

# Status and population viability of Icelandic Greylag Geese *Anser anser* in Scotland

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## Abstract

During 2003–2007, the Icelandic Greylag Goose *Anser anser* population increased from c. 73,000 to c. 100,000 individuals (reversing a decline in numbers recorded during the 1990s), the wintering distribution shifted northwards (c. 60% to Orkney) and breeding success (the proportion of adults which successfully raised young) increased. Count, productivity and re-sighting data were analysed to identify any important relationships between the demographic variables (survival and productivity) influencing population trends and intrinsic and extrinsic covariates. In particular, a population model was developed to permit exploration of the effects of recent changes in UK shooting pressure and predict how the population may respond to possible future shooting scenarios. The model suggested that the shooting of Icelandic Greylag Geese in the UK has declined since 1999, to the extent that by 2007 around 8,000 fewer birds were being shot annually there, probably as a consequence of northward shifts in wintering distribution. Model projections based on this reduced shooting level predicted a median population size of c. 220,000 birds after 25 years, with no risk of decline to below 50,000. In contrast, a return of shooting levels in the UK to previous levels (c. 15,000–25,000 birds *per annum*) gave a predicted fall in the median population size to c. 55,000 geese after 25 years, with 6% of simulated populations falling below 25,000. The model suggested that a reduction in shooting of 2,000 geese annually (considerably fewer than the estimated reduction of 8,000) would permit population growth in ≥ 50% of simulations. In order for > 95% of simulated populations to have positive population growth, a reduction in shooting of 8,500 birds would be required. Loss of breeding habitat as a result of hydro-power developments in Iceland may reduce the overall productivity of the population, although the estimated current extent of habitat loss appears unlikely to have a significant impact on the population. This result is based on limited data however, and further developments may change this situation.

**Key words:** *Anser anser*, Greylag Goose, population dynamics, population viability analysis.

Three Greylag Goose *Anser anser* populations are recognised in the UK. Two are largely resident, of which one is confined to northwest Scotland and the other “re-established” population occurs throughout much of the remainder of Britain (Madsen *et al.* 1999). The third population breeds in Iceland and winters mostly in Scotland, with smaller numbers wintering in north England, southwest Norway, Ireland, the Faeroe Islands and Iceland. Organised annual autumn counts of the Icelandic population, started in 1960, suggest a population increase from *c.* 36,000 birds in the early 1960s to *c.* 110,000 in the late 1980s (Hearn & Mitchell 2004). Numbers declined in the early 1990s, however, apparently due to the large number of birds shot each year notably in Iceland (Frederiksen *et al.* 2004), and *c.* 86,000 were counted in winter 1994/95. A northward shift in wintering range started in the 1940s, increasing the importance of sites in east-central Scotland for the birds in the 1960s, and in north and northeast Scotland during the 1980s. Several autumn roosts in northeast Scotland became far more important than formerly, both for the actual numbers and for the proportion of the total population which they supported. From the mid 1990s onwards overall numbers continued to decrease, reaching a low of *c.* 73,100 birds in 2002/03, but more recently have increased again to an average population size of *c.* 98,300 geese recorded in winters 2004/05–2008/09. The northward range shift continued and, since the mid 1990s, increasing numbers of Greylag Geese have wintered on Orkney, reaching *c.* 60,000 (more than half the total winter population) by 2008/09.

Trinder *et al.* (2005) established the need to distinguish the resident UK Greylag Goose population from the migratory Icelandic population in order to estimate reliably the size of the latter. This has been addressed to some extent by recent surveys of the resident population in Scotland, which found an estimated 47,000 Greylag Geese present during the summer, with large numbers in the north and west of Scotland. The greatest concentration was found on Orkney (*c.* 10,000) an area also used by the wintering Icelandic population (Mitchell *et al.* 2010). Adjustments to the counts of the Icelandic population were undertaken accordingly. Assuming that the resident birds are relatively sedentary (for which there is some support; see Mitchell *et al.* 2010; Bowler *et al.* 2005), there appears to be little mixing of the two populations since the resident population currently has a more westerly distribution than that of the Icelandic one.

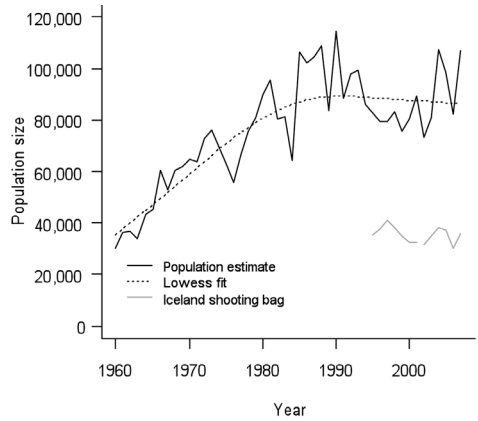
Given the population size (*c.* 100,000 birds based on recent winter counts) and the estimated total shooting bag (up to *c.* 60,000 birds annually in UK and Iceland combined, see below) it is likely that shooting has had a considerable influence on this population's trend in numbers over the last two decades. The percentage of the population counted on Orkney first exceeded 10% in 1996; it is now estimated to be around 60%. This northward range shift has almost certainly reduced the UK shooting bag, since less shooting takes place on Orkney than in other parts of the wintering range (C. Shedden, pers. comm.), with perhaps as many as 15,000 fewer birds currently being shot each winter. During

the 1990s, after thirty years of population growth, the population began to decline in numbers, but in the last five years it has increased again. Our hypothesis is that the fall and subsequent increase in Icelandic Greylag Goose numbers has been a result of the recent reduction in numbers shot in the UK, coincident with the shift to wintering on Orkney. We attempted to find support for this hypothesis by developing a population model to predict the effects of changes in shooting. Specifically, population counts and demographic data were used to develop a population viability analysis (PVA) model for the Icelandic Greylag Goose population, including analysis of the consequences of the recent winter distributional changes and associated changes in shooting pressure on population trends. Results from this model are presented here, and form the basis for a discussion of the likely future status of this population.

