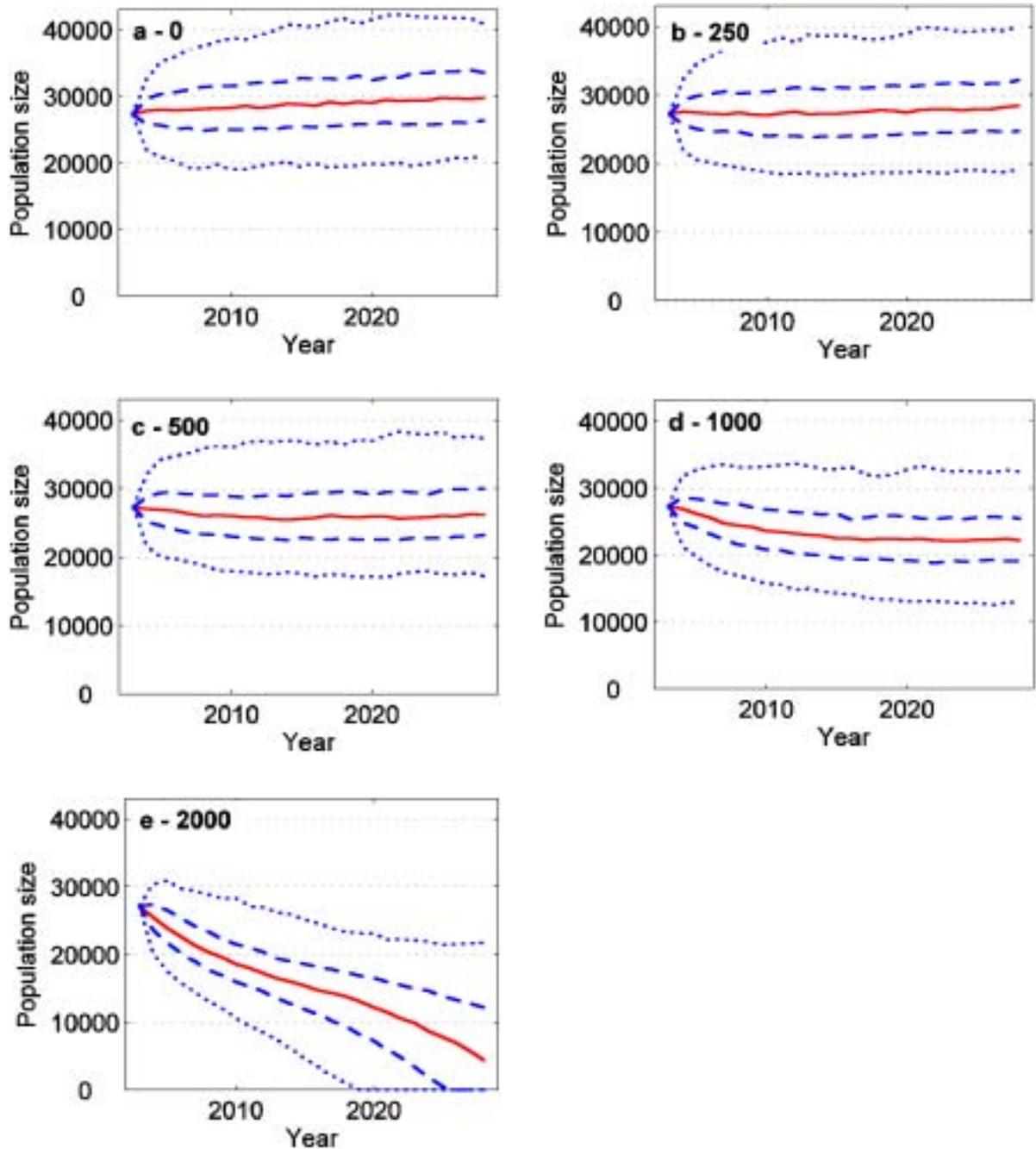
