Estimation of Demographic Parameters for New Zealand Sea Lions Breeding on the Auckland Islands
- Final Report: 1997/98-2008/09

Objective 3: POP2007/1

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Executive Summary

Similar methodology to last year was used to analyse the updated data, although additional models were considered that included annual variation in demographic parameters.

Results indicate that survival probabilities were relatively low between the 2007/08 and 2008/09 breeding seasons compared to previous years (survival probability lower by approximately 0.05). Breeding probabilities in 2008/09 were also relatively low for females that had bred in the previous year.

As the age profile of the tagged population is changing though time, it is cautioned that some apparent temporal effects may be due to changes in the age distribution, or vice-versa.

A model-based method for estimating the number of females alive in each year that been exposed to tagging was applied to the data and suggested that the number may have reduced in 2008/09 by approximately 700 individuals to between 4100-5200. These estimates may be sensitive to the specific model used, however, and it is recommended that field methods be trialled that will enable direct estimates of population size.

Introduction

This report provides an update on the estimation of demographic parameters for New Zealand sea lions breeding on the Auckland Islands from data collected up to the 2008/9 field season. In addition to the estimation models agreed upon previously, models that allow annual variation in demographic parameters have also been fitted to the data.

Survival and Reproduction

Estimation methods

The tag-resight data was analysed using mark-recapture methods implemented in the software WinBUGS. This allows the simultaneous estimation of survival and breeding rates with the ability to easily account for tag-loss. Unaccounted for, tag loss will result in estimated survival rates being biased low (i.e., mortality will be overestimated). This was illustrated in MacKenzie (2009).

Whether an animal survives between breeding seasons $t-1$ and t could be considered as a Bernoulli random variable (i.e., a coin flip) where the probability of survival is S, which may vary by age, year or breeding status of the animal in year $t-1$ (eqn 1). Similarly, whether an animal breeds in year t could also be regarded as a Bernoulli random variable, with probability of breeding equal to B, which may also vary by age, year or breeding status in the previous year (eqn 2). The number of flipper tags remaining on an animal in year t, given the number of tags in the previous year could be represented as a multinomial random variable with only 1 trial (i.e., the outcome from a single roll of a dice), The probability of the number of tags in year t is now a vector, $\mathbf{T}$ because of the multiple potential outcomes (eqn 3).

$$Survive\ to\ year\ t \mid alive,\ age\ and\ breeding\ status\ in\ year\ t-1 \sim Bernoulli\left(S_{age,t-1,bred}\right) \quad (1)$$

$$Breeds\ in\ year\ t \mid alive\ in\ year\ t,\ age\ and\ breeding\ status\ in\ t-1 \sim Bernoulli\left(B_{age,t,bred}\right) \quad (2)$$

$$Tags\ in\ year\ t \mid alive\ in\ year\ t,\ number\ of\ tags\ in\ t-1 \sim multinomial\left(\mathbf{T}_{tags},1\right) \quad (3)$$

Using WinBUGS, the estimation problem can be defined in terms of the underlying random variables which mitigates the need to define the model likelihood explicitly.

Survival and breeding probabilities were allowed to vary in accordance with animal age. Based upon the results of previous work, 3 age classes are considered here: 0-3, 4-14, 15+. There are no breeding individuals in the 0-3 age class hence these survival and breeding probabilities were set to 0. Rarely, an individual that was aged 3 in the previous year has bred for the first time as a 4-year old, hence the breeding probability in year t for a non-breeder aged 0-3 in year $t-1$, was allowed to be non-zero, but was assumed to have no annual variation. Tag loss probabilities were assumed constant with respect to animal age and year. Note that survival and breeding probabilities depend upon the age of the individual in the previous year (see eqns 1 and 2).

Three models were considered representing different patterns of annual variation in the demographic parameters for the older cohorts; 1) no annual variation; 2) variation that was different depending upon breeding status in previous year, but not age; and 3) variation that was different for breeding status and age groups. Model 1 was the model recommended and agreed upon in MacKenzie (2009). Variation was incorporated assuming a logit-normal random effect model, that is demographic parameters were defined as random values from a normal distribution on the logistic scale with a certain mean and standard deviation, that were then transformed to the probability scale. That is, the demographic parameter for an individual in age class a, in year t, and previous year breeding status b (generically denoted as $\theta_{a,t,b}$) was modelled by the relationships:

$$y_{a,t,b} = \text{logit}\left(\theta_{a,t,b}\right) = \mu_{a,b} + \varepsilon_{a,t,b}, \quad \varepsilon_{a,t,b} \sim N\left(0, \sigma_{a,b}^2\right)$$

$$\theta_{a,t,b} = \frac{e^{y_{a,t,b}}}{1 + e^{y_{a,t,b}}}.$$

The following constraints therefore give rise to the 3 models:

1. $\varepsilon_{a,t,b} = 0$

2. $\varepsilon_{t,b} \sim N\left(0, \sigma_b^2\right)$

3. $\varepsilon_{a,t,b} \sim N\left(0, \sigma_{a,b}^2\right)$

Within a breeding season, attempts are made to resight previously tagged individuals. There are a limited number of days of field effort each year (generally less than 80-90), and on any given day individuals may or may not be observed. Therefore, the number of times an individual is seen during a breeding season could be considered as a binomial random variable with a daily sighting probability of p. The sighting probability depends upon whether the animal is currently alive, breeding status, age class, number of flipper tags, presence of a brand and PIT tag. It is assumed that:

1. Animals that have no flipper tags can not be resighted unless they are chipped or branded.
2. Whether an unbranded animal is chipped or not has no effect on the resight probability if the animal has 1 or more flipper tags.
3. Branded animals have the same resight probability regardless of number of flipper tags.
4. There is a consistent odds ratio (δ) between resighting animals with 1 and 2 flipper tags (eqn 5).
5. Resight probabilities are different for breeding and non-breeding animals.
6. Resight probabilities are different for animals aged 0-3 and those 4+.
7. Resight probabilities vary annually.

$$\frac{p2_{t,bred}}{1-p2_{t,bred}} = \frac{p1_{t,bred}}{1-p1_{t,bred}} \times \delta \tag{5}$$

With the exception of the resight probability for animals with 2 tags ($p2$), all other probabilities are estimated independently.

Two definitions of 'breeding' (see below) are used to compare how that may influence results.

Markov chain Monte Carlo methods were used to obtain approximate posterior distributions for all parameters. Two chains of 30,000 iterations were run and checked for convergence and good mixing. If there were doubts about convergence, an additional 20,000 iterations were run. Values from the final 25,000 iterations were retained for final inferences. Vague prior distributions were used for all parameters:

$$\mu's \sim N\left(0, 3.78^2\right)$$

$$\sigma's \sim U\left(0, 10\right)$$

$$\mathbf{T}_2 \sim Dirichlet\left(1,1,1\right)$$

$$\text{Other probabilities} \sim U\left(0,1\right)$$

$$\ln\left(\delta\right) \sim N\left(0, 10^2\right)$$

The WinBUGS code that was used to fit the model to the data has been included in Appendix 2.

Model Fit

Model fit was assessed using Bayesian p-values (Gelman et al. 2003) with the model deviance being used as the test statistic. For each iteration in the MCMC procedure, the deviance for the observed data is calculated given the current values of model parameters, and compared to the deviance for a set of simulated data that has been generated using those current values. The p-value is determined as the fraction of iterations where the generated deviance is greater than the observed deviance. Extreme values (close to 0 or 1) may indicate the estimating model is not a good fit for the observed data.

Simulated data sets were created based upon the observed data. For each individual, given the year, their age and breeding status when they were tagged, the 'observations' in the subsequent years (whether they survived, bred, number of tags remaining and number of resights each season) were simulated based upon the sequence of random variables defined above. This creates a generated set of data for which we know that the model being applied to the real data must be reasonable. Therefore, the range of deviance values obtained from the simulated data sets indicates what values could be expected if the estimating model is a reasonable fit to the real data.

The posterior distribution of the deviance value for the observed data could also be used as a relative measure of fit among models, with smaller values indicating a better model. However, one cannot use the same guidelines to compare models as when performing a maximum-likelihood analysis. The deviance values obtained when using maximum-

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likelihood is analogous to the minimum value in the posterior distribution, whereas in a Bayesian context one may look at the entire distribution of deviance values to compare models.

Data used

The data used by MacKenzie (2009) was initially extracted from the Auckland Island sea lion database by Laura Boren (DOC contractor) with additional verification by Darryl MacKenzie (Proteus), for females tagged between 1989/90 – 2002/03 and resighted during the period 1989/90-2007/08. Due to the inconsistent field effort prior to 1997/98, data from 1989/90-1996/97 was not considered by MacKenzie (2009). This data was updated for the current analysis with the resightings for the 2008/09 field season, along with all resightings for females tagged as pups in 2003/04 (Table 1; additional data supplied by Louise Chilvers, DOC). Hence the youngest age of an animal included in the analysis was five. Younger animals were not included as resightings are rare, and resighting probabilities are likely to exhibit a high degree of heterogeneity making their inclusion more problematic than their exclusion given the information they will likely provide on demographic rates. Pups that did not survive the first 8 weeks, or were found dead prior to the end of that years field season, are excluded from the analysis. Only encounters inside of the primary field season on Enderby Island were used.

Breeders were defined according to the status allocated to females in the sea lion database. In the primary analysis 'breeders' were defined by those animals given a status of '3' in that year (i.e., 3 = adult female confirmed to have pupped (seen nursing, or giving birth) for that breeding season). A more liberal secondary definition was also used with 'breeders' being defined as those animals given a status of either '3' or '15' in that year (15 = Adult female probably pupped – female seen on three or more occasions including at least one sighting in the presence of a pup, but not seen giving birth, or nursing a pup).

Results

Examples of Convergence

Due to the large number of parameters, traces of the MCMC chains are not presented here for all parameters, though examples are given in Figures 1-3. The traces for all demographic

parameters where checked for each model. Generally, convergence appears to have been reached within the first 1000-3000 iterations, well within the 5000 burn in period. Figures 1-3 also includes the Gelman-Rubin-Brooks plot for convergence (Brooks and Gelman 1998) with convergence being suggested once the lines approach the value of 1.

Strict Definition of 'Breeder'

Posterior distributions for the resight probabilities were relatively consistent regardless of the model fitted to the data, hence those from the model with annual variation that is consistent across age groups are presented here (Figures 4-7). In all cases, the daily probability of resighting a tagged breeder (red-shaded) is higher than a tagged non-breeder (grey-shaded). Daily resight probabilities for individuals in the 0-3 age group are very low, as are the probabilities of resighting tagged individuals by PIT tag.

Deviance values and deviance-based Bayesian p-values for models with the different age-structures are presented in Figures 8 and 9. These results indicate that the model with the most flexible structure is the best fitting model, and the model with no annual variation is the worse. The Bayesian p-values indicate that the observed deviance values for the model with no annual variation in the demographic parameters are slightly unusual (0.095; but not extreme), and are judged as satisfactory for the other two models. While it could be argued that the most complicated model appears to be the best overall, some of the estimates raise concerns about the potential reliability of the results (e.g., Figure 10) and also highlight that sample sizes in some years for certain age groups can be small (e.g., Figure 11). This raises concerns about the possibility of potential spurious results being identified. Therefore, results are presented for the model of intermediate complexity where annual variation was different depending only on previous years breeding status.

Figures 12-14 present the posterior distributions for survival of non-breeders in each age-class. Recall that survival is denoted in terms of the beginning period. Relatively extreme values are estimated for the first 4 years (1997/98-2000/01), before settling down to a relatively consistent range of values for the period 2001/02-2006/07. The final value (2007/08) is estimated to be noticeably lower than the preceding 6 years. Generally, annual survival probabilities for the 4-14 age-class are estimated to be the highest (2001/02-2006/07 average $\approx$ 0.87), followed by the 0-3 age class (average $\approx$ 0.77) then the 15+ age-class (average $\approx$ 0.70). The equivalent results for breeders are given in Figures 15 & 16. The

estimated values for both age-classes are relatively consistent, especially for the period 1997/98-2006/07, though survival probability in 2007/08 is again estimated to be lower than previously. Overall the survival probabilities for the 4-14 age-class are estimated to be higher (1997/98-2006/07 average ≈ 0.92) than the 15+ age class (average ≈ 0.75). In all cases females that bred the previous year are estimated to have higher survival than females that did not breed. A numerical summary of the random effect mean and standard deviation (on the logistic scale) for survival probabilities are given in Table 2.

The posterior distribution for probability of breeding in year t for non-breeders in year $t-1$ is given in Figure 17 for those aged 4-14 in year $t-1$ and in Figure 18 for those aged 15+ in $t-1$ (*note that x-axes are currently labelled in terms of $t-1$ but text describes results in terms of year t, which is more correct. Figures will be updated in final copy*). There has been an apparent decline in breeding probability until 2004/05 (from ≈ 0.60 to ≈ 0.2), with an apparent increase in the last few years (to ≈ 0.4). Estimated values are similar for both age groups. For females that bred in year $t-1$ (Figures 19 & 20), the estimated probability of breeding in year t appears to be relatively constant initially (≈ 0.7), suddenly dips in 2004/05 (to ≈ 0.4) and increases until 2007/08 (to ≈ 0.7), then dips again in 2008/09 (to ≈ 0.5). Estimated values are again similar for both age groups. A numerical summary of the random effect mean and standard deviation (on the logistic scale) for breeding probabilities are given in Table 3. Pup production numbers (supplied by L. Chilvers, DOC) are given in Appendix 1 for comparison with years of mass mortality events indicated.

Tag loss and retention probabilities (per year) rates are given in Table 4. These results suggest that flipper tags are not lost independently as the probability of losing both tags is not approximately the probability of losing 1 tag, squared (e.g., $0.07 \neq 0.09^2$). Furthermore, if tag loss was not accounted for survival would be underestimated by approximately 0.08, although the presence of branded and PIT tagged animals partially mitigates this.

Liberal Definition of 'Breeder'

Posterior distributions for the resight probabilities when using the liberal definition of breeder are essentially identical to when using stricter definition, hence are not presented again.

Deviance values and deviance-based Bayesian p-values for models with the different age-structures are presented in Figures 21 and 22, with similar conclusions to using the stricter definition of a breeder.

Using the more liberal definition of breeder has essentially no impact on the observed pattern of annual variation in both demographic parameters. Annual estimates of survival are essentially unchanged (Figures 23-27), while breeding probability estimates tend to be higher, as would be expected (Figures 28-31). A numerical summaries of the random effect mean and standard deviation (on the logistic scale) for demographic parameters are given in Tables 5 and 6.

Tag loss and retention probabilities (per year) are virtually unchanged using the liberal definition of breeder (Table 7).

Discussion

Even though the results presented here do not come from the 'best' model, the model used is biologically realistic in that whether a particular year is good or bad for sea lions, that effect is likely consistent across age groups. There was no indication of poor model fit for this model. There is also the fact that samples sizes in certain years are getting very small in some age classes for the 'best' model, hence attempting to separately estimate parameter values for those cases will yield unreliable estimates (e.g., Figures 10 and 11).