## Methods

### Analysis of demographic variables derived from population counts

A coordinated census of the Icelandic Greylag Goose population has been carried out in autumn since 1960, traditionally in November each year. During the early 2000s, however, Greylag Geese migration from Iceland occurred later in the autumn (Rowell 2005), leading to the introduction of an additional December count from 2005 onwards. Based on the highest count from the autumn census, the estimated population size increased steadily until the late 1980s, then declined during the 1990s



**Figure 1.** Autumn population estimate for the Icelandic Greylag Goose each year (black line). The dotted line is a locally smoothed regression (lowess) and the grey line is the number of geese reported shot in Iceland between 1995 and 2007.

and has since shown signs of recovery (Fig. 1). A sample of flocks has been checked each autumn to determine the juvenile proportion (PJ; 'birds of the year') and the mean brood size (BS). The overall productivity (P) and the minimum number of adults (aged three years or older) which bred in the preceding summer (PB) can be estimated using these data in conjunction with the population estimate (N; see Appendix 1 for details).

Oscillating fluctuations in the difference in atmospheric pressure at sea level between the Icelandic low and the Azores high (North Atlantic oscillation; NAO) control the strength and direction of westerly winds and storm tracks across the North Atlantic. The NAO index can be broadly divided between positive and negative phases. Positive periods are associated with

enhanced westerly winds at mid latitudes, leading to comparatively mild and wet winters, while negative periods are associated with cooler temperatures and less windy conditions. Strong winds experienced during migration periods may delay departure or increase energy expenditure, thus potentially compromising reproductive success if encountered during spring migration. Tests were conducted to identify any significant relationships between the demographic rates (PJ, BS, P) and environmental conditions (NAO) experienced during both spring and autumn migration and on the breeding grounds in Iceland (monthly mean temperature and monthly total precipitation at Akureyri, Iceland, 65°41'N 18°05'W, from March–September). Akureyri was selected due to its location within the birds' breeding range, although it should be noted that the breeding range extends across most of Iceland's lowlands. Climate data typically contain both inter-annual variability and also show long-term temporal trends. To minimise the risk of confounding long-term trends in the climate data with those in the demographic rates, both datasets were de-trended prior to analysis. This process fits a trend through a dataset, the value of which is then removed from the variables, leaving only the variation around the trend, thereby retaining the between-year variability in the data without any of the potentially confounding effects of the trend itself (Turchin 2003).

All model fitting was conducted using R software (<http://www.R-project.org>). For each analysis, starting models included only

main effects in order to minimise the risk of detecting spurious interactions and to simplify model interpretation. Minimal adequate models were selected in a two stage process. Backward step-wise model refinement of linear models using the Akaike Information Criterion (function `stepAIC` in MASS library, R) reduced the initial candidate set of variables to only those which were significant or close to significance (Crawley 2005). Further model simplification then proceeded by serial deletion of the least significant term. At each stage the least significant variable was identified using `dropterm` (MASS library, R), which provides information on the fit of each term when added last to the model, thus maintaining marginality. Confirmation of improved model parsimony after each deletion was obtained by pair-wise *F*-tests of the fit of the previous and updated models. Final models contained only those variables which explained a significant amount of the variation in proportion of juveniles (at  $\alpha < 0.05$ ).

### Tests for density-dependence

The presence of density-dependence in the population time series was tested for using the Pollard *et al.* (1987) randomisation test and the Dennis & Taper (1994) bootstrap test. In addition, linear regression of the proportion of juveniles, mean brood size and proportion of breeding birds against the population size (logged and offset backwards one year) were undertaken in order to identify any negative trends which might indicate declines in reproduction as a consequence of increasing population density.

### Population adjustments to allow for the change in winter distribution within the UK

In recent years, the Orkney component of the Icelandic population has been adjusted to allow for the number of Greylag Geese resident on the islands (Mitchell 2008). The summer Greylag Goose survey found 10,000 resident birds on Orkney in 2008, twice the previously estimated value (Mitchell *et al.* 2010). Growth in the numbers of geese resident on Orkney was inferred from the current estimate (10,000), and based on an exponential increase in the number of breeding pairs on Orkney since the 1990s (Meek 2008). Correction of the Icelandic population estimate using this updated Orkney-resident population estimate resulted in only modest changes in all but the most recent years (difference > 1,000 in only 9 years; > 3,000 in only 2 years; Table 1).

### Survival analysis of marked individuals

Annual survival over the period 1992–2000 was estimated using re-sightings of marked birds. These data comprised *c.* 14,000 observations of 1,137 birds caught as adults (535 females, 602 males) and 1,009 birds caught as juveniles (489 females, 520 males) marked in Scotland between 1993 and 2008, mainly at Loch Eye, Highland but also at other Scottish sites. Over 450 of the marked geese were reported dead, including 211 recovered in Iceland. Both the number of birds caught and marked each winter (mean = 153, range: 0–330), and the level of re-sighting effort, has varied considerably between years.

Barker survival models (Barker 1997) were fitted to the data and implemented using the Rmark library in R. The Barker model, an extension of the Burnham model used by Frederiksen *et al.* (2004), combines live re-sightings and dead recoveries in the analysis to make efficient use of capture-mark-recapture data. This is a considerable advantage over traditional survival models which use either re-sightings (*e.g.* Cormack-Jolly-Seber (CJS)) or recoveries (*e.g.* Brownie) and are more prone to bias resulting either from permanent emigration or ring loss. The Barker model has the additional benefit of using re-sightings made between discrete re-sighting periods, treating them as ‘live’ recoveries. Consequently, estimates of survival are considered closer to ‘true’ survival than those obtained using only live re-sightings or dead recoveries (with these data, survival estimates obtained using a CJS model were 3–6% lower than those obtained from the Barker model). A winter re-sighting period of October to April was used to accommodate goose catches that occurred throughout the winter. Although such a long re-sighting period violates the assumption made in the modelling process of there being a short re-sighting period relative to the survival period, the bias in survival estimates resulting from the violation of this assumption has been found to be minimal and far outweighed by the improved precision offered by increasing the sample size (O’Brien *et al.* 2005).