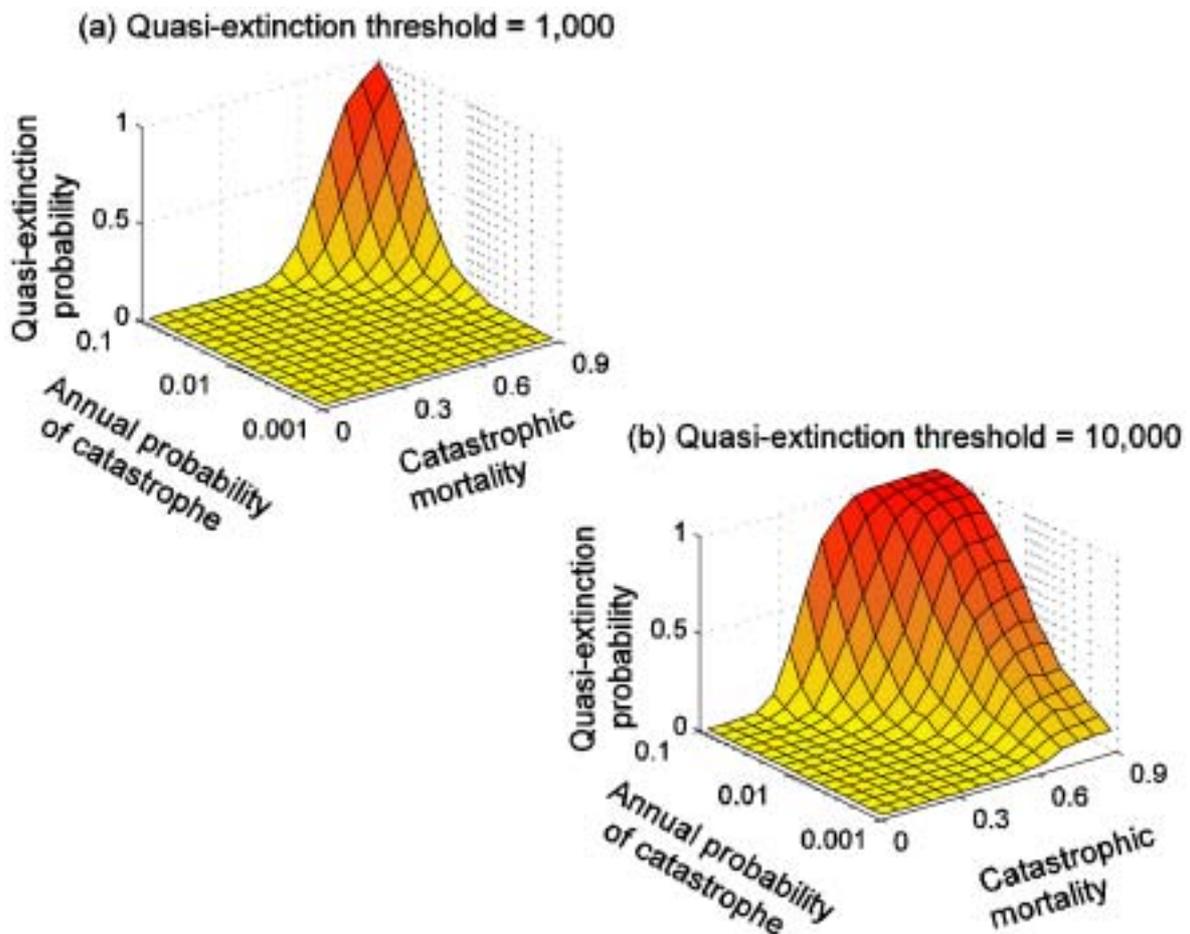