Information on different types of flipper tag loss comes from different groups of animals. All females will contribute information on the rates of retaining the same number of tags for a whole year, and on the probability of losing 1 of 2 tags. Information on losing either both or a single remaining tag (i.e., going from starting the year with either 2 tags or a single tag, to ending the year with no tags) comes primarily from branded individuals and, to a lesser extent because of lower resight probabilities, PIT tagged individuals.

It should be noted that as the age profile of the tagged individuals is not relatively constant (as might be expected if one randomly selected females each year rather than just resighting individuals tagged as pups; e.g., Table 1), then there is the possibility that some of the observed temporal effects may actually be the result of the changing age profile, rather than a

true temporal change. The converse is also possible in that some of the observed difference may be (at least partially) due to changing age profiles within an age class.

An example of this may be the apparent U-shaped pattern in the non-breeder breeding probabilities (Figures 17, 18, 28 and 29). The apparent decline may be symptomatic of a generally aging group of animals within this timeframe (Table 1) if the probability of breeding is not approximately similar across the entire age-class, or if there is a subset of individuals that are dedicated non-breeders. Younger individuals begin to enter this age class in significant numbers in 2003, but if the majority of females do not begin to breed until age 6 or 7, this would be an explanation for why the breeding probability does not begin to increase until 2006. Alternatively, this U-shaped may be accurate, possibly indicating that due to the current population status, fewer individuals were breeding during the late 1990's-early 2000's, but in the late 2000's more individuals decided to breed.

The apparent dip in non-breeder survival for the 3rd and 4th years may also be symptomatic of a changing age structure within the tagged population. Alternatively, the dip may be a lagged-effect of the 1997/98 mass mortality event, i.e., the mortality actually occurred primarily in 1997/98, but as juvenile sea lions do not tend to be resighted until age 5 that mortality gets spread or averaged over subsequent years to some degree.

The results indicate that survival (particularly of adults, for both breeders and non-breeders) was approximately 0.05 lower in between 2007/08 and 2008/09 compared to most other years, which is very large change for long-lived species such as New Zealand sea lions. Breeding probability was as also relatively low for females that had bred in the previous year.

Population Size

Estimation Methods

The existing, available data can not be used to directly estimate total population size as tagging (marking) has been primarily of pups. However, using the above results it is possible to estimate the number of females alive each year from each tagged pupping cohort. Essentially, given the number of female pups produced in year *t*, the corresponding estimated survival probabilities can be used to predict the number that survive through to years *t*+1, *t*+2,

t+3, etc. As survival appears to depend upon breeding status in the previous year, a prediction must also be made about whether the female bred or not each year, given they survived.

More formally, given the age and breeding status of a female in year *t*, they may be in 1 of 3 mutually exclusive states in year *t*+1:

1. Alive and breeding, with probability $S_{age,t,bred} \times B_{age,t+1,bred}$

2. Alive and not breeding, with probability $S_{age,t,bred} \times \left(1 - B_{age,t+1,bred}\right)$

3. Dead, with probability $1 - S_{age,t,bred}$

Therefore, the number of females in each state in year *t*+1, given the number of females of the specific age and breeding status in year *t*, will be a multinomial random variable. Hence,

$$N_{cohort,t+1,bred|age,t,bred} \sim multinomial\left(N_{cohort,t,bred}, \Psi_{age,t,bred}\right)$$

and

$$N_{cohort,t+1,bred} = \sum_{age,t,bred} N_{cohort,t+1,bred|age,t,bred}$$

where $\Psi_{age,t,bred}$ is the multinomial probability vector formed by the 3 state probabilities given above. Total number alive each year is then obtained by summing across cohorts and breeding status.

As demographic parameters are not known and have been estimated, this uncertainty must be accounted for. This achieved by generating random values for $N_{cohort,t+1,bred|age,t,bred}$ for each iteration of the MCMC analysis, hence the resulting distributions of $N_{cohort,t+1,bred|age,t,bred}$ incorporate both parameter estimation uncertainty and stochastic variation. For years with no direct estimates of survival or breeding probabilities (e.g., 1995/96) values were predicted based upon the estimated mean and standard deviation of the random effects terms.

In addition to the pup counts from 1994/5 onwards, and the pup tagging cohorts of 1997/98 onwards, there are also older known-age females from pupping cohorts in the early 1990's. Rather than predict the number of survivors from those cohorts (which may be prone to too many compounding prediction errors), a more direct estimation method was used. If it can be assumed that the fraction of the total number of females alive in the Auckland Islands that are observed at Sandy Bay, is approximately consistent across all ages for females aged 4+, then this estimated fraction for the younger females in combination with the number of older

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females observed at Sandy Bay each year, can be used to estimate the total number of older females in the Auckland Islands population. That is, if

$$N_t^{4+,*} = \sum_{\substack{age,bred \\ 4 \leq age \leq t}} N_{cohort,t,bred}$$

is the estimated number of females alive in year t aged 4+ from the identified pupping cohorts (1997/98 onwards), and $n_t^{4+,*}$ is the number of females from those cohorts observed at Sandy Bay, then

$$f_t = \frac{n_t^{4+,*}}{N_t^{4+,*}}$$

is the estimated fraction. The number of older females can then be estimated as

$$N_t^{4+,\#} = \frac{n_t^{4+,\#}}{f_t},$$

where $n_t^{4+,\#}$ is the number of older females observed at Sandy Bay, which is then add to the estimated number of survivors from the pup count data to estimate the number of females alive belonging to cohorts that had been exposed to tagging. This will be a biased low estimate of population size because not all cohorts within the population have been accounted for, but the degree of bias will decrease through time assuming continuing tagging and counting of pups.

Data used

Survival and breeding probability were estimated as described above using the 1997/98 onwards tagged pup cohorts. Pup count data extends from 1994/95 to date and a 50:50 sex ratio has been assumed. Counts relate to the number of female pups that survived the first 8 weeks (Table 7). 2001/02 is the first year in which pups from the 1997/98 cohort are observed to be 4-years old, hence estimated numbers of older females only occurs from 2001/02 onwards. At that time 157 females aged 9-12 were also observed at Sandy Bay, which correspond to the 1989/90-1992/93 pup cohorts (Table 7). Therefore, annual estimates relate to estimates of the number of surviving females in the 1989/90-1992/93 (from 2001/02 onwards) and 1994/95-2008/09 cohorts rather than true population size estimates. Hence, by 2008/09 the 'population' corresponds to females aged from 0-14 and 16-19 years old.

Results

Annual estimates obtained from the demographic model where annual variation in demographic parameters depends only on breeding status in previous year, are given in Figure 32 (using the strict definition of a breeder). The overall curvature to the estimates is a result of the constant tagging of new pups, although the degree of curvature appears to have flattened off into the mid-2000's, suggesting that perhaps most have the age groups within the Auckland Islands population are now represented in the various pupping cohorts. The high estimate for 2001/02 is the first year in which the estimated number of older surviving females was included and is likely an overestimate due to only a few of the more recently tagged females being observed in this year (i.e., f_t was unuslally small in this year). In the mid-2000's, the estimates stabilised at approximately 5500 females (95% credible intervals of approximately 4500-6000), however in 2008/09 the estimate decreased by approximately 700 females. Results are essentially identical if the liberal definition of a breeder is used.

Discussion

The method presented above is an attempt to use existing information to obtain a 'ballpark' estimate of population size. Resulting estimates from the mid-2000's onwards are believable and correspond well (in terms of orders of magnitude) with values based on assuming a stable population and annual pup counts (Gales and Fletcher 1999). However, they do display less annual variation than the latter approach as they explicitly incorporate the survival of adult females which, ecological theory suggests, is likely to exhibit less annual variation than breeding or reproduction rates for a longer-lived species. The lower estimate in 2008/09 is the combination of lower pup production and estimated lower adult survival. It should be noted however that these results may bee sensitive to choice of model for the demographic parameters (e.g., Figure 33).

At the working group meeting on 6 May 2010 it was suggested to use an integrated model or back-extrapolate the final age distribution through to the beginning of the time series to obtain a series of values that maybe more indicative of true population size. Such approaches will require the assumption of a relatively stable age-structured population, and that the age structure is relatively consistence across the Auckland Islands. These options will be evaluated more fully during the analysis of the 1997/98-2009/10 data.

Direct estimation of population size is likely to result in more robust values, but would require other data to be collected during the field season. Exactly what information should be collected, and how this might be done, requires some careful thought and discussions with field personnel. However, one option would be to do something similar to what is presently conducted to estimate pup production in some areas. For example, count the number of females on a (section of) beach and mark some number of them (e.g., 100 with a temporary mark). A few days later, repeat the survey and count the number of females on the beach, and the number that are marked. This data would provide the type information required to obtain a direct estimate of population size.

While having reliable estimates of survival and breeding rates is very useful information as they provide important insights into how a population may be functioning, they do not indicate how well a population may be performing at a particular point in time which is likely to be very important information from a management perspective (i.e., management actions could be very different if population size is relatively large or small, all else being equal). Furthermore, efforts to identify any density dependent effects on survival and/or breeding would be aided greatly by having independent estimates of population size. Therefore, it is recommended that serious consideration be given to assess whether the collection of additional information would be feasible in the upcoming field seasons.