The downside of the Barker model’s greater flexibility is the addition of four secondary (so-called ‘nuisance’) probabilities: site fidelity ( $F$ ), temporary immigration ( $F'$ ),

**Table 1.** Previous and revised Icelandic Greylag Goose population estimates, allowing for growth in the numbers of geese resident on Orkney. <sup>1</sup>WWT adjustment applied to figures reported each year since 2001. <sup>2</sup>Growth of resident population modelled as an exponential increase, based on increase in counts of breeding pairs (Meek 2008; Mitchell *et al.* 2010). <sup>3</sup>Column 3 – column 4. <sup>4</sup>Revised population estimate used in this report (column 2 – column 5).

Year	Previous total Icelandic Greylag Goose population	Previous adjustment to allow for numbers resident on Orkney <sup>1</sup>	Projected numbers resident on Orkney <sup>2</sup>	Difference between old and new adjustments <sup>3</sup>	Revised total Icelandic Greylag Goose population <sup>4</sup>
1985	106,670	0	100	100	106,570
1986	102,000	0	123	123	101,877
1987	104,790	0	152	152	104,638
1988	108,700	0	187	187	108,513
1989	83,577	0	231	231	83,346
1990	114,678	0	285	285	114,393
1991	88,272	0	351	351	87,921
1992	98,144	0	433	433	97,711
1993	99,253	0	534	534	98,719
1994	86,132	0	658	658	85,474
1995	82,722	0	811	811	81,911
1996	79,576	0	1,000	1,000	78,576
1997	79,477	0	1,233	1,233	78,244
1998	83,096	0	1,520	1,520	81,576
1999	75,866	0	1,874	1,874	73,992
2000	80,324	1,500	2,310	810	79,514
2001	89,628	1,500	2,848	1,348	88,280
2002	73,115	1,500	3,511	2,011	71,104
2003	81,131	4,000	4,329	329	80,802
2004	107,207	4,000	5,337	1,337	105,870
2005	98,243	4,000	6,579	2,579	95,664
2006	82,339	5,000	8,111	3,111	79,228
2007	107,137	5,000	10,000	5,000	102,137

re-sighting outside the core re-capture period (R) and a bird being seen alive and then subsequently recovered during the same period (R'). This considerably increases the number of possible models, complicating identification of the most parsimonious model. For the current analysis the secondary probabilities were considered to be of limited value, adding little to the primary aim of estimating survival. In addition, there are often too few data for reliable estimation of the nuisance probabilities and the guidance is therefore to use simple structures (*i.e.* constant rate models rather than time-dependent ones) and treat the results obtained with caution (Richard Barker, pers. comm.). Preliminary analysis was conducted in order to determine the most appropriate structures for the secondary probabilities. This entailed keeping the probabilities of primary interest (survival, re-sighting and recovery) as constant rates and testing for the degree of support for time dependence in the secondary probabilities. This found that models with constant rates for the secondary probabilities (termed 'dot' models) received more support (based on the AIC score) than more complicated, time-varying ones. Hence, dot models were used for the secondary probabilities for the remainder of the analyses.

As a first step, the goodness of fit of a general model ( $S_{a2t}$   $p_t$   $r_{a2t}$   $R_{dot}$   $R'_{dot}$   $F_{dot}$   $F'_{dot}$ ) was determined using the parametric bootstrap approach implemented in programme MARK (where transition probabilities were: survival 'S', resighting 'p', recovery 'r'; modelled as either time dependent 't' or

constant 'dot', with age structure in survival and recovery 'a2', denoting first year survival modelled separately from adult). While this test found no evidence for a significant lack of fit, there was some over-dispersion in the data. Hence a variance inflation factor ( $\hat{c}$ ) of 1.03 was calculated and used during model selection.

Survival model fitting concentrated on the re-sighting rate (p), the recovery rate (r) and the survival rate (S). The relative fit of each model to the data was determined using Akaike's Information Criterion (AIC), corrected for over-dispersion (hence Quasi AIC; QAIC) and sample size (hence 'c'; QAICc). AIC balances the number of parameters in the model against the model deviance (*i.e.* the amount of variance left unexplained by the model) and is the accepted standard for survival model selection. The model with the lowest QAICc score provides the best-fit to the data. Competing models with a  $\Delta$ QAICc score of less than 2 (*i.e.* within 2 QAICc units of the best model) are judged to have received some support from the data (Burnham & Anderson 1998). These 'close' models therefore are also used to infer parameter values (*e.g.* survival and re-sighting rates) using the model averaging processes incorporated in MARK, thereby taking model uncertainty into account.

## Population model development

Recent productivity estimates still lie within the distribution described by the mean estimate (and its variance) used by Trinder *et al.* (2005). Thus, the productivity rates used remained the same (Table 2). There was little evidence for density-dependent



**Table 2.** Icelandic Greylag Goose demographic parameters: mean (and standard deviation).

	Previous estimate (1998–2002)	Recent estimate (2003–2007)	Overall estimate (1966–2007)
Proportion juveniles (PJ)	0.18 (0.03)	0.23 (0.03)	0.18 (0.06)
Mean brood size (BS)	2.74 (0.15)	2.47 (0.37)	2.32 (0.37)
Productivity (P)	0.26 (0.05)	0.38 (0.07)	0.29 (0.12)
Proportion breeders (PB)	0.20 (0.04)	0.31 (0.06)	0.24 (0.08)

population regulation (see density dependent results below), so the population was modelled as density independent. The model had a matrix formulation with a three age class structure (juveniles, yearlings, adults). Environmental stochasticity was included by randomly drawing each demographic rate (survival and reproduction) from appropriate probability distributions (beta for survival, lognormal for reproduction) at each time step. The probability distributions were derived from analysis of the population data, as described in detail by Trinder *et al.* (2005).

Demographic stochasticity was incorporated by using the value from the random number generation described above as the probability value in a binomial probability estimator. All modelling was carried out using R. The population was simulated for a period of 25 years, with each run repeated 5,000 times to generate summary results. The starting year for these simulations was 2007, and the initial population size was that recorded in the autumn of that year.