Figure 11 Plots of the probability of quasi-extinction within 100 years for the Svalbard barnacle goose resulting from catastrophic mortality events, derived using the density-dependent version of the model. The annual probability of a catastrophe occurring (y-axis, lower-left) varies between an average of once in every 10 years (0.1) to once in every 1000 years (0.001). The occurrence of a catastrophe in any particular year of a population simulation is determined by a random 'coin-toss' process. The proportion of the population removed by a catastrophe (x-axis, lower right) varies between 0–0.9 (ie 0–90% of the population dies). Quasi-extinction probabilities (z-axis, vertical) are derived from the proportion of simulations (out of 1000) which fall below population thresholds of 1,000 and 10,000 individuals within 100 years. For example, the risk of the population falling below 1000 individuals within 100 years (Figure 11a) when catastrophes occur on average once every 10 years ('annual probability of catastrophe' = 0.1) is negligible when less than 50% of the population is killed ('catastrophic mortality <= 0.5), but rises rapidly as a greater proportion of the population is removed. However, the likelihood of the population being reduced below 10,000 (Figure 11b) is almost certain ('quasi-extinction probability' = 1) when 50% or more of the population is removed on average once every 10 years.



APPENDIX 1

Calculation of demographic data and age class sizes for the Svalbard barnacle goose using the annual population count (N), proportion of juveniles (j) and mean brood size (bs) data collected on the Solway. In all of the following equations subscript 't' is used to denote the current year, 't-1' the previous year.

Number of juveniles:

$$J_t = j_t * N_t$$

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

$$S_t = \frac{N_t - J_t}{N_{t-1}}$$

Number of birds in their second year:

$$N2_t = J_{t-1} * S_t$$

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:

$$PB_t = \frac{J_t / bs_t}{0.5 * N3_t}$$

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

Threshold density-dependence:

(Parameters: Nlim = threshold population size of breeding age birds;
MaxPB = maximum proportion of breeders)

If $N3_{t-1} < Nlim$

$$DDpropB_t = MaxPB$$

If $N3_{t-1} > Nlim$

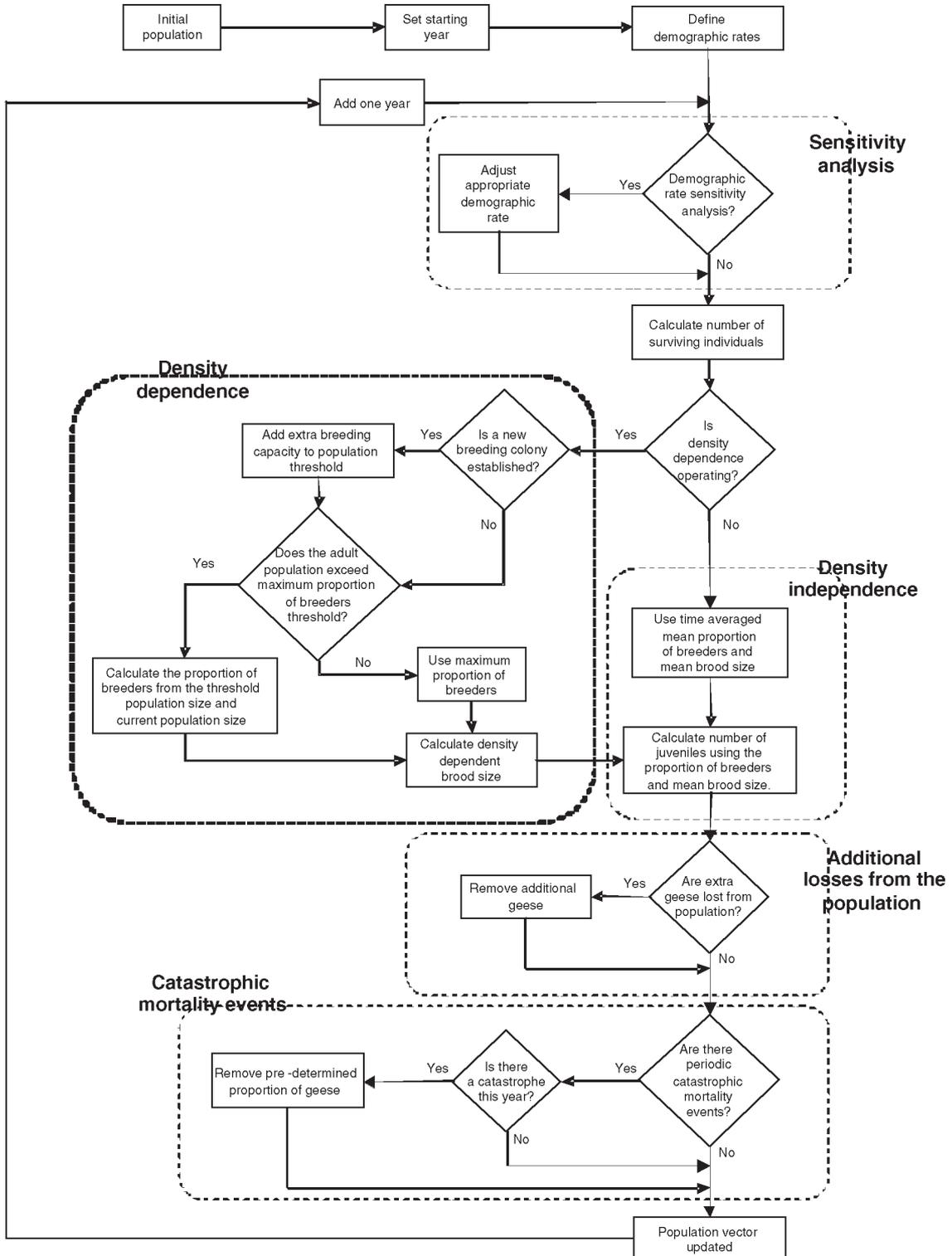
$$DDpropB_t = MaxPB * \frac{Nlim}{N3_{t-1}}$$