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Figures

Figure 1: Example diagnostic plots of mean annual survival for females that did not breed and were aged 15+ in previous year. Upper panel is a trace plot of the 2 chains and lower panel is the Gelman-Rubin-Brooks plot for convergence.
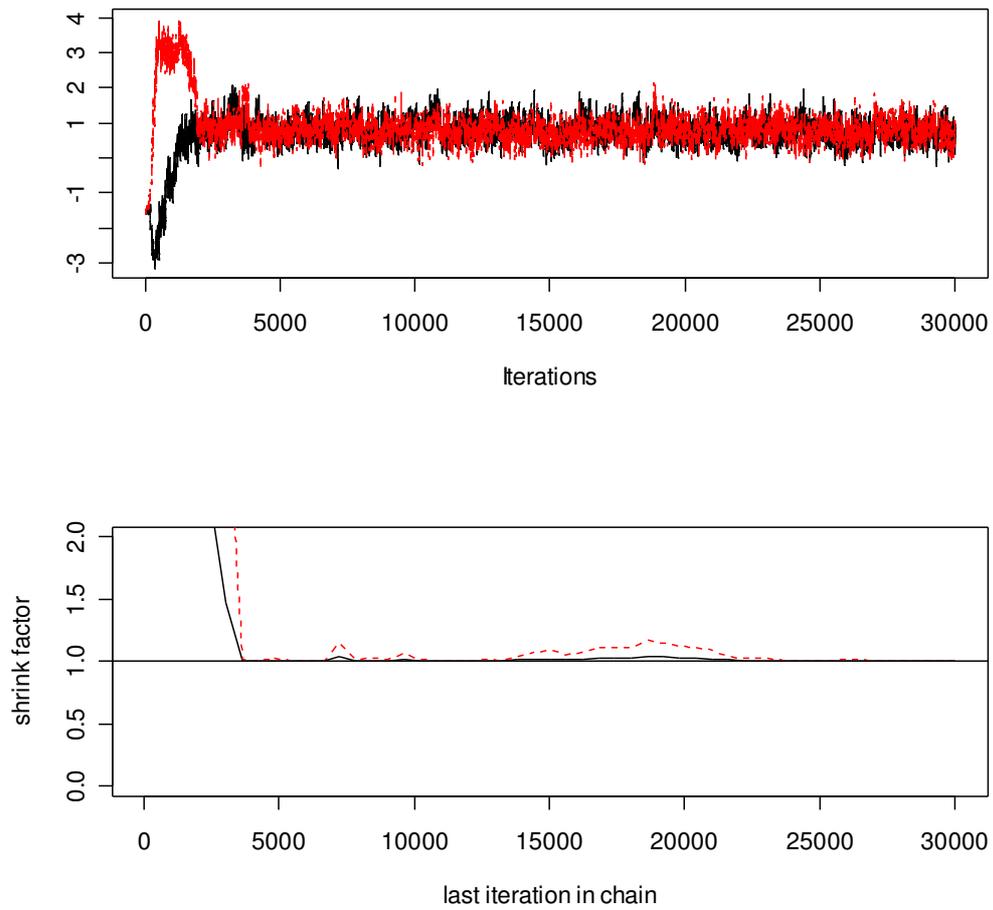
Figure 2: Example diagnostic plots of mean annual breeding probability for females that did bred and were aged 4-14 in previous year. Upper panel is a trace plot of the 2 chains and lower panel is the Gelman-Rubin-Brooks plot for convergence.
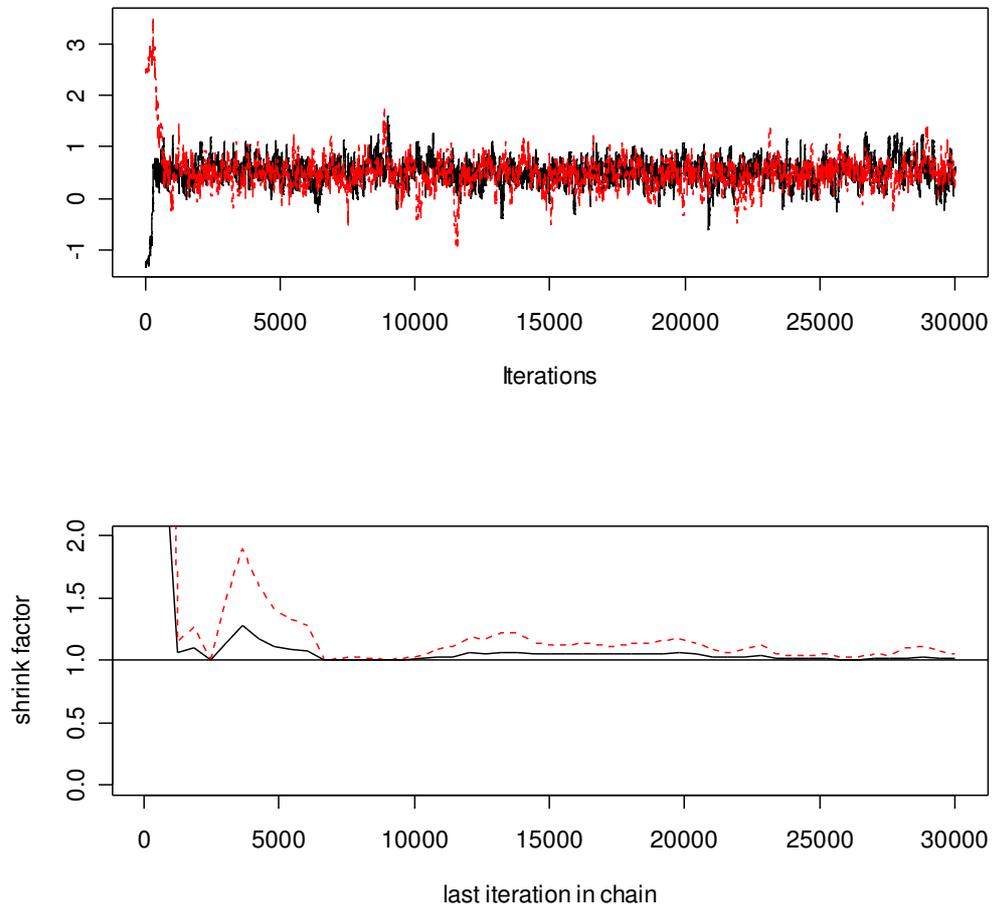
Figure 3: Example diagnostic plots of the standard deviation of annual survival for females that bred in the previous year. Upper panel is a trace plot of the 2 chains and lower panel is the Gelman-Rubin-Brooks plot for convergence.
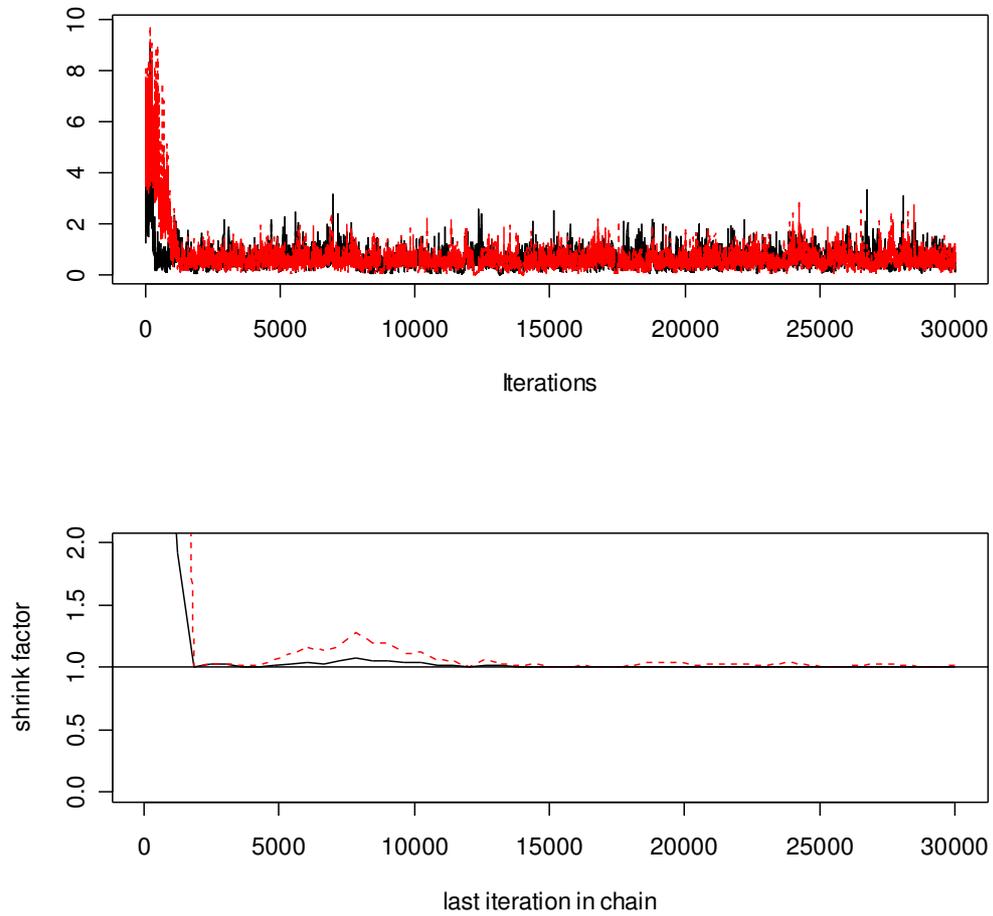
Figure 4: Posterior distribution for the daily probability of sighting a branded individual in each year by age class. Resight probabilities for which there was no information in the data are not indicated. Grey-shaded distributions indicate non-breeders and red-shaded distributions breeders. Years are denoted in terms of the calendar year associated with the January portion of the field season.
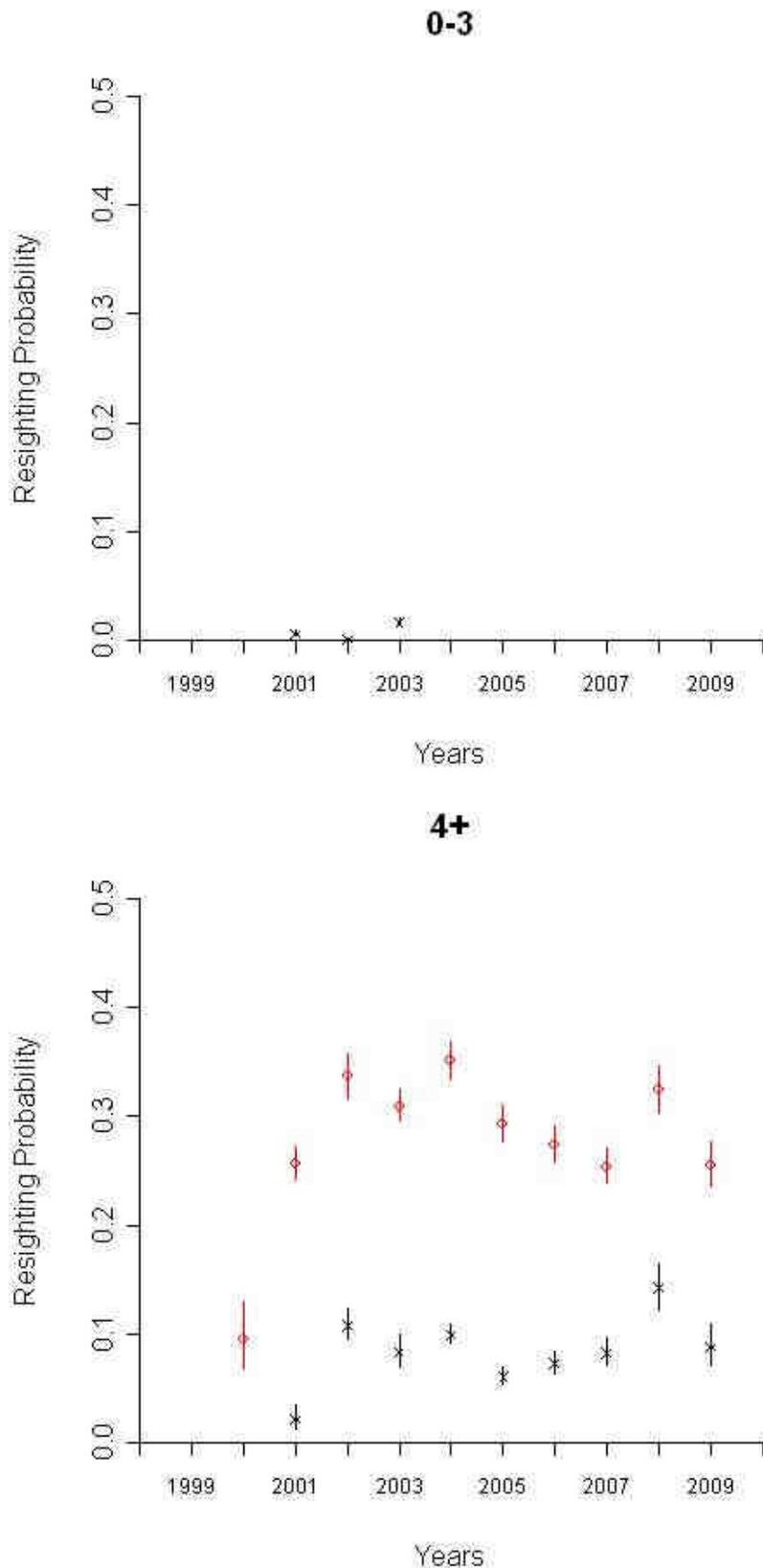
Figure 5: Posterior distribution for the daily probability of sighting a PIT tagged individual with no flipper tags in each year by age class. Resight probabilities for which there was no information in the data are not indicated. Grey-shaded distributions indicate non-breeders and red-shaded distributions breeders. Years are denoted in terms of the calendar year associated with the January portion of the field season.
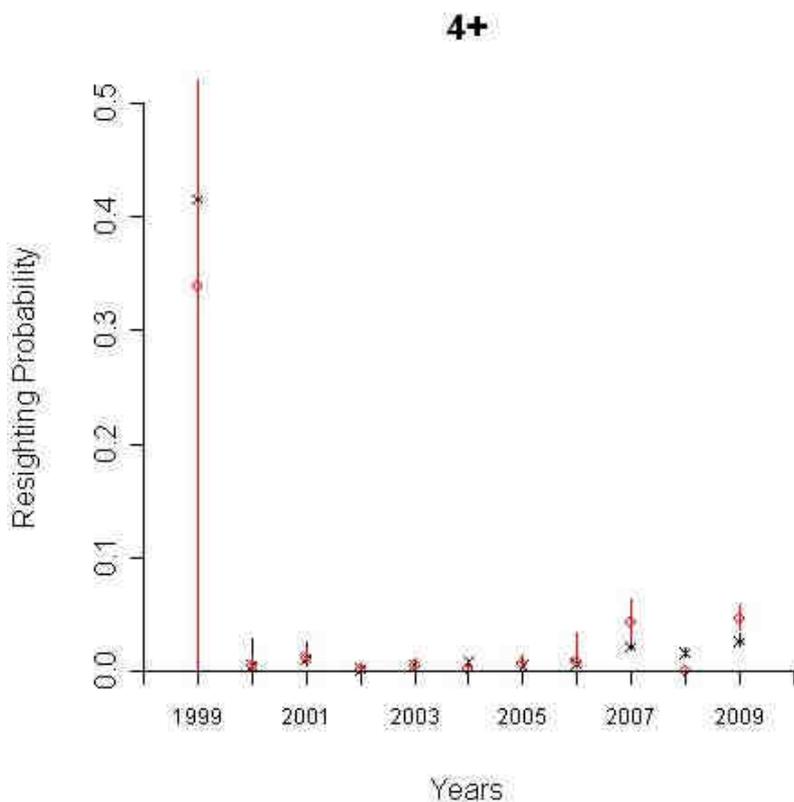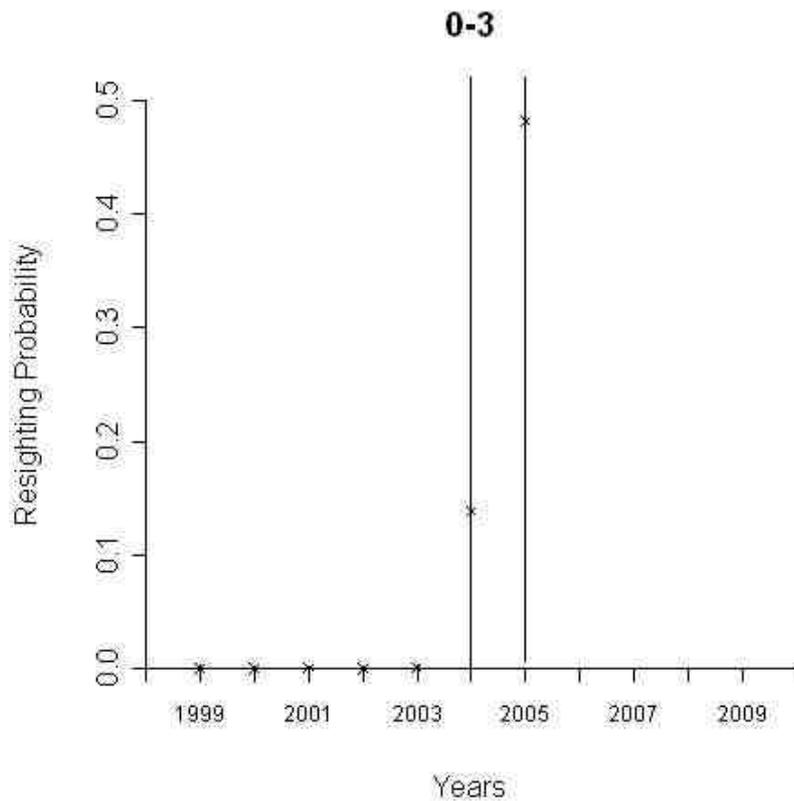
Figure 6: Posterior distribution for the daily probability of sighting an individual with 1 flipper tag in each year by age class. Resight probabilities for which there was no information in the data are not indicated. Grey-shaded distributions indicate non-breeders and red-shaded distributions breeders. Years are denoted in terms of the calendar year associated with the January portion of the field season.

0-3

4+
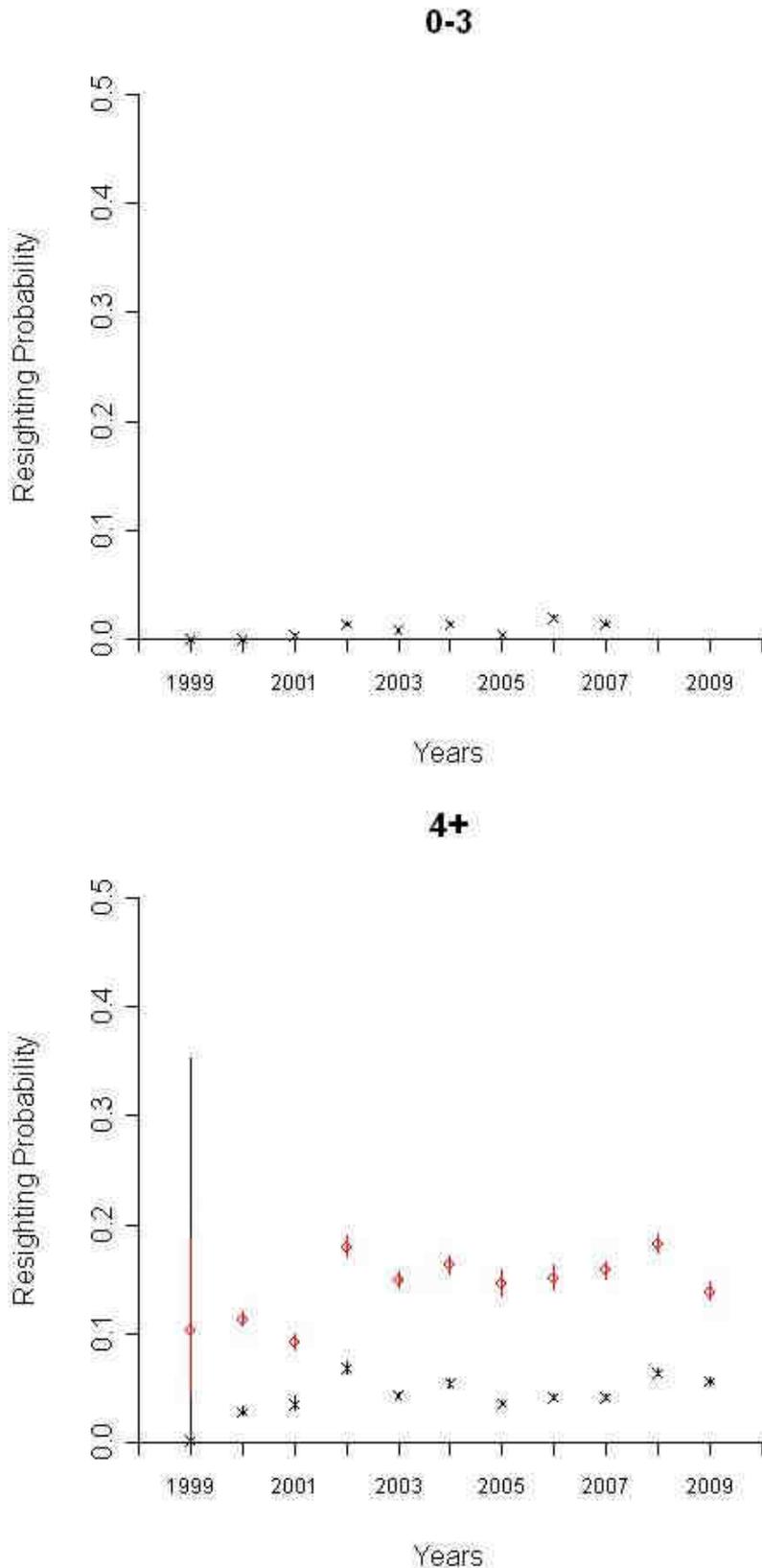
Figure 7: Posterior distribution for the daily probability of sighting an individual with 2 flipper tags in each year by age class. Resight probabilities for which there was no information in the data are not indicated. Grey-shaded distributions indicate non-breeders and red-shaded distributions breeders. Years are denoted in terms of the calendar year associated with the January portion of the field season.