The results of the survival analysis reported here (see Results) indicated that survival rates have changed very little since the previous PVA model for this population was produced (Trinder *et al.* 2005). The previous model used annual survival rates estimated by Frederiksen *et al.* (2004). The survival analysis conducted here found that annual survival rates have remained the same (see below), therefore the previous estimates remained valid. In addition to annual survival rates, Frederiksen *et al.* (2004) also reported seasonal survival. These seasonal rates were used in the current population model in order to facilitate simulation of changes in the number of birds being shot in Scotland and to model these changes. This was achieved through removal of individuals during the period of the annual cycle which corresponded to the survival period in Scotland. Further details of this procedure are provided in the following section.

Icelandic Greylag Geese are legal quarry throughout their range. Since 1995, hunters in Iceland have been required to report the



number of each species shot in order to renew their licences (Fig. 1). Despite a small amount of over-reporting in these data, the figures are thought to be free of significant bias (Frederiksen & Sigfusson, 2001). No equivalent reporting scheme exists in the UK, so estimates of the number of Greylag Geese shot there annually rely on less precise indirect methods (*e.g.* Frederiksen 2002) or sampled responses from hunters (Hart & Harradine 2003). Between the mid 1990s and early 2000s, the UK annual shooting bag was estimated at between 20,000–25,000 birds (for the years 1995–2000; Frederiksen 2002) and between 15,000–20,000 birds (for winters 2001/02–2002/03; Hart & Harradine 2003). In its baseline form the population model implicitly assumed a constant shooting off-take, corresponding to these estimates (15,000–25,000 geese). Changes to this baseline level were modelled by either adding or removing individuals from the population (*i.e.* respectively reducing or increasing the number shot). In other words, shooting was simulated as the *difference* from the implicit baseline (15,000–25,000), rather than the actual overall number shot. The maximum number of birds which could be ‘reinstated’ in this way was limited so that the survival rate during the UK hunting season (1 September–14 February) could not exceed 0.95 (this approximates to an annual survival rate of 0.9), which represents a precautionary approach to modelling changes in shooting. It would be preferable to model the total shooting bag explicitly, rather than as changes to an unknown (but estimated) ‘baseline’. However, this would only be possible if annual estimates of the

total number shot were available for a period coincident with independent survival estimates. This would permit estimation of the relative contributions of natural and shooting mortality to the overall mortality rate.

One of the assumptions of the approach taken here is that shooting mortality is completely additive to natural mortality. Thus, changes in the shooting level are not compensated for through variations in natural survival. The alternative – compensatory mortality, whereby deaths resulting from shooting are substituting for deaths that would occur naturally – could only be estimated if annual bag data were available. However, while this is a necessary simplification, at the level of shooting experienced by this population it is probably appropriate, at least over relatively small differences in the shooting level.

### Model validation

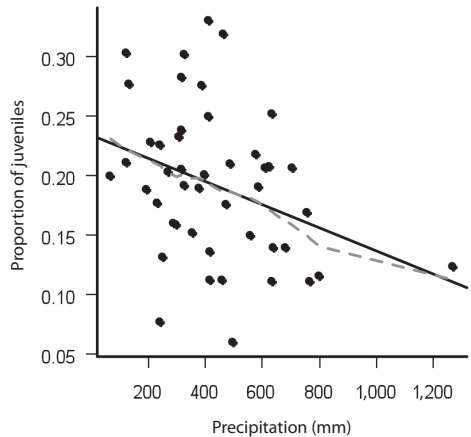
To replicate the recent population trend using the model, two parameters were incremented across a range of values until the combination which yielded the closest match (between the real population trends and the median prediction generated by the population model) was identified. This was performed by means of summing the squared deviations between the population time series and the median model prediction, with the best-fit parameters identified as the ones which gave the smallest overall difference (*i.e.* a least squares approach). The first parameter was the total reduction in the shooting bag which occurred over the period 1993–2007 (1993 was chosen as the starting point as this

coincided with the beginning of a marked decline in the population). The second was the delay (in years) after 1993 before the reduction began. For example, over the 15 years (1993–2007) of a simulation with a total bag reduction of 10,000 birds annually and a six year delay, the reduction in the number shot in each year of the simulation would be modelled as:

0, 0, 0, 0, 0, -1111, -2222, -3333, -4444, -5555, -6666, -7777, -8888, -10000, -10000.

### Loss of breeding habitat

When Trinder *et al.* (2005) produced the previous PVA for this population two hydro-power developments in Iceland were considered as having the potential to reduce breeding and moulting habitat availability for Greylag Geese. Since this time, one of these proposals has been refused planning permission, while the second development has been completed. It has been estimated that the area downstream of this development which may be affected by changes in hydrology contains around 10% of the breeding population of Greylag Geese (Birdlife International *et al.* 2003; at the 2003 population size, 10% of the breeding population equated to around 700 pairs). We used the population model to investigate the possible outcomes of reducing the number of pairs able to breed each year. In these simulations the best-fit reduction in UK shooting (–8,000 birds *per annum*) was used throughout. These simulations represented a ‘worst case’ scenario, in which the displaced geese were unable to breed elsewhere.



**Figure 2.** Relationship between the proportion of juveniles recorded in autumn amongst Icelandic Greylag Geese and the total precipitation in the preceding March at Akureyri, Iceland (65°41'N 18°05'W). The close agreement between the least-squares fit (black line) and lowess local fit (dashed line) indicates the robustness of this relationship. Note: this plot used the original data; however, statistical analysis was conducted using de-trended data. The local regression fitted through these data (dashed line) indicated that this relationship was unaffected by the outlier to the right of the graph.