APPENDIX 2

Significant results of statistical analysis of Svalbard barnacle goose demographic data. The explanatory variables were: $\text{Log}_e(N_{t-1})$ – the natural log of the total population size in the previous year, May temperature – the average temperature for May each year (1960–2001) recorded at Svalbard airport (Longyearbyen), May NAO – the value for the North Atlantic Oscillation index for May each year (1960–2001) and June snow – the number of days with at least 50% of the ground covered in snow in June (1976–1994, 2000–01) recorded at Svalbard airport. The length of dataset used was determined by the duration of each weather variable from Svalbard, 'Long' with temperature and NAO data and 'Short' with snow data. In all instances Generalised Linear Models (GLM) were used first to check for the presence of significant interaction terms. If none were identified the remaining model refinement was carried out using Robust Regression (Robust), which is less sensitive to outliers in the data. All tests were conducted using Matlab (MathWorks, Inc.). No significant relationships were identified between survival and any explanatory variable, similarly none were found between the mean brood size and the short dataset.

Test rate (transformation)	Dataset	Test	Significant explanatory variables	t	p	Parameter estimate	Standard error
Mean brood size (none)	Long	GLM	Constant	5.443	<0.001	8.601	1.58
			$\text{Log}_e(N_{t-1})$	-4.003	<0.001	-0.712	0.178
			May temperature	2.152	0.037	0.802	0.372
			$\text{Log}_e(N_{t-1})$ * May temperature	-2.026	0.049	-0.087	0.042
Proportion breeders (square root)	Long	Robust	Constant	6.516	<0.001	1.945	0.299
			$\text{Log}_e(N_{t-1})$	-4.754	<0.001	-0.146	0.031
			May temperature	3.011	0.005	0.042	0.014
			May NAO	-2.47	0.018	-0.047	0.019
	Short	Robust	Constant	6.081	<0.001	2.995	0.493
			$\text{Log}_e(N_{t-1})$	-5.221	<0.001	-0.276	0.053
Proportion juveniles (arcsine)	Long	Robust	Constant	6.272	<0.001	1.126	0.18
			$\text{Log}_e(N_{t-1})$	-5.118	<0.001	-0.095	0.018
			May temperature	3.365	0.002	0.028	0.008
			May NAO	-2.135	0.039	-0.025	0.012
	Short	Robust	Constant	6.574	<0.001	1.892	0.288
			$\text{Log}_e(N_{t-1})$	-6.061	<0.001	-0.187	0.031
Productivity (square root)	Long	Robust	Constant	7.489	<0.001	2.415	0.323
			$\text{Log}_e(N_{t-1})$	-5.81	<0.001	-0.193	0.033
			May temperature	3.473	0.001	0.053	0.015
			May NAO	-2.313	0.026	-0.048	0.021
	Short	Robust	Constant	7.02	<0.001	3.783	0.539
			$\text{Log}_e(N_{t-1})$	-6.219	<0.001	-0.36	0.058
		June snow	-4.196	0.001	-0.031	0.007	

APPENDIX 3 – Flow chart describing the density dependent, stochastic population model for the Svalbard barnacle goose



ANNEX 1 – Guide to goose population viability analyses

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Population Viability Analysis encompasses a range of statistical and mathematical techniques used to make predictions about the prospects for a particular population of animals, such as the probability of decline and/or extinction within specified time periods. For the purposes of this work on Scottish goose populations, PVA refers to models which produce simulated population trajectories over multiple time steps (eg 25 years), using the randomly varying vital rates (survival and reproduction) derived from population data. In other words, based on data already collected, we can estimate the probability that the population will reach a given size at some point in the future. A crucial aspect of the simulation process is that the vital rates employed by the model vary by the same amount as the vital rates observed in the field data. In addition to this variation in the vital rates, other important features of natural population dynamics can be incorporated into the simulations if appropriate. Such factors include density-dependent regulation of vital rates and co-variation between different rates.