0-3

4+
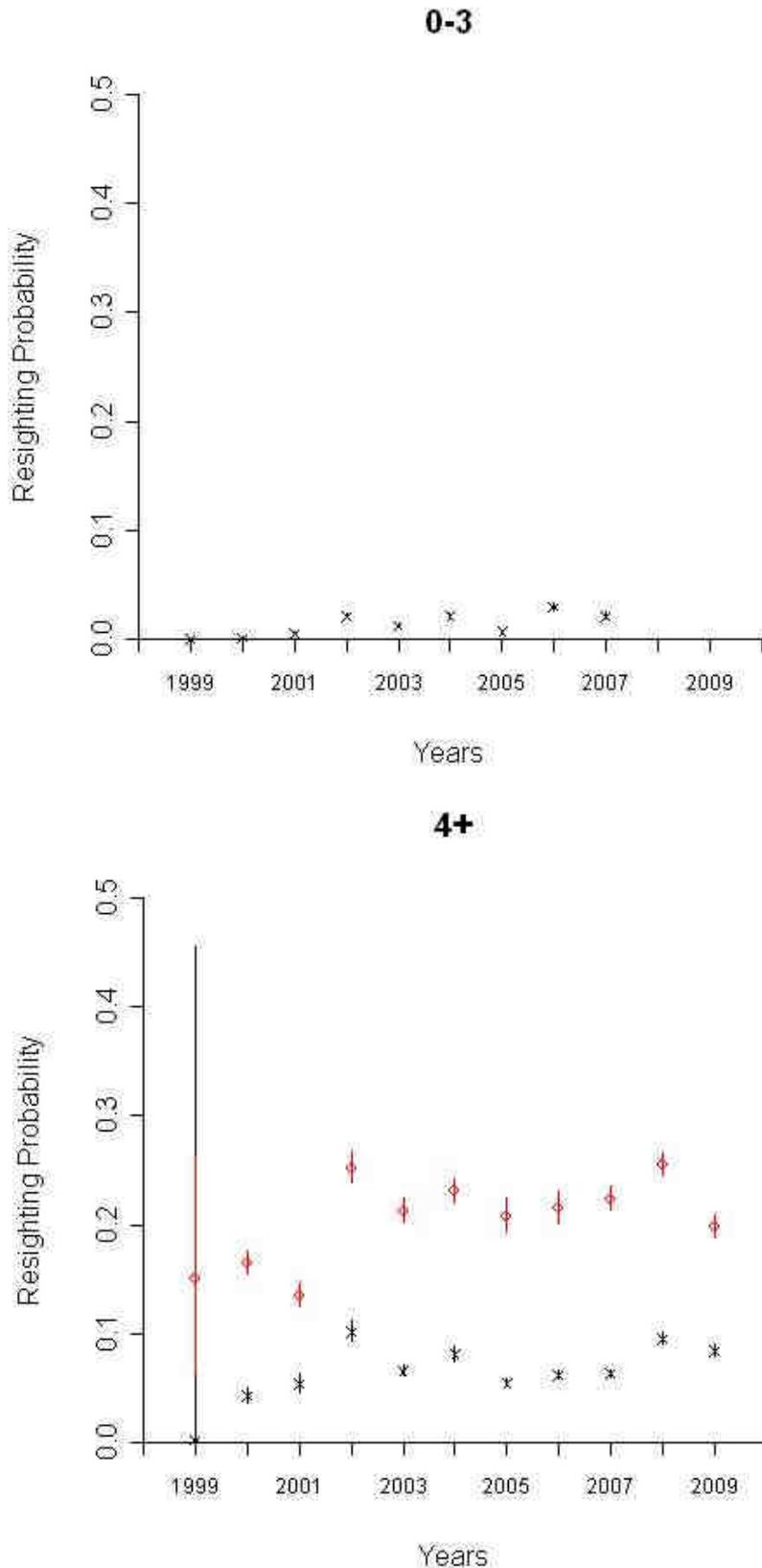
Figure 8: Posterior distributions for the deviance value from models with no annual variation (light grey), variation depending on previous year breeding only (mid-grey), and variation depending on previous year breeding and age (dark grey), using the strict definition of breeder. Smaller values indicate a better fit to the data.
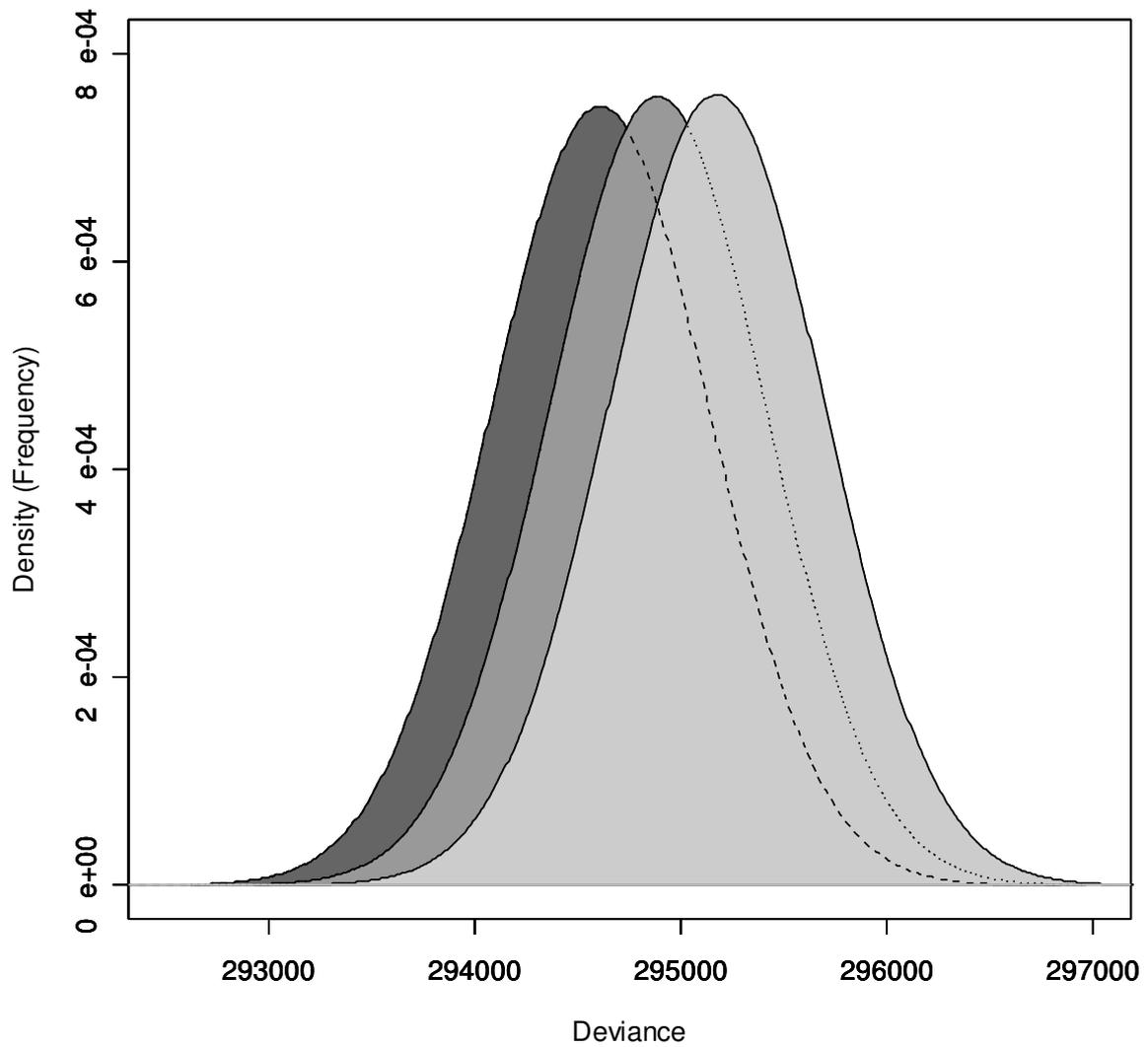
Figure 9: Plots of posterior (light grey) and predicted (dark grey) deviance values from each model; a) no annual variation; b) variation depends on previous year breeding status only; and c) variation depends on previous year breeding status and age. Bayesian p-values are indicated.
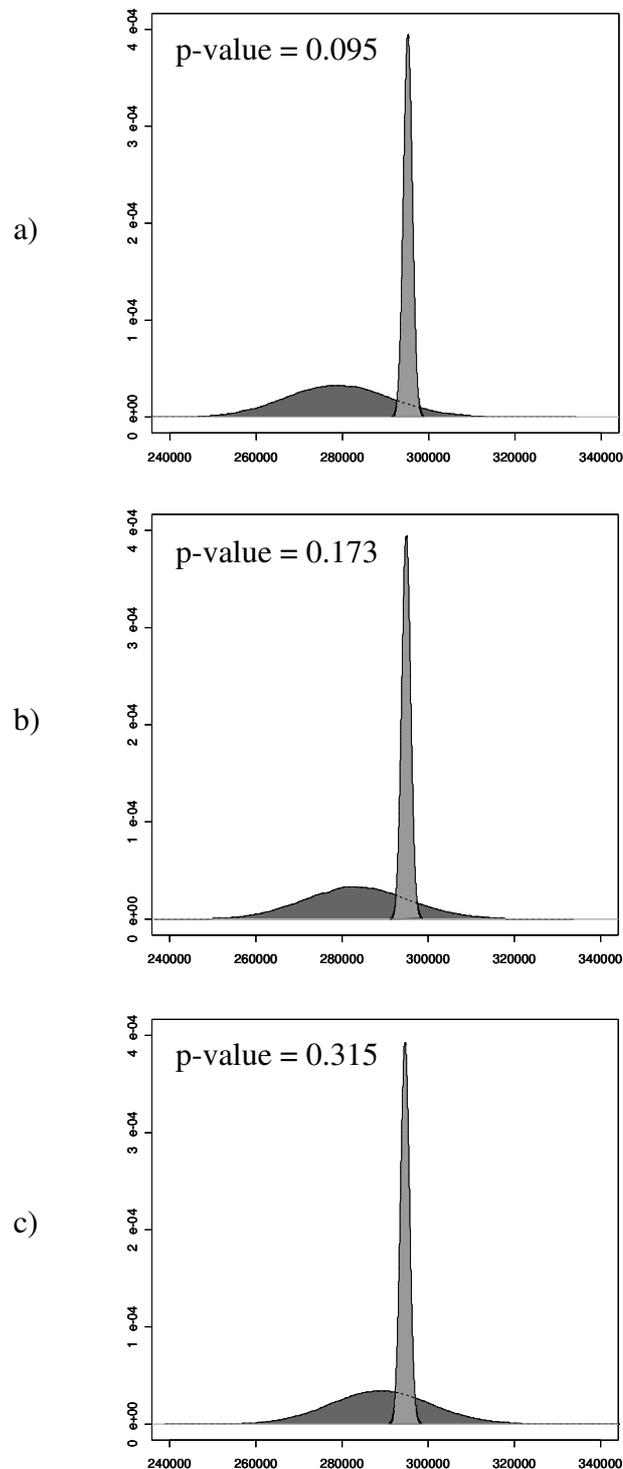
Figure 10: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were non-breeders aged 0-3 in year *t*, from model with annual variation depending on breeding status and age class in year *t*, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year *t*.
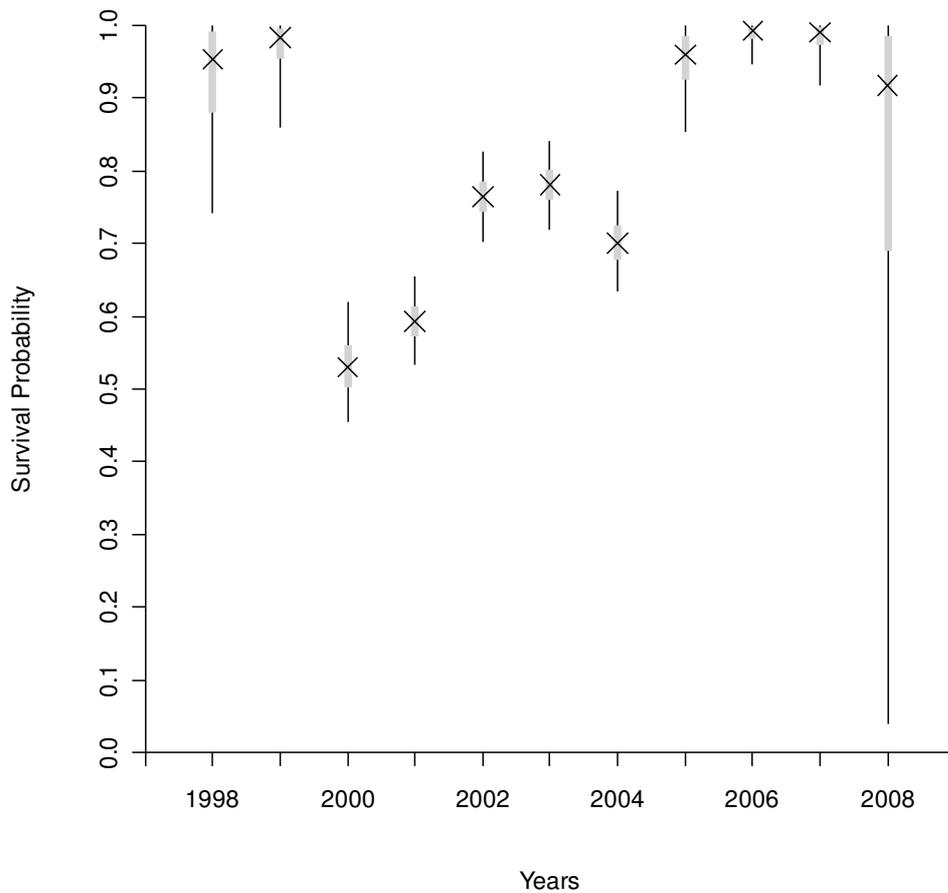
Figure 11: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were breeders aged 15+ in year *t*, from model with annual variation depending on breeding status and age class in year *t*, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year *t*.
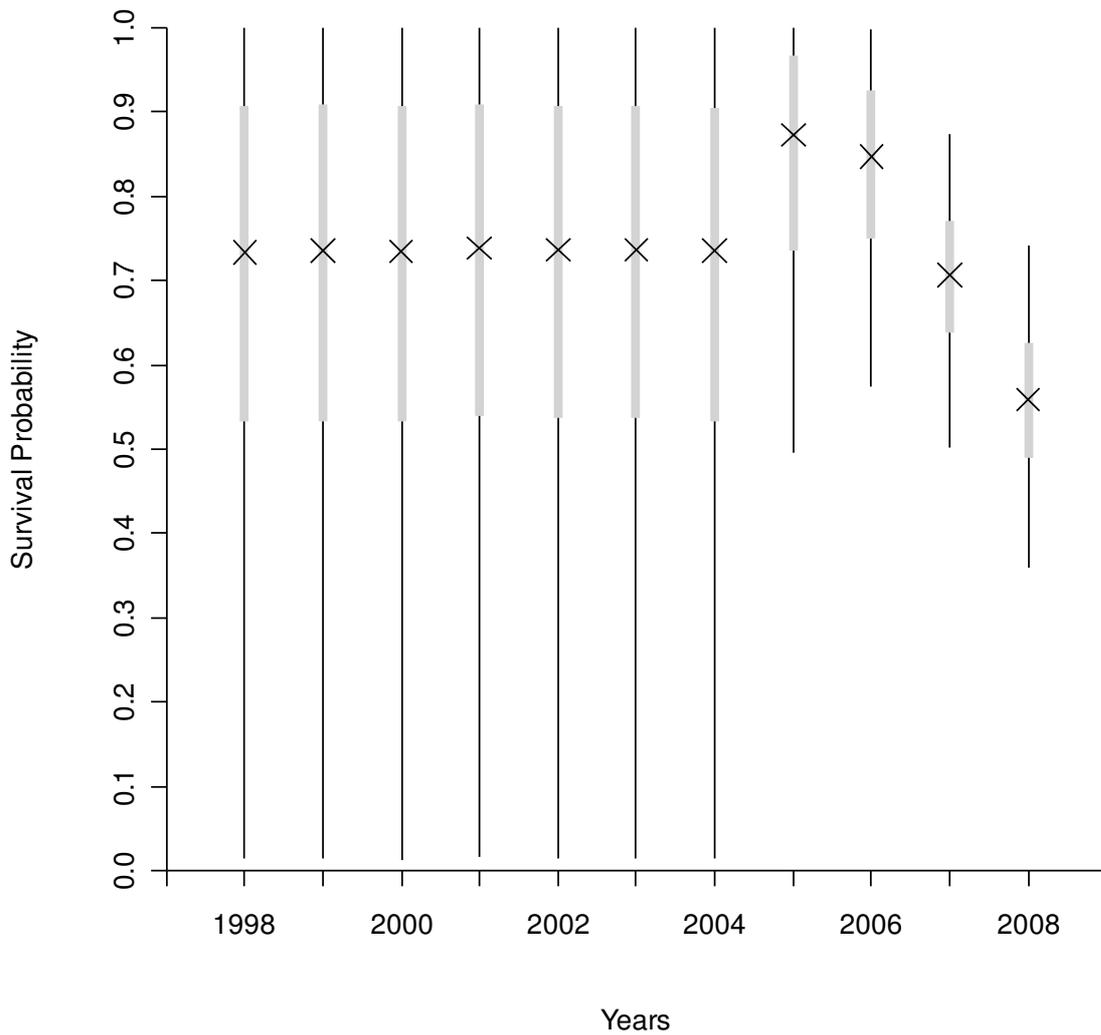
Figure 12: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were non-breeders aged 0-3 in year t, from model with annual variation depending on breeding status in year t, but consistent across age classes, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year t.
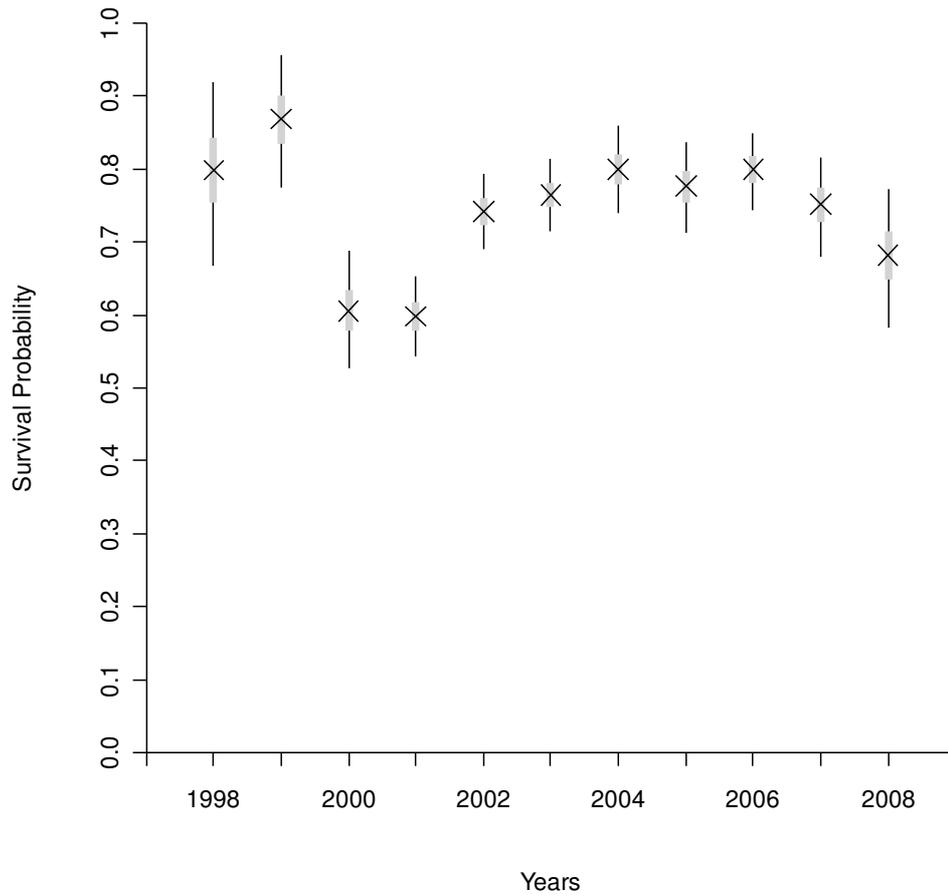