## Results

### Relationships between demographic rates and environmental covariates

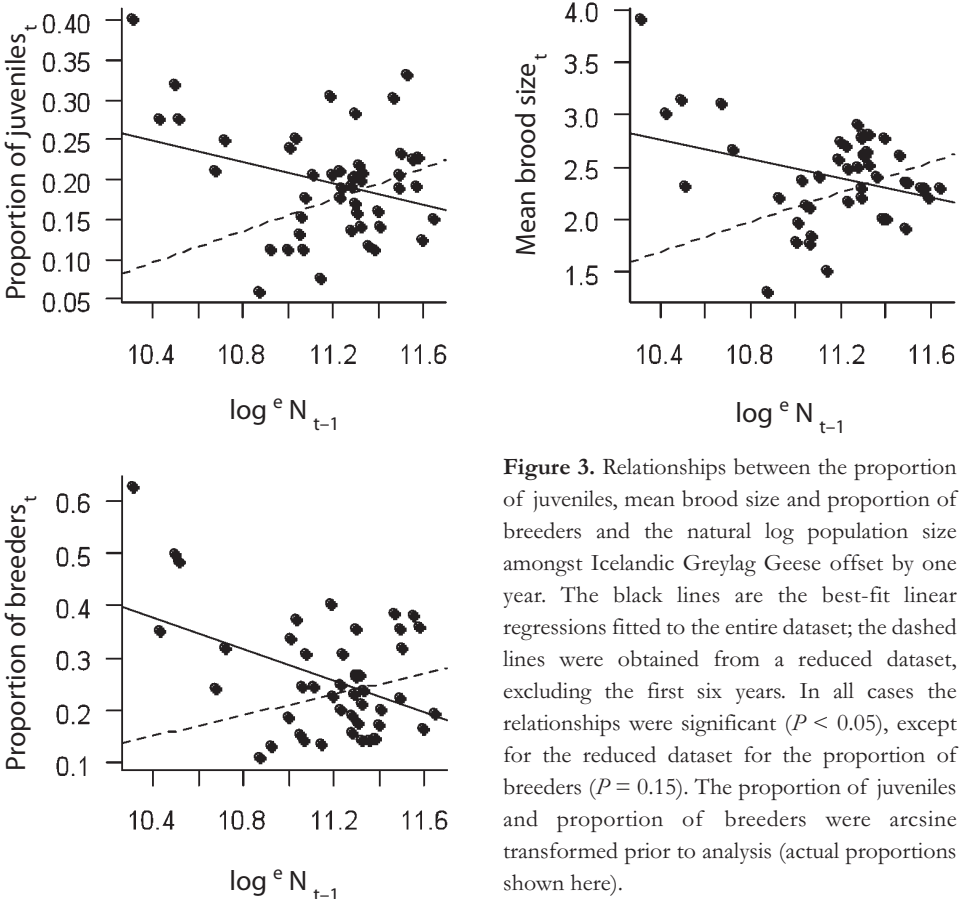
Only one significant result was obtained between the count based demographic rates and the environmental variables tested: the proportion of juveniles recorded in autumn was negatively related to the total precipitation in Iceland in the preceding March ( $F_{1,44} = 5.14$ ,  $r = 0.29$ ,  $P = 0.03$ ; Fig. 2). This may reflect a relationship between the commencement of breeding and the timing of the spring thaw, which may be

delayed in years of additional spring snow accumulation, as found for other Arctic breeding goose populations (Boyd & Fox 2008; Trinder *et al.* 2009).

### Tests for density-dependence

Both the Pollard *et al.* (1987) and Dennis & Taper (1994) tests gave positive results, suggesting that the population growth rate may have been regulated by population density (Pollard test,  $P = 0.04$ ; Dennis and Taper test,  $P = 0.02$ ). Regression of the

productivity rates (PJ, BS, PB) against the logged population size in the previous year revealed the same patterns for each rate: across the whole 48 year dataset (1960–2007) there were significant negative trends in reproduction (Fig. 3). However, in each case the negative relationship was found to be dependent on the first six years (1960–65) of data, when the population size was < 46,000 birds. Repeating the same tests using data from 1966 revealed the opposite trend: all the rates increased



**Figure 3.** Relationships between the proportion of juveniles, mean brood size and proportion of breeders and the natural log population size amongst Icelandic Greylag Geese offset by one year. The black lines are the best-fit linear regressions fitted to the entire dataset; the dashed lines were obtained from a reduced dataset, excluding the first six years. In all cases the relationships were significant ( $P < 0.05$ ), except for the reduced dataset for the proportion of breeders ( $P = 0.15$ ). The proportion of juveniles and proportion of breeders were arcsine transformed prior to analysis (actual proportions shown here).

**Table 3.** Results of linear regression of Icelandic Greylag Goose population size against reproductive parameters, comparing results from the full dataset with those minus the first six years.

Dependent variable	All years: 1960–2007			Reduced years: 1967–2007		
	<i>t</i>	<i>P</i>	Direction of relationship	<i>t</i>	<i>P</i>	Direction of relationship
Proportion juveniles (PJ)	−2.14	0.04	−ve	2.08	0.04	+ve
Mean brood size (BS)	−2.17	0.03	−ve	2.41	0.02	+ve
Proportion breeders (PB)	−3.08	0.004	−ve	1.39	0.17	NA

In all cases the independent variable was the natural log of total population size, offset by one year to test for a lagged effect of population size on reproduction. The proportion of juveniles and proportion of breeders were arcsine transformed prior to analysis. Degrees of freedom (d.f.) were 1, 45 for all years; d.f. = 1, 39 for reduced years.

with increasing population size (Table 3). Evidence for density-dependence was therefore equivocal.

### Survival of marked individuals

Four models were considered to receive equal support, based on AIC score (difference < 2, models 1–4 in Table 4). All included the two age class structure (a2) in survival, while the top placed model included an additive sex difference and the third an additive time component. Thus there was weak support for differences in survival for males and females. There was strong support for the re-sighting rate having varied through time (models 14–16, Table 4), while the recovery rate was best modelled as a constant rate, although model 4 indicated weak support for

different recovery rates for juveniles and adults.

Final parameter estimates, taking account of model selection uncertainty, were obtained by model averaging. This approach weights parameter estimates by their support across all candidate models. For this model set this effectively meant averaging across the top five models, since these accounted for > 99.9% of the total model weights (Table 4).