The simulation models employed for this goose work calculate the population size at yearly intervals, from one autumn to the next (autumn was chosen as this is the period during which most population data has been collected). The following equation is a summary of how the number of individuals present in the current year (N_t) together with the annual survival rate (S) and the annual reproductive rate (P), determine the number present in the following year (N_{t+1}):

$$N_{t+1} = (N_t * S) + (N_t * S * P)$$

The most important aspect of a population model used for PVA is that the vital rates (here, S and P) are not fixed constants in all years of a simulation, but are random variables, taking on new values in each year of a population projection. The range over which the vital rates vary in the model is defined by the ranges observed in the population in question. For example, while the average annual survival rate for the Scottish population of Greenland white-fronted goose between 1982–2002 was 0.89 (ie on average 89% of the population survived from one year to the next), the minimum and maximum annual values recorded during this period were 0.77 and 0.99 respectively. This variation is a reflection of many factors, not least variability in the environment. In practical terms, in each year of a model simulation random number generators are used to pick out a value for survival and a value for reproduction, and these values are then used to determine how many individuals survive to the following year, and how many young are born.

The overall survival and reproduction rates for a population vary in response to changes in the environment (known as environmental stochasticity), as described above, but individuals within the population also vary in their own probabilities of survival and breeding (referred to as demographic stochasticity). Demographic stochasticity is particularly critical for small populations and is typified by chance events, such as a small population only producing male offspring in a breeding season. This form of randomness is simulated in the models using the statistical equivalent of a 'coin toss' process to determine for example, whether any particular bird lives or dies. The magnitude of a vital rate in any particular year may also be related to the

magnitude of other rates. For example, a good year for survival may also be a good year for reproduction (perhaps in response to above average temperatures during the breeding season), and these rates are then said to 'co-vary' with one another. This is an example of positive co-variance, but negative covariance is also possible. For instance, elevated survival might be accompanied by poorer breeding. Where analysis of the field data indicated the presence of co-variance in the vital rates this was also incorporated into the models.

Density-dependence

The last major component of the simulation models is density-dependence. This is based on the principle that individuals must compete with one another in order to obtain all the resources (eg food, mates, breeding space) they require to live and breed successfully. As a population grows the level of this resource competition increases, causing the population growth rate to reduce, until a point is reached at which there is no more net expansion of the population. By this means natural populations are prevented from expanding in size indefinitely. During analysis of the goose population data it was found in some cases that, for example, the proportion of the adults which bred in a particular year was negatively related to the population size. If appropriate, this relationship was incorporated into the simulation models so that the proportion of the population which breeds in any particular year, while still retaining a random element, is also determined by the size of the population.

Quasi-extinction probabilities

Each completed simulation represents one possible path which the population could take. By repeatedly running the model (eg 1000 times) the average predicted population growth is obtained, and perhaps more importantly, the full range of possible population sizes which could be expected is also acquired. The proportion of the simulation runs which fall below a particular threshold population size within a specified number of time steps are referred to as quasi-extinction probabilities. These are a useful way to express the range of population sizes produced by the model and form the basis of much of the prediction in the goose PVA information papers.

Analytical steps for PVA

In summary, the steps for turning the goose population data into simulation models were as follows.

- 1 Estimation of the annual rates of survival and reproduction for all years of available data. The reproductive rates were broken down into the following components:
 - a proportion of juveniles in the population,
 - b average brood size,
 - c proportion of the adult population accompanied by juveniles
 - d overall productivity (defined as number of juveniles divided by number of breeding age birds).

[NB: a & b above were obtained as field estimates, while c & d were derived using the population counts and a & b].

- 2 Statistical testing of the vital rates described in 1, looking for evidence of changes in their values over time or in relation to the population size (the latter is used as an indication of the presence of density-dependent population regulation).
- 3 Development of biologically meaningful ways to describe any density-dependent relationships identified in 2.
- 4 The averages and standard deviations for the vital rates identified in 1, and any relationships between the rates and population size described in 3, were used to develop a population simulation model.
- 5 The simulation model was used to make predictions of the future population size based on conditions either:
 - a remaining as they were during the period of data collection, or;
 - b changing by some defined amount in response to different possible scenarios.