Figure 13: Posterior distribution for probability of survival from year *t* to *t+1* for individuals that were non-breeders aged 4-14 in year *t*, from model with annual variation depending on breeding status in year *t*, but consistent across age classes, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year *t*.
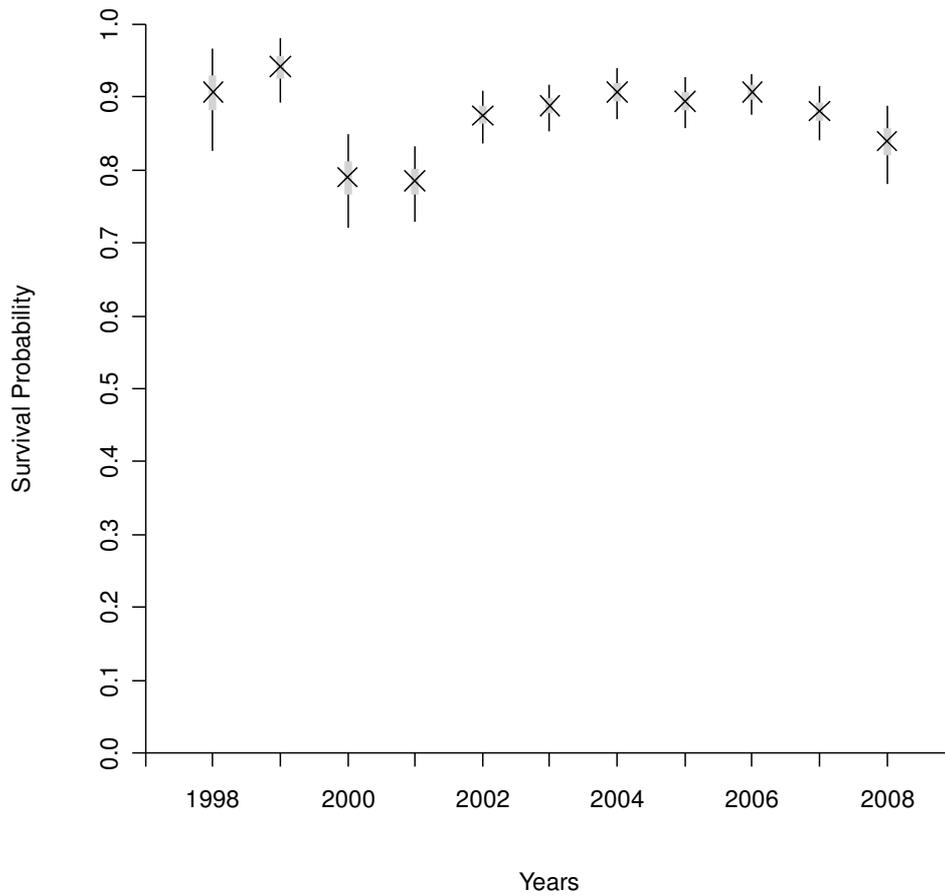
Figure 14: Posterior distribution for probability of survival from year *t* to *t+1* for individuals that were non-breeders aged 15+ in year *t*, from model with annual variation depending on breeding status in year *t*, but consistent across age classes, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year *t*.
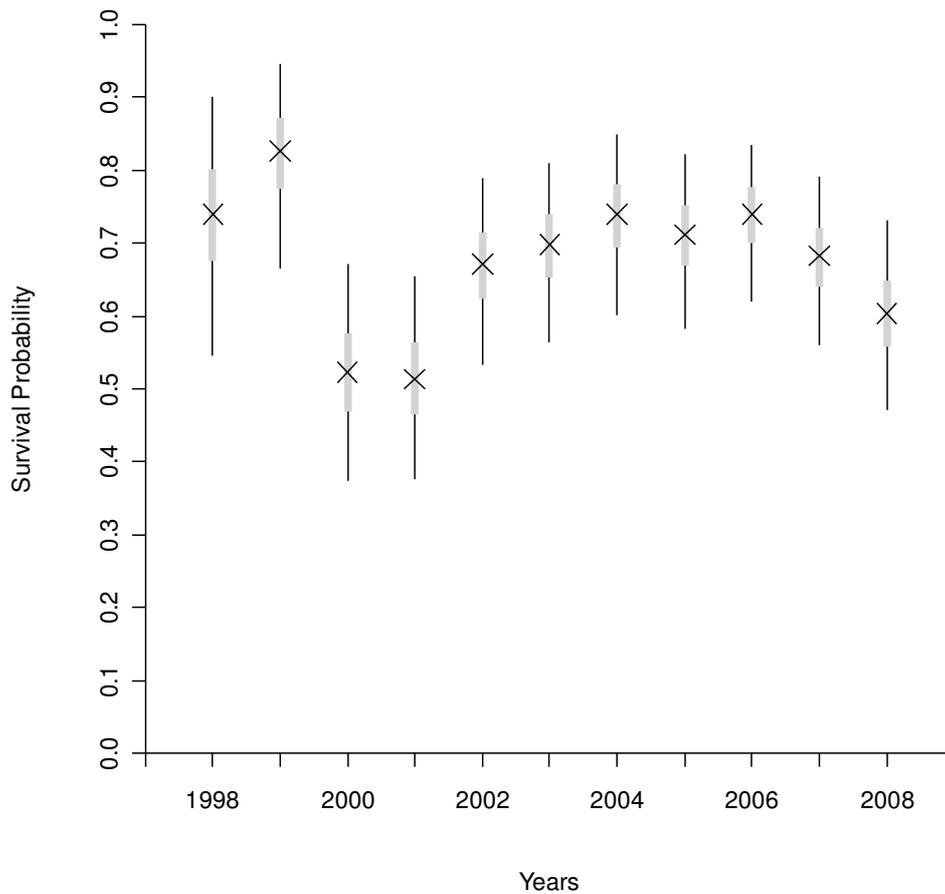
Figure 15: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were breeders aged 4-14 in year *t*, from model with annual variation depending on breeding status in year *t*, but consistent across age classes, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year *t*.
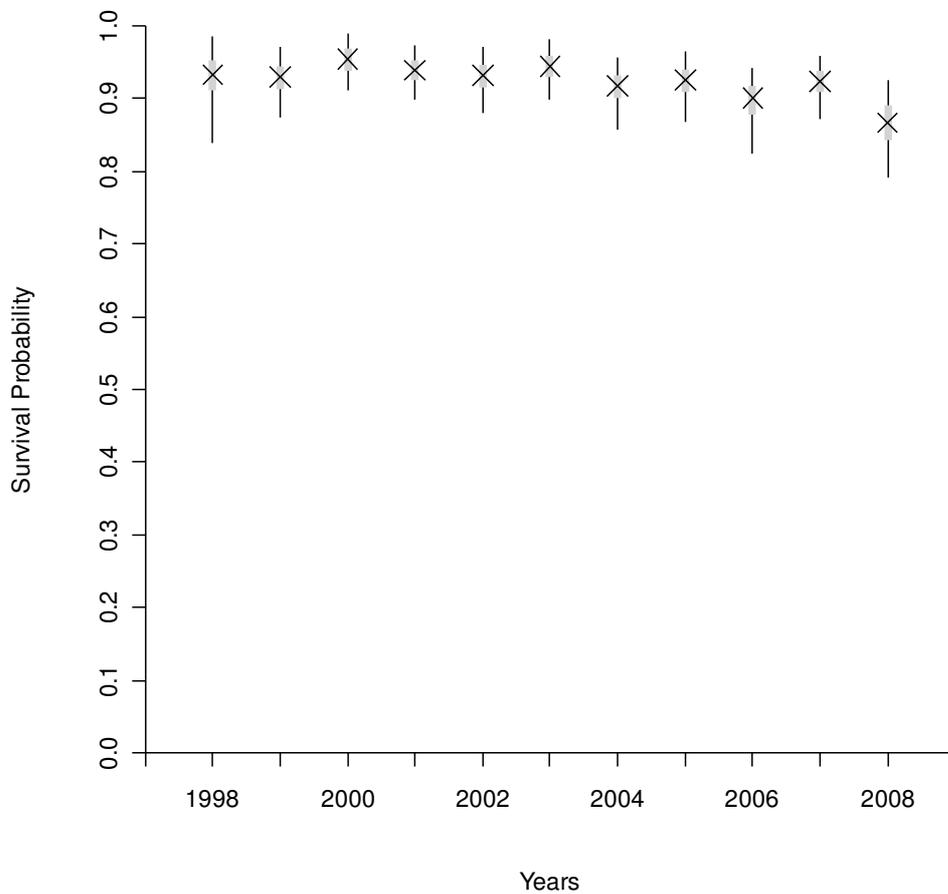
Figure 16: Posterior distribution for probability of survival from year *t* to *t+1* for individuals that were breeders aged 15+ in year *t*, from model with annual variation depending on breeding status in year *t*, but consistent across age classes, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year *t*.
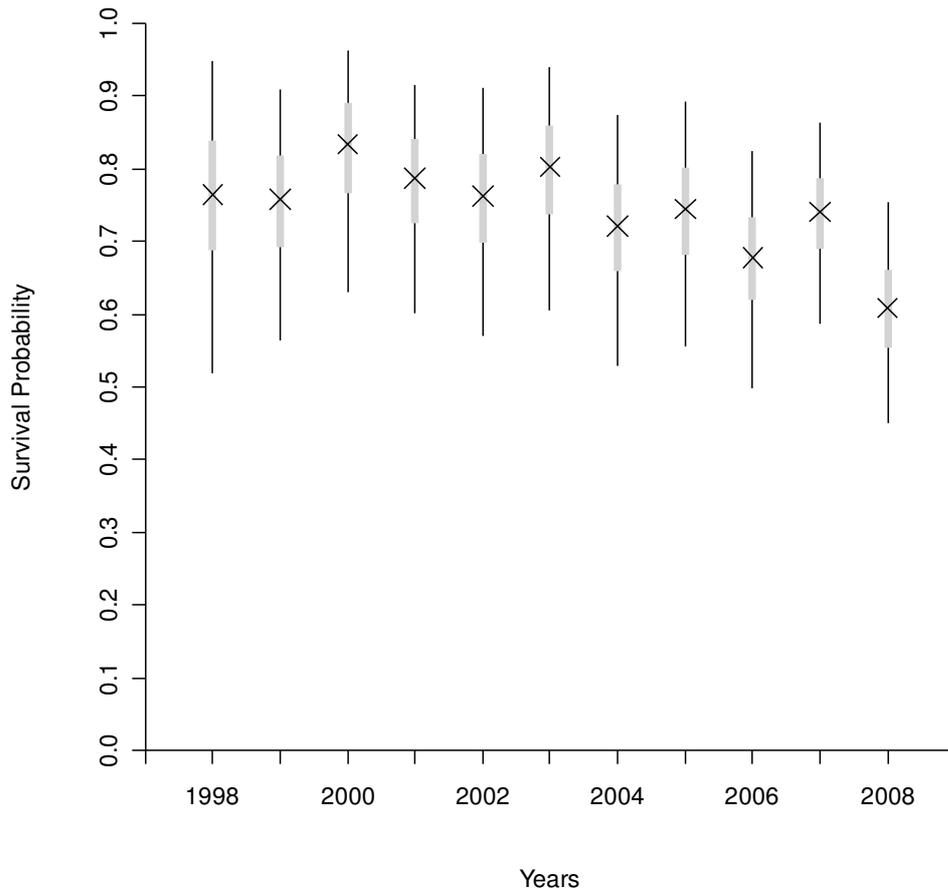
Figure 17: Posterior distribution for probability of breeding in year *t*+1 for individuals that were non-breeders aged 4-14 in year *t*, from model with annual variation depending on breeding status in year *t*, but consistent across age classes, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year *t*+1.