Mean adult survival over the period 1993–2008 was 0.7 (range = 0.67–0.77) and mean juvenile survival was 0.56 (0.53–0.66; Fig. 4a). While the best fit model suggested that females had slightly higher survival (~2%) on average than males, the support for this was not strong (models 1 and 2, Table 4). These autumn to autumn survival

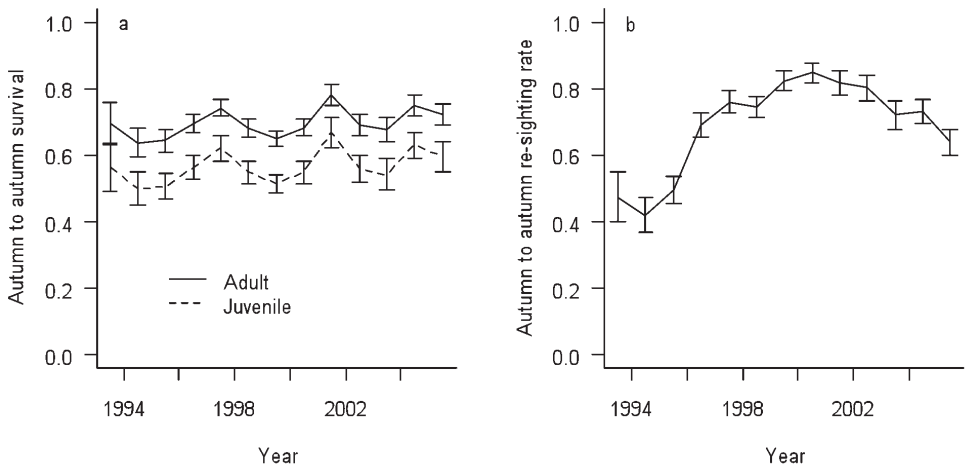
**Table 4.** Order of Barker model fits to the Icelandic Greylag Goose re-sighting data from Scotland 1993-2008. Model fit decreases down the table.

Model no.	S	P	r	No. pairs	QAICc	ΔQAICc	Model weight	Qdeviance
1	a2+sex	time	dot	22	13,137	0.000	0.353	3,915
2	a2	time	dot	21	13,138	0.537	0.270	3,918
3	a2+time	time	dot	36	13,139	1.432	0.172	3,889
4	a2	time	a2	22	13,139	1.970	0.132	3,917
5	a2+time	time	a2	37	13,140	3.135	0.073	3,888
6	a2*time	time	dot	51	13,158	21.049	9.48e-06	3,878
7	a2*time	time	dot	51	13,158	21.049	9.48e-06	3,878
8	a2*time	time	a2	52	13,160	22.845	3.86e-06	3,877
9	time	time	a2	36	13,173	35.704	6.23e-09	3,923
10	a2*time	time	time	66	13,178	41.372	3.66e-10	3,867
11	dot	time	a2	21	13,179	42.288	2.32e-10	3,960
12	dot	time	dot	20	13,182	44.905	6.26e-11	3,964
13	sex*a2*time	time	dot	81	13,187	49.755	5.54e-12	3,845
14	a2*time	time	time	82	13,189	51.851	1.94e-12	3,845
15	a2*time	dot	time	68	13,348	211.362	0.00e+00	4,033
16	a2*time	a2	time	69	13,350	213.056	0.00e+00	4,033

estimates were very similar to those reported by Frederiksen *et al.* (2004) for the period 1993–2000: adult survival of 0.69 (0.62–0.75), and juvenile survival of 0.58 (0.46–0.64). The mean winter re-sighting rate was 0.68, but with considerable variation over the period (range = 0.42–0.85; Fig. 4b). The recovery rate was best modelled as a constant value of 0.22, although the third and fourth best models suggested there may have been a small difference between juveniles (0.23) and adults (0.22).

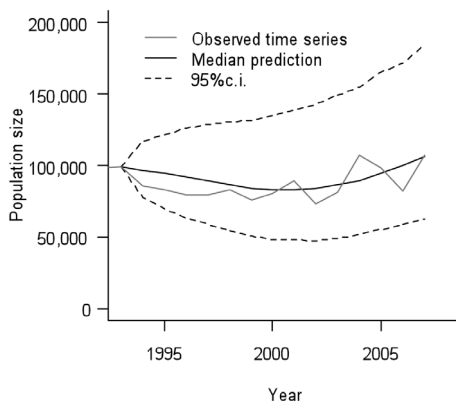
**Simulated changes in UK shooting**

The best-fit parameters identified during the model validation exercise suggested that there has been an overall reduction in the UK shooting total of 8,000 birds annually. The model suggested that, since 1999, an average of 1,000 fewer birds were shot in the UK each winter than in the preceding winter, leading to a slight recovery in numbers in recent years (Fig. 5). Over this period the estimated proportion of the



**Figure 4.** (a) Icelandic Greylag Goose survival estimates (and s.e. bars) from the best-fitting model which included time as a parameter (model 3 in Table 4:  $S_{a2+t} p_t r \cdot R \cdot R' \cdot F \cdot F'$ ); (b) estimated re-sighting rates (and s.e. bars) from the best fitting model (model 1 in Table 4).

population wintering on the mainland halved in size, while numbers on Orkney increased almost threefold, changes which

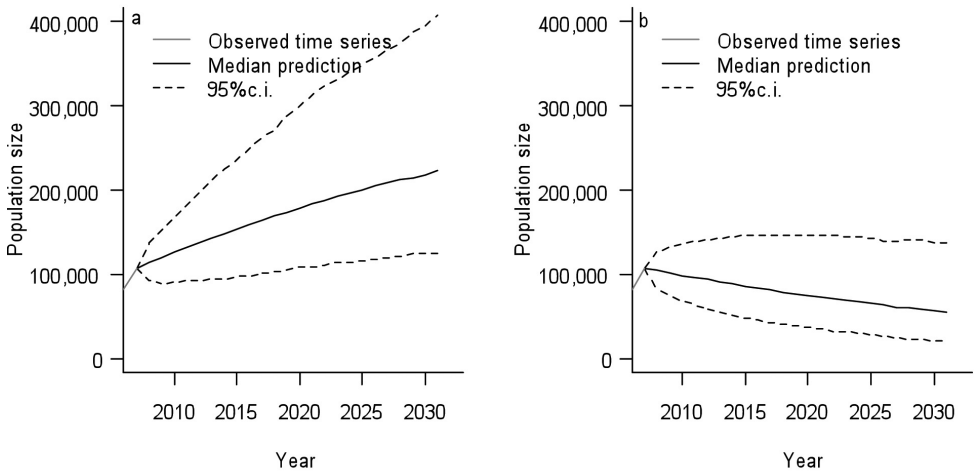


**Figure 5.** Best-fit of model to the observed population of Icelandic Greylag Goose over the period 1993–2007. In the model, UK shooting was reduced from 1999, reaching a maximum reduction of 8,000 fewer geese shot in 2007.

are consistent with the modelled reduction in shooting bag.

Maintaining the reduced number of birds shot at 8,000 annually for the next 25 years the model predicted the population will grow at an average annual rate of 3%, reaching a median size of 220,000 (Fig. 6a). Ninety-nine percent of simulations under these conditions exceeded 110,000 after 25 years. In contrast, simulations in which the number shot each winter in the UK was set at the nominal mean value (*i.e.* around the late 1990s levels of shooting, *c.* 15,000–25,000 geese *per annum*) predicted the population would decline at an average annual rate of 3%. Under these conditions the median population size in 25 years was predicted to be 55,000 and 6% of simulations had populations below 25,000 in 25 years (Fig. 6b).

The risk of population decline below



**Figure 6.** (a) Predicted Icelandic Greylag Goose population growth with a constant reduction of 8,000 in the number of birds shot per year relative to late 1990s levels; (b) predicted population growth with the number shot maintained at late 1990s level (*i.e.* between *c.* 15,000–25,000 geese *per annum*).

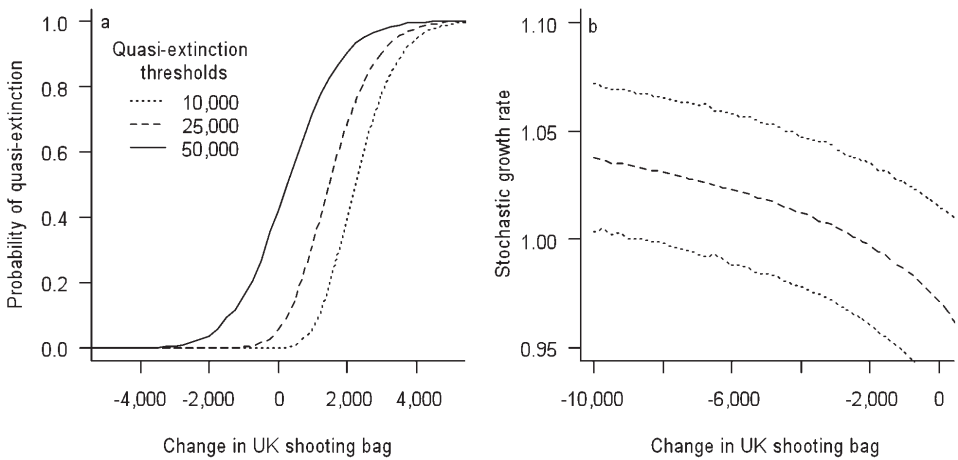
specific thresholds ('quasi-extinction') within 25 years was investigated across a range of changes to the UK bag size. In these simulations zero change implied continuation of shooting at the mean level experienced during the 1990s, as illustrated in Fig. 6b. The estimated reduction in shooting which has occurred in the last ten years (8,000 *per annum*) is far greater than the minimum reduction of 3,000 annually which the model predicted to be necessary in order for fewer than 0.5% of simulations to decline below 50,000 in 25 years (Fig. 7a). The average stochastic growth rate was greater than 1 (*i.e.* positive population growth) for all UK shooting bag reductions in excess of 2,500 *per annum*. However, a bag reduction of at least 8,500 annually was required in order for 95% of all simulations to achieve positive growth (Fig. 7b).

### Loss of breeding habitat

The risk of population decline to below 50,000 after 25 years remained at < 1% until more than 2,000 pairs were prevented from breeding each year. Above this figure the risk of decline increased rapidly and exceeded 50% if more than 3,300 pairs were prevented from breeding (Fig. 8). The risks of population decline to below 25,000 and 10,000 remained at < 1% until the number of pairs prevented from breeding exceeded 2,400 and 2,600, respectively.

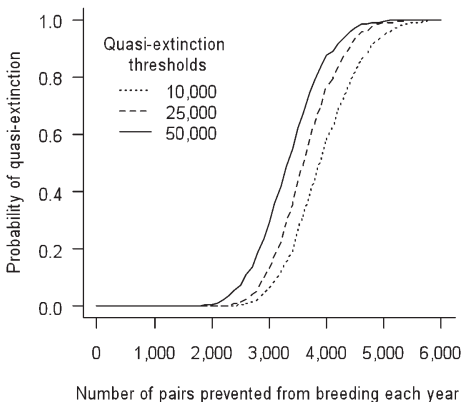
The exact figures reported above are also strongly dependent on measures of the change in shooting used in the models (in this example a reduction of 8,000 was used). However, the slope of the lines (*i.e.* the sensitivity of the population to a change in the number of pairs prevented from breeding) remains consistent across other





**Figure 7.** (a) Risk of population decline below specific threshold sizes in 25 years with changing shooting levels in the UK. Negative values on the x-axis represent reduced numbers shot each year, while positive values represent increases in bag size; (b) average stochastic growth rate of Icelandic Greylag Geese (dashed line) and 95% confidence intervals (dotted lines) resulting from changes to the UK shooting bag.

levels of UK shooting. Thus, if shooting in the UK is higher than that used here (*i.e.* closer to the baseline, or increased above it)



**Figure 8.** Probability of the Icelandic Greylag Goose population declining below specific thresholds, resulting from a reduction in the numbers of breeding pairs.

then the lines on the graph will move left, representing greater risks of population decline with loss of breeding pairs. The converse is true if UK shooting is reduced further.