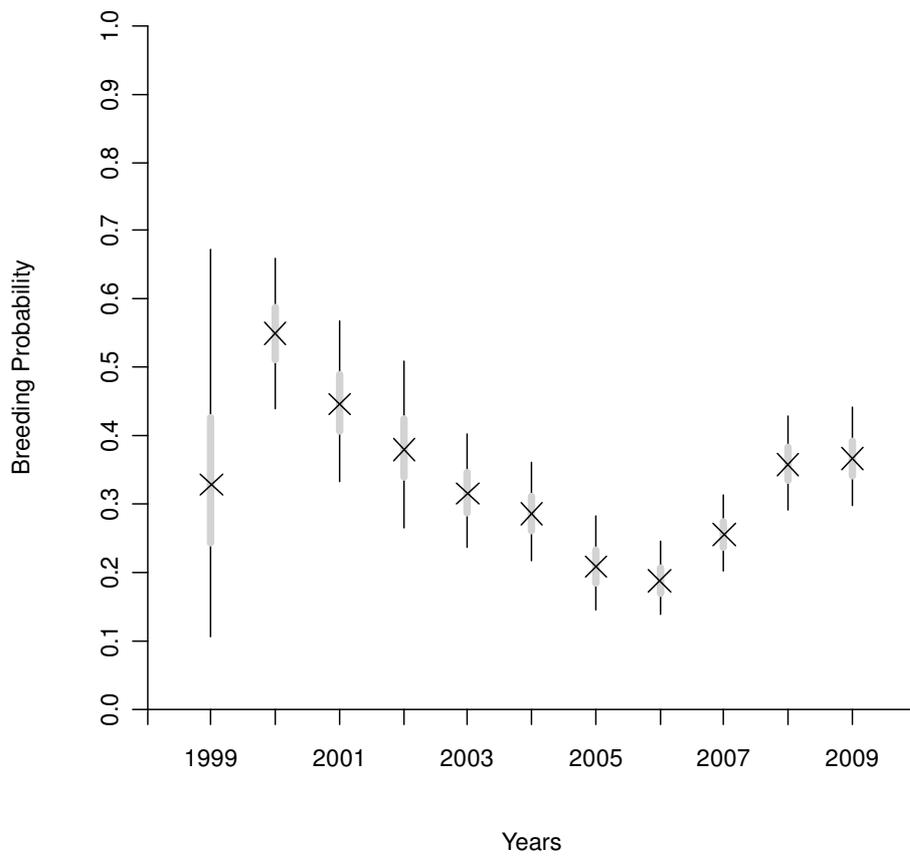
Figure 18: Posterior distribution for probability of breeding in year *t*+1 for individuals that were non-breeders aged 15+ in year *t*, from model with annual variation depending on breeding status in year *t*, but consistent across age classes, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year *t*+1.
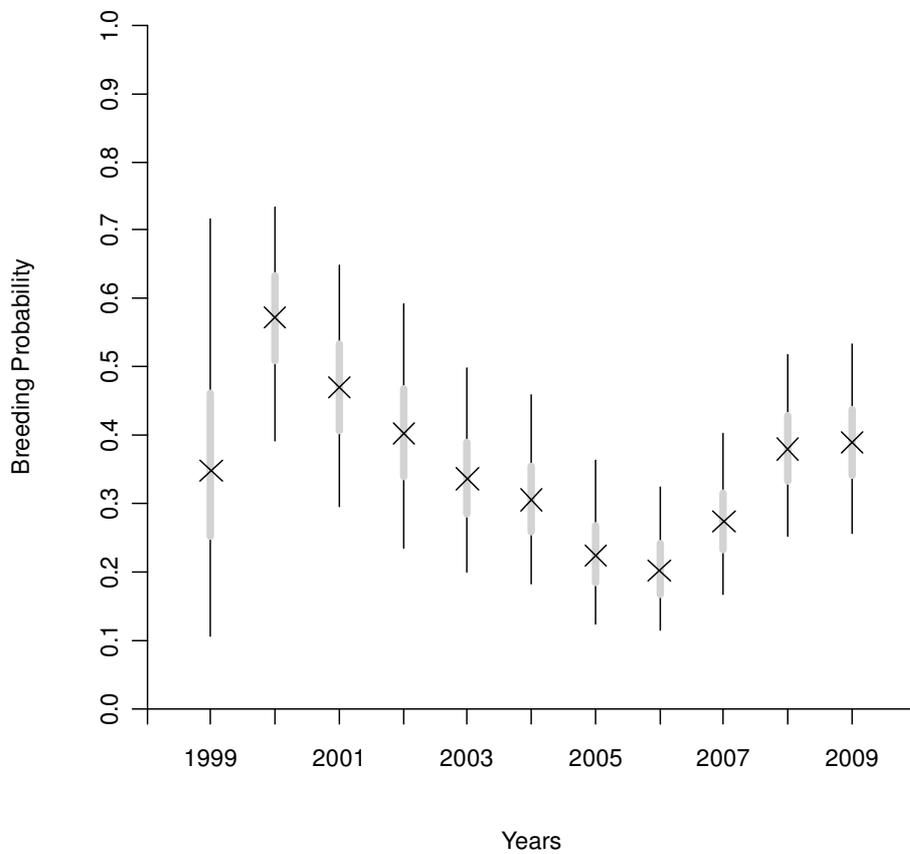
Figure 19: Posterior distribution for probability of breeding in year *t*+1 for individuals that were breeders aged 4-14 in year *t*, from model with annual variation depending on breeding status in year *t*, but consistent across age classes, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year *t*+1.
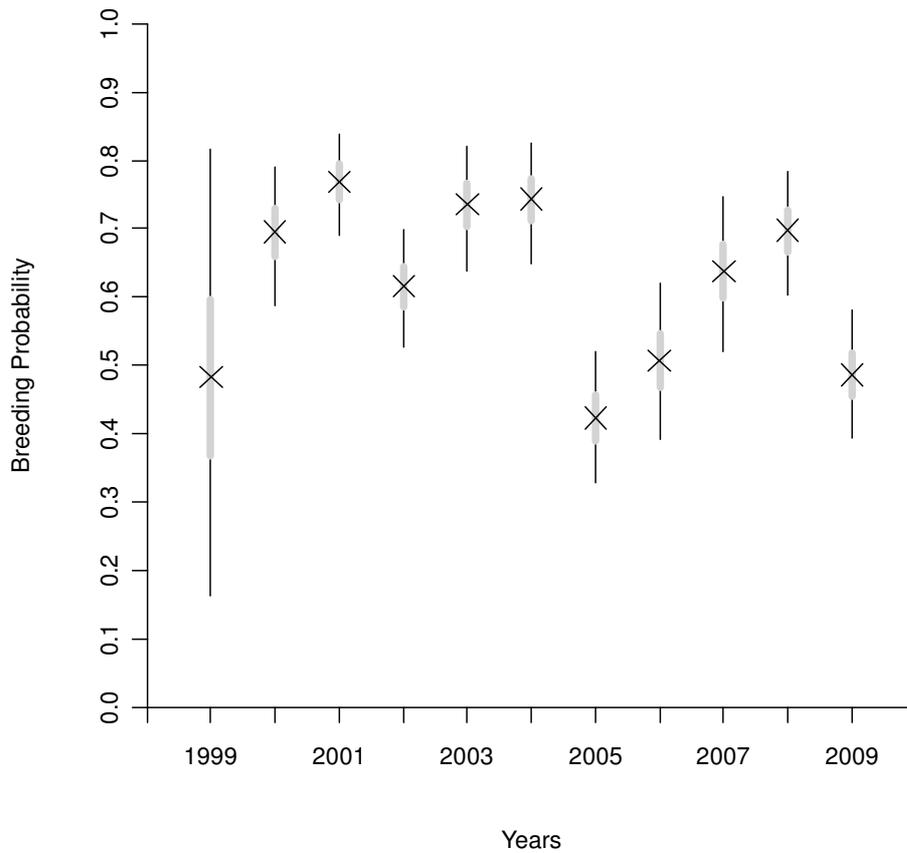
Figure 20: Posterior distribution for probability of breeding in year *t*+1 for individuals that were non-breeders aged 15+ in year *t*, from model with annual variation depending on breeding status in year *t*, but consistent across age classes, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year *t*+1.
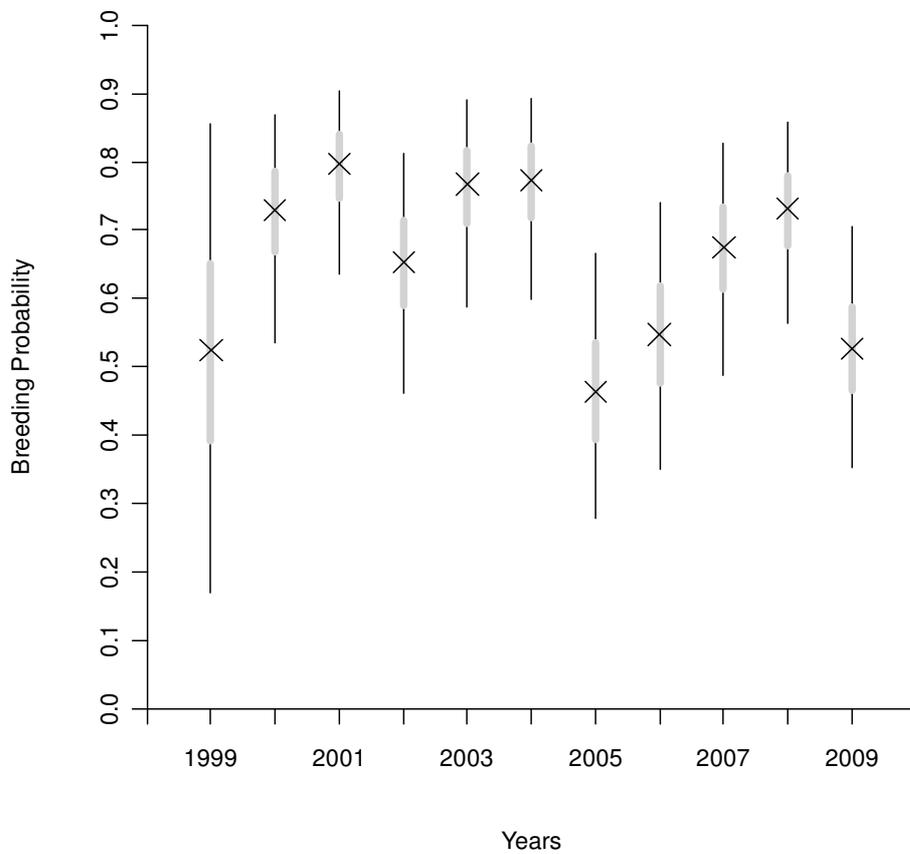
Figure 21: Posterior distributions for the deviance value from models with no annual variation (light grey), variation depending on previous year breeding only (mid-grey), and variation depending on previous year breeding and age (dark grey), using the liberal definition of breeder. Smaller values indicate a better fit to the data.
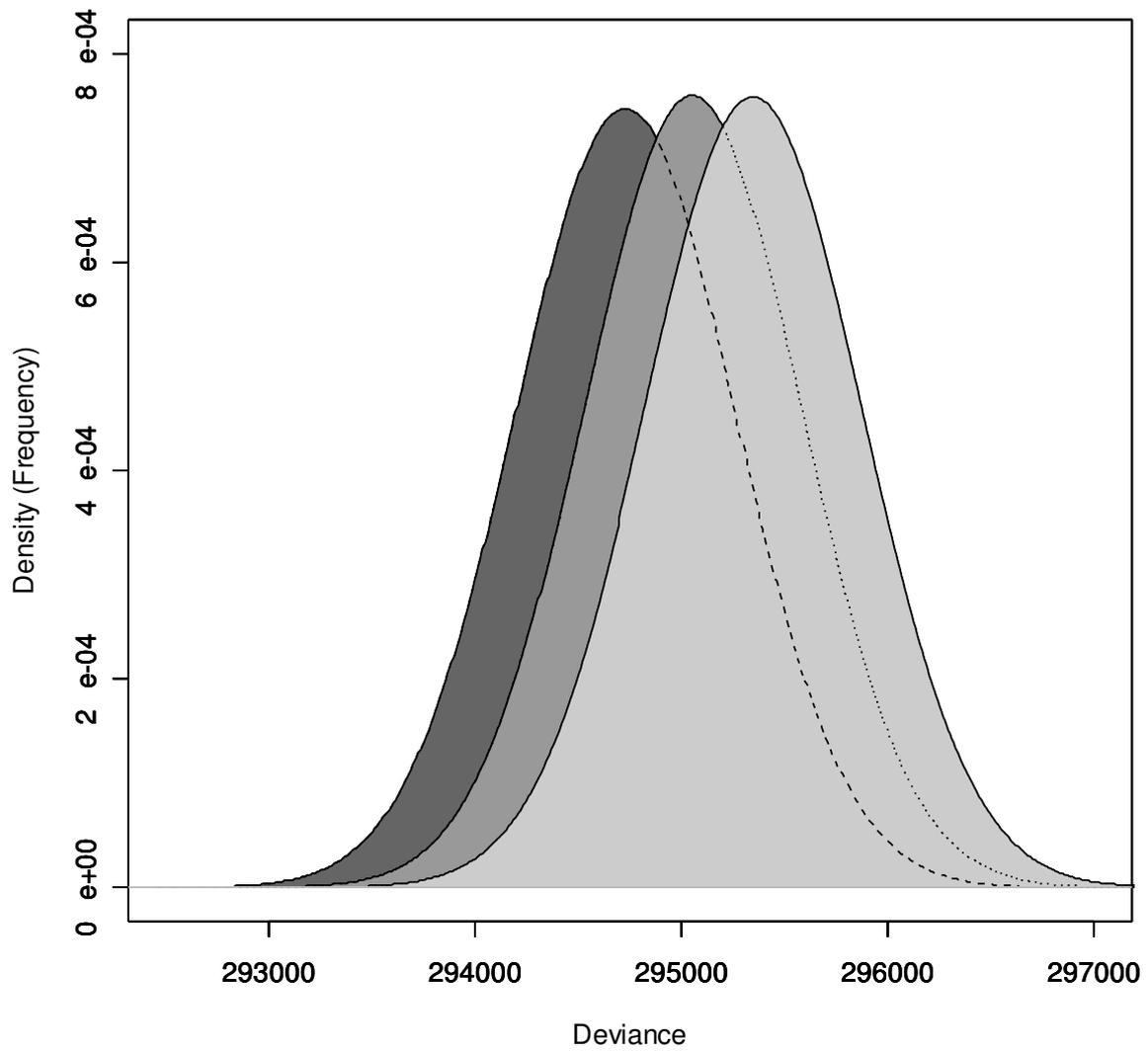
Figure 22: Plots of posterior (light grey) and predicted (dark grey) deviance values from each mode using the liberal definition of breeder; a) no annual variation; b) variation depends on previous year breeding status only; and c) variation depends on previous year breeding status and age. Bayesian p-values are indicated.
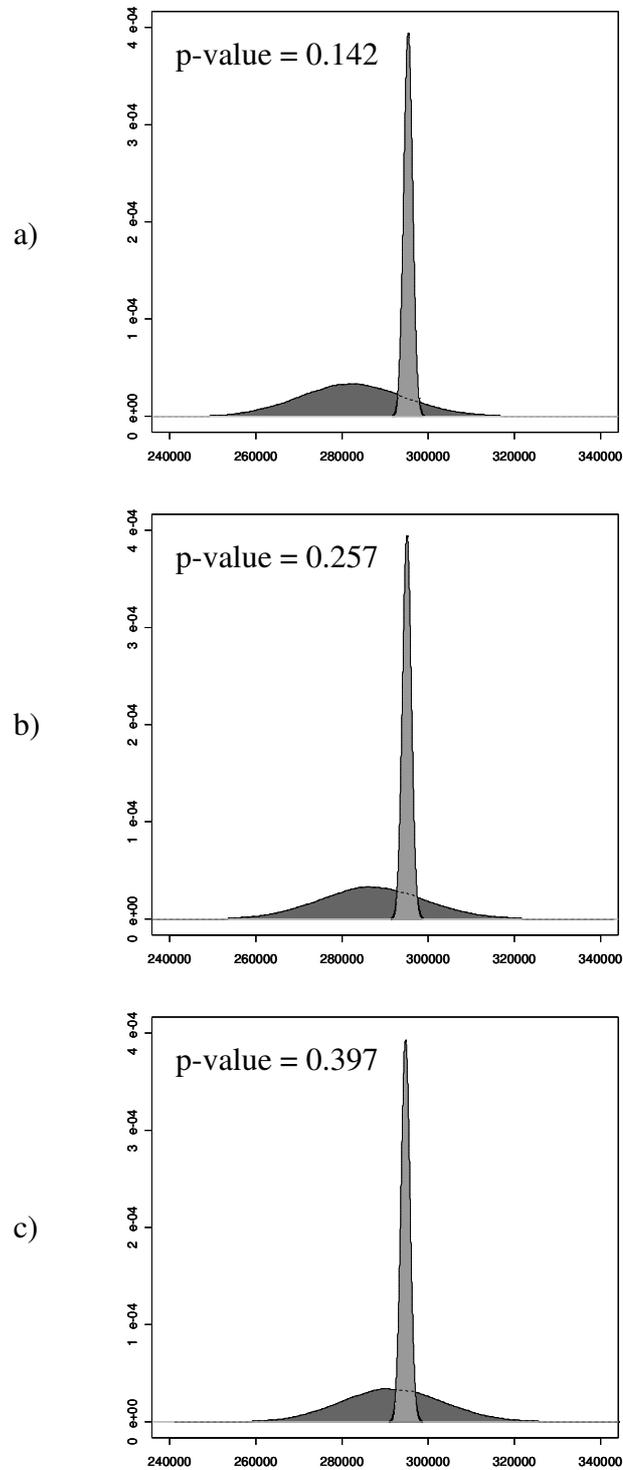
Figure 23: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were non-breeders aged 0-3 in year t, from model with annual variation depending on breeding status in year t, but consistent across age classes, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year t.
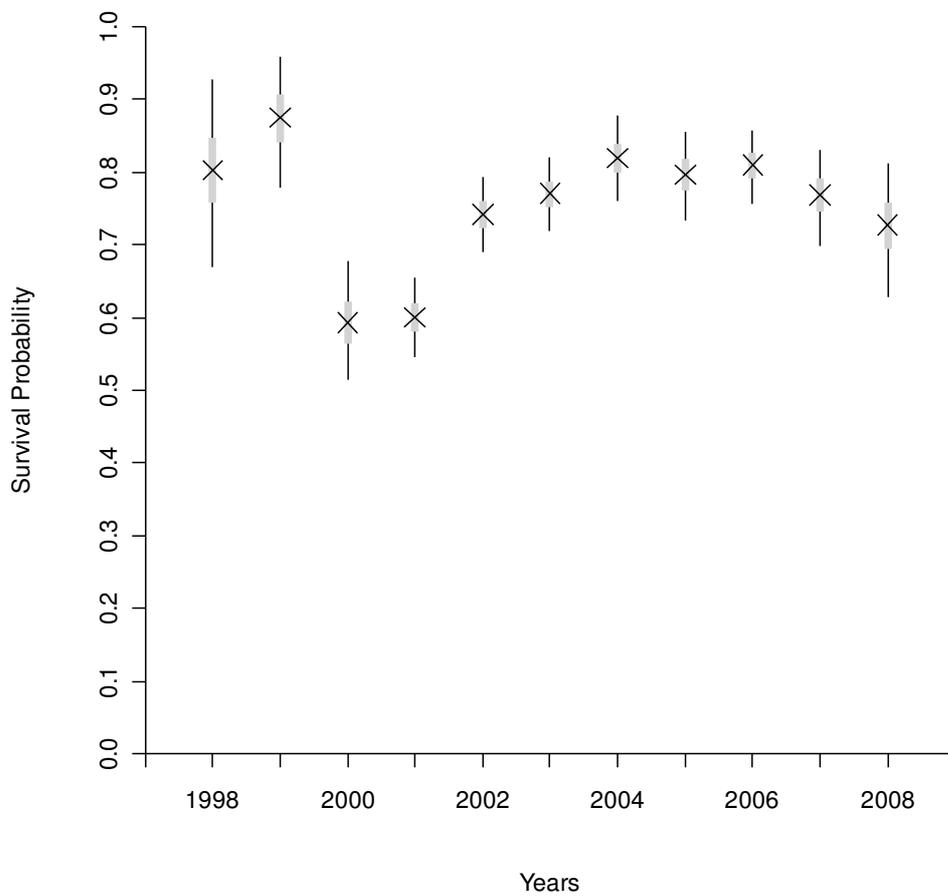
Figure 24: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were non-breeders aged 4-14 in year *t*, from model with annual variation depending on breeding status in year *t*, but consistent across age classes, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year *t*.
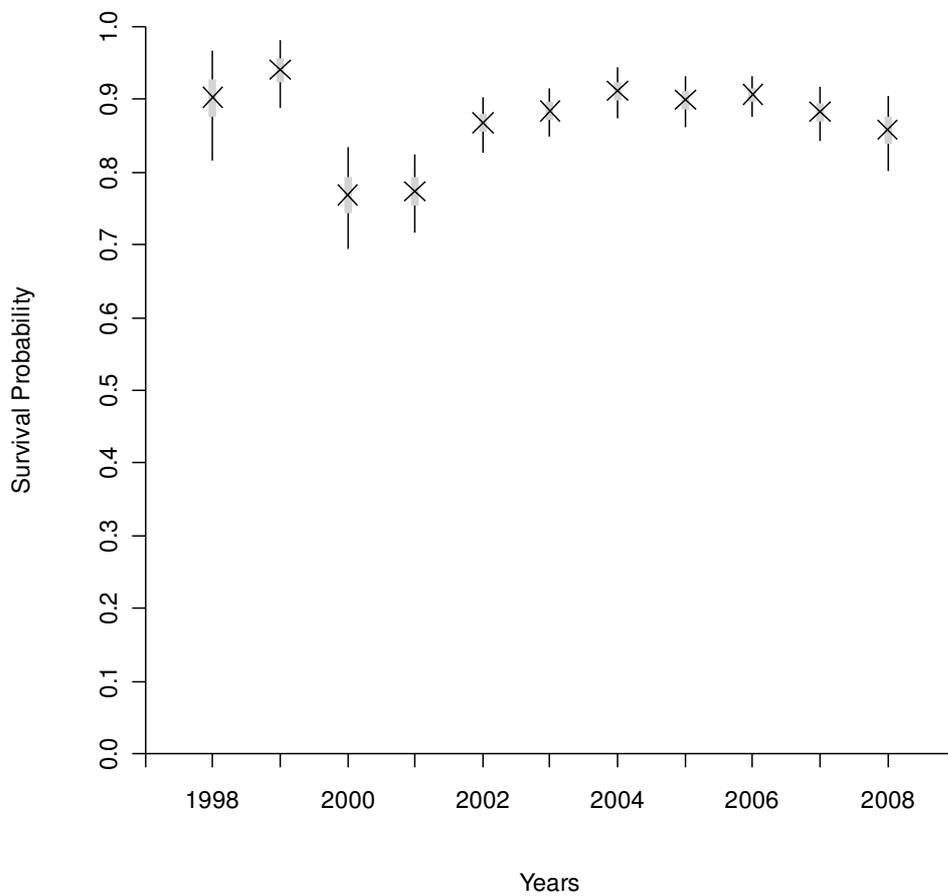
Figure 25: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were non-breeders aged 15+ in year t, from model with annual variation depending on breeding status in year t, but consistent across age classes, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year t.
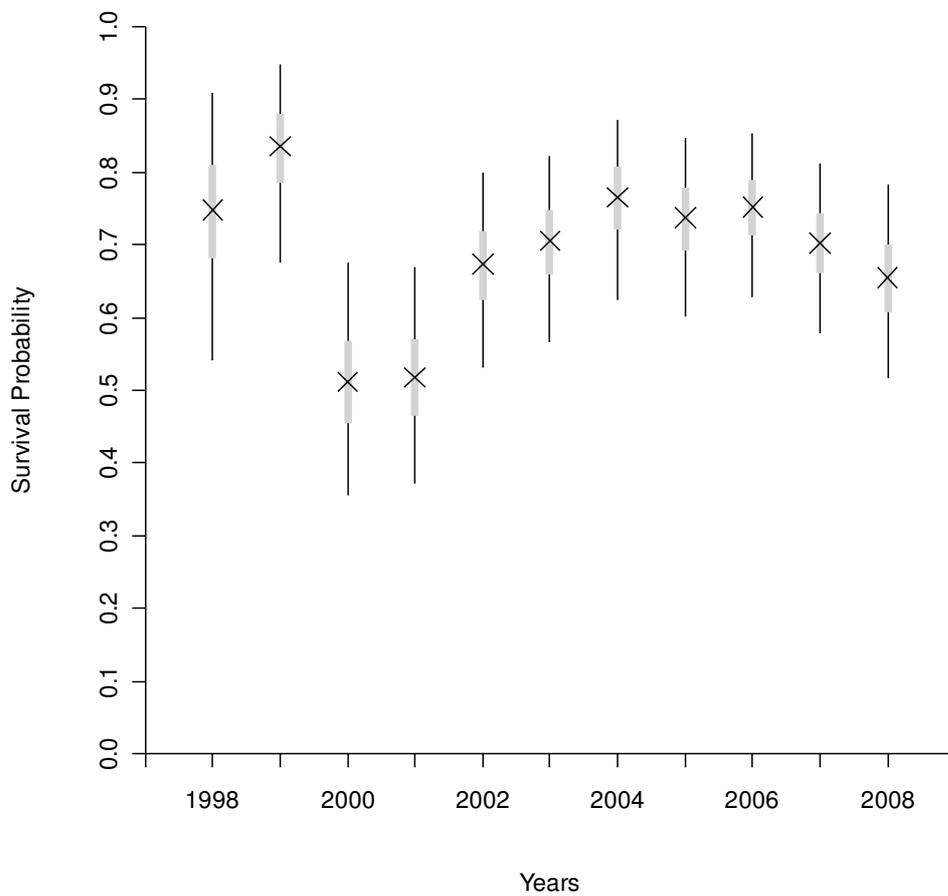
Figure 26: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were breeders aged 4-14 in year *t*, from model with annual variation depending on breeding status in year *t*, but consistent across age classes, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year *t*.
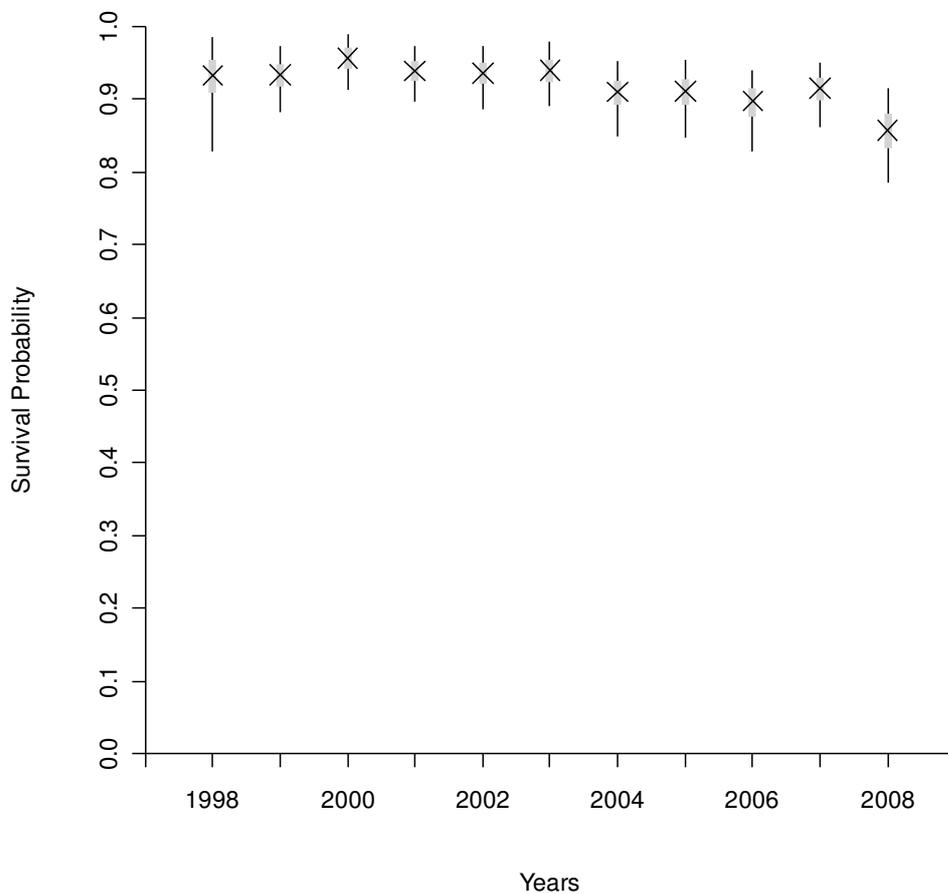
Figure 27: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were breeders aged 15+ in year t, from model with annual variation depending on breeding status in year t, but consistent across age classes, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year t.