## Discussion

The number of Iceland Greylag Geese overwintering on Orkney has increased considerably in the last 20 years, from < 1,000 birds in the mid 1980s to > 60,000 in 2007 (Meek 2008). The reasons for this shift are not well understood, but given that northward range shifts in wintering ranges have been noted for other bird species (*e.g.* <http://www.stateofthebirds.org/habitats/north-shifts>) in response to climate change, it seems likely that the trend towards milder winters has been an important factor. Several other wintering goose populations in

the UK have exhibited 'short-stopping' in the last 20–30 years, where geese have progressively deserted more southerly areas as conditions closer to the breeding grounds become favourable (Mitchell *et al.* in press). This increase appears to have been at the expense of sites further south in Scotland. Areas traditionally associated with heavy shooting pressure (*e.g.* Aberdeenshire and Perthshire) now host < 10% of the population (in 2007), compared with > 50% in 1997 (Mitchell 2008). While accurate shooting data are not available, this shift has probably had a large effect on the number of Greylag Geese shot in the UK.

Given the extensive area over which the birds are located in the winter it seems probable that observation error exists in the population estimates, and tests for density-dependence are known to be liable to Type I errors (*i.e.* false positives) in the presence of observation error (Shenk *et al.* 1998). Therefore, while these results suggest density-dependent regulation of population growth has occurred, the possibility that these results have been obtained due to confounding factors cannot be ruled out. Furthermore, the analysis of reproduction in relation to population density suggested that any change related to increasing population size has been in the opposite direction to that which would be expected under density-dependent regulation. While density-independent models are inherently simplistic, in this case it appears to be the more appropriate approach to take.

Using the population model to explore how the UK shooting bag may have changed over the last few years leads to the suggestion that the population growth rate

has been regulated by shooting. The UK annual shooting bag for Icelandic Greylag Geese was estimated at 20,000–25,000 birds in the late 1990s (Frederiksen 2002) and at 15,000–20,000 birds in the early 2000s (Hart & Harradine 2003). Extrapolating from these estimates, using the reduction in the population exposed to shooting in mainland Scotland (down from 81% between 1996–2000 to 47% between 2002–2007), and using information provided by shooting guides on Orkney (which indicates an annual shooting bag of 3,000–4,000 in recent years; C. Shedden, pers. comm.), the total number shot in the UK may now be around 10,000–15,000. This represents a decline in the UK shooting bag of up to 15,000 birds. The bag size may rise again, however, if shooting increases on Orkney. With recent local complaints of agricultural damage due to the presence of increasing numbers of over-wintering geese on Orkney, an increase in the number of birds shot there is likely.

The biggest single enhancement to the monitoring of this population would be the collection of robust shooting bag estimates for the UK. Without these data it is possible only to estimate an approximate number shot, with no annual variation. Furthermore, without bag estimates it becomes difficult to use the outputs of this modelling exercise for its main purpose, namely improved goose management. The reduction in shooting estimated anecdotally and the simulation model results reported here are in broad agreement. However, given the large number of geese in this population which appear to be shot each year, shooting remains the single greatest determinant of

the populations' status. Reliable figures for the number shot would provide an early warning of changes in hunting pressure that could impact on the population as well as greatly enhancing our ability to make predictions of future population trends. The rate of growth in this population is likely to be dependent on the extent of shooting on Orkney in future years. If shooting remains lower than that experienced during the late 1990s then the population is likely to grow. However, if shooting begins to increase once more then it is likely that growth will be reduced and may become negative once more.

In Iceland, where the bag recording system has now operated for 15 years, accurate annual bag data are available. These data suggest that approximately one-third of the post breeding population are shot each year prior to migrating to the winter quarters in Britain (mean = 41,600 from 2005–2009, range = 36,360–49,790, data from the Wildlife Management Institute, Akureyri, Iceland, <http://www.ust.is/Veidistjornun/Almennt/Veiditolur/>). Both the average number shot in Iceland and any trends in this figure have an important role to play in determining the status of this population. Although the numbers shot in the UK appear to have changed, apparently influencing the recent population trend, this must be set against the consistently higher numbers shot in Iceland. A comparatively modest reduction in UK shooting appears to have permitted the population to begin to increase. A similar reduction in Iceland would be expected to further permit population increase. However, a long term increase in Icelandic shooting could readily

compensate for the UK reduction, leading once more to population decline. This highlights the critical importance of flyway level monitoring and management for migratory species which cross international boundaries.

The potential for loss of breeding habitat in Iceland is real (as witnessed by flooding of areas under hydro-electric schemes), and the model suggested that over 2,000 pairs would need to be stopped from breeding to adversely affect population levels. In some cases, affected individuals would likely be displaced to other breeding areas rather than removed from the breeding cohort. Currently developments (existing or proposed) on the breeding grounds do not appear to represent a significant threat to the population; however, coupled with an increase in hunting levels, the long term effect of loss of breeding habitat could play a significant part in population regulation.

The number of geese counted at sites outside the UK in the autumn, including Iceland, has increased in recent years. If this represents a real expansion of range, greater efforts to coordinate counts across countries will be needed in future to ensure estimation of the population is as accurate as possible.

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**Appendix 1.** Demographic rate calculations.

Calculation of demographic data and age class sizes for the Icelandic-breeding population of Greylag Goose using the annual total population count (N), proportion of juveniles (PJ) 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.

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Number of juveniles:	$J_t = PJ_t * N_t$
Crude annual survival rate (from year t-1 to year t):	$CS_t = \frac{N_t - J_t}{N_{t-1}}$
Number of birds in their second year:	$N2_t = J_{t-1} * CS_t$
Number of birds in their third year or older:	$N3_t = N_t - (J_t + N2_t)$
Productivity:	$P_t = \frac{J_t}{N3_t}$
Proportion of breeders: (i.e. the minimum number of third year and older birds required to have bred to account for the estimated number of juveniles)	$PB_t = \frac{J_t / BS_t}{0.5 * N3_t}$
Mean number of adults (post-breeding, pre-shooting):	$Na' = \frac{Ht * (1 - pHj)}{1 - Sa}$
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 no. of two year old birds:	$N2' = Nj' * Sj$
Mean no. of three years and older birds:	$N3' = Na' - N2'$
Mean productivity derived from survival and shooting bag estimates:	$P = \frac{Nj'}{N3'}$

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