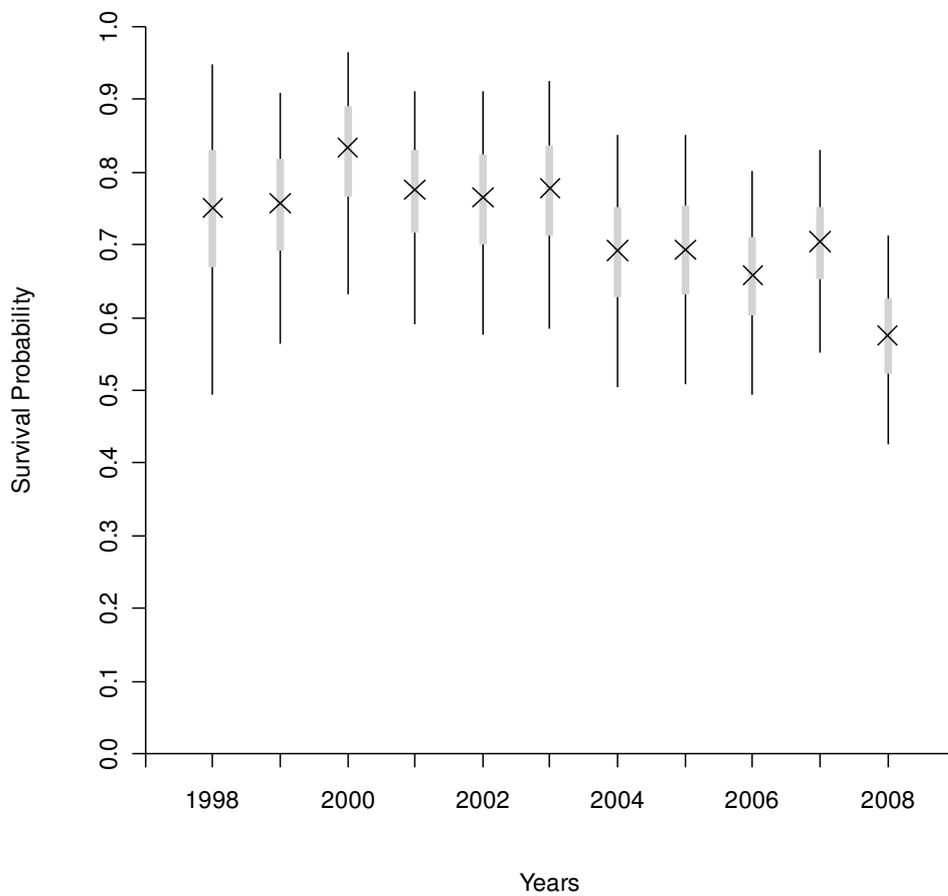
Figure 28: Posterior distribution for probability of breeding in year *t*+1 for individuals that were non-breeders aged 4-14 in year *t*, from model with annual variation depending on breeding status in year *t*, but consistent across age classes, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year *t*+1.
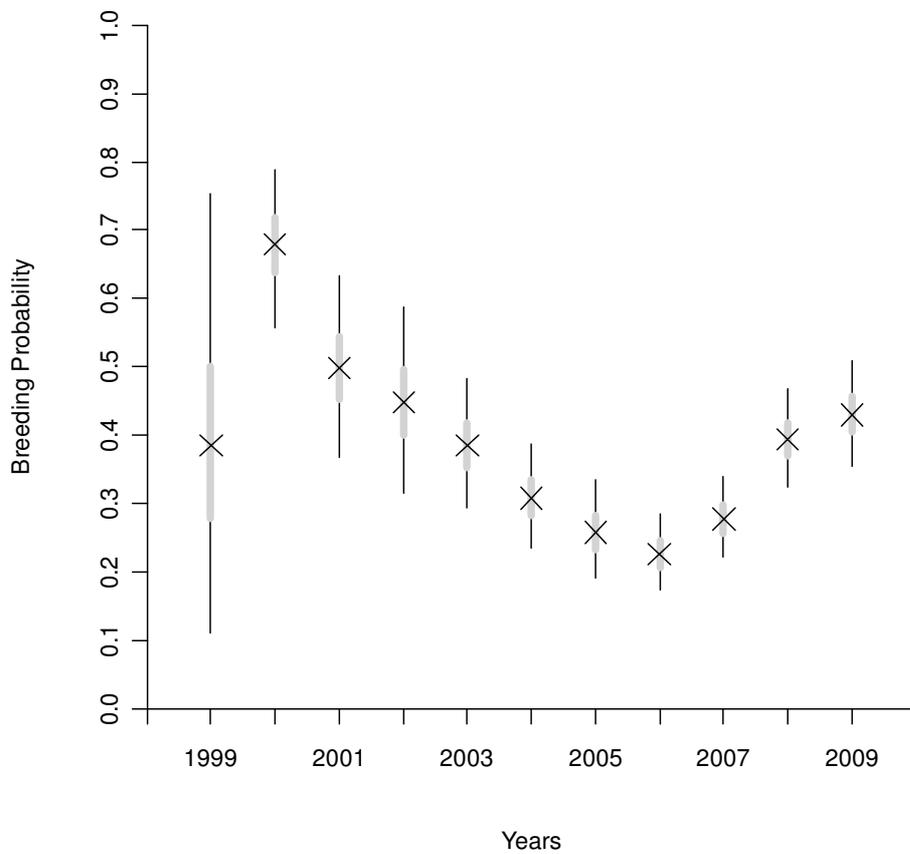
Figure 29: Posterior distribution for probability of breeding in year *t*+1 for individuals that were non-breeders aged 15+ in year *t*, from model with annual variation depending on breeding status in year *t*, but consistent across age classes, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year *t*+1
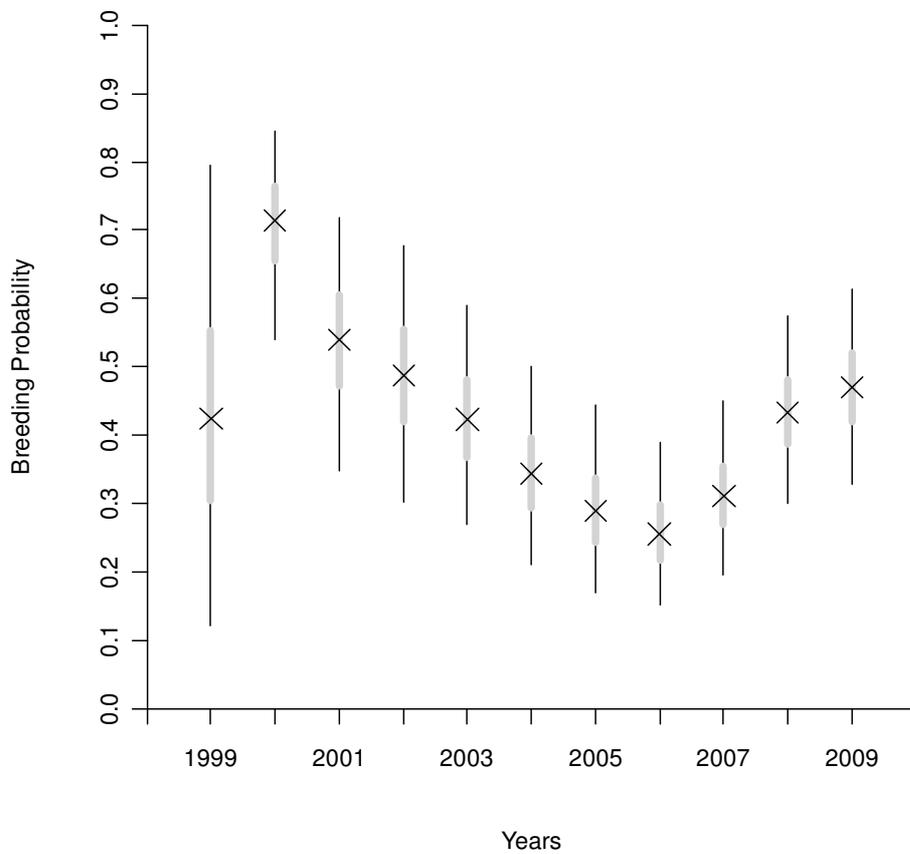
Figure 30: Posterior distribution for probability of breeding in year *t*+1 for individuals that were breeders aged 4-14 in year *t*, from model with annual variation depending on breeding status in year *t*, but consistent across age classes, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year *t*+1.
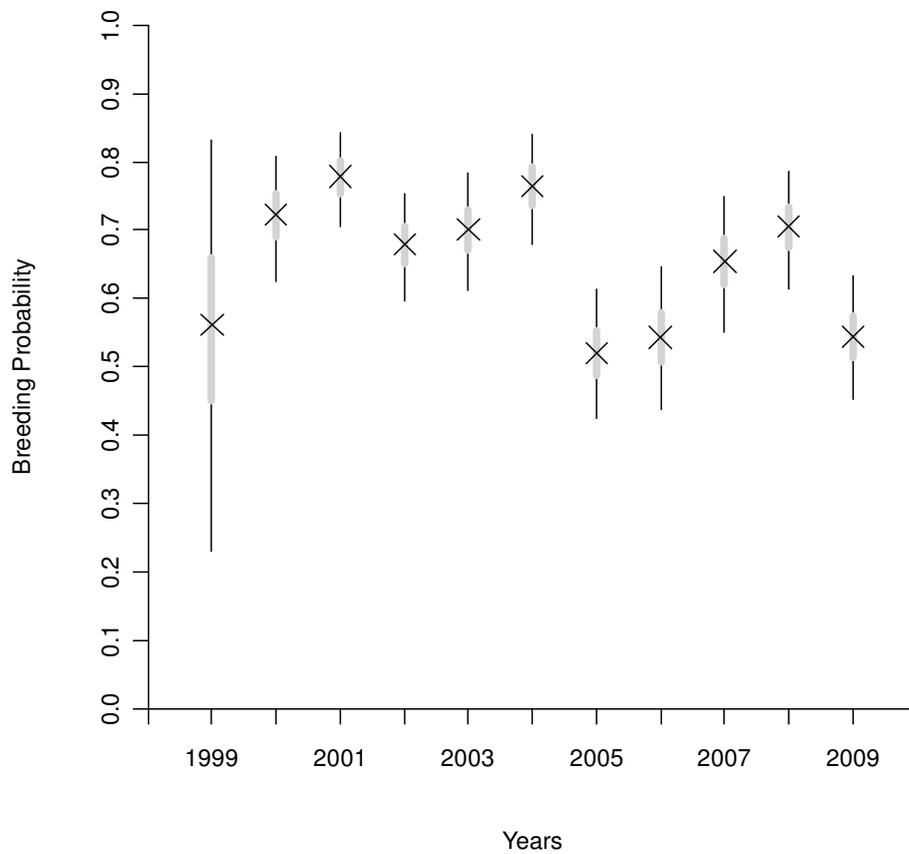
Figure 31: Posterior distribution for probability of breeding in year *t*+1 for individuals that were non-breeders aged 15+ in year *t*, from model with annual variation depending on breeding status in year *t*, but consistent across age classes, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season and indicate the year *t*+1.
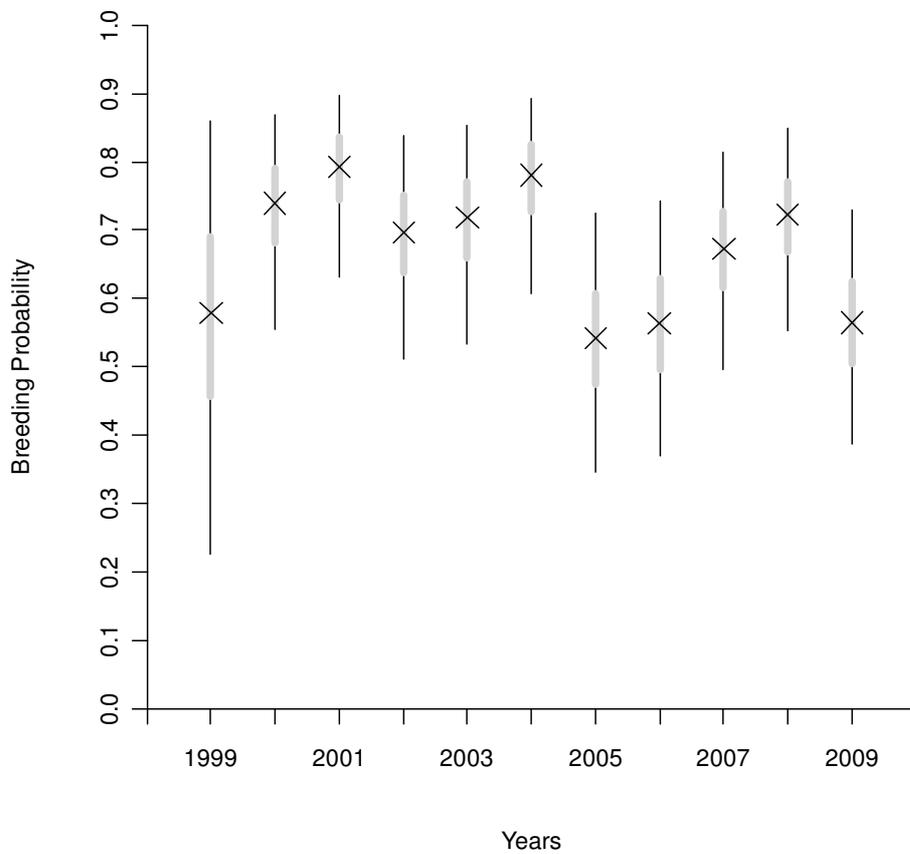
Figure 32: Posterior distribution for estimated number of females alive in year *t* belonging to cohorts that had been exposed to tagging. Model assumed annual variation depending on breeding status in year *t*-1, but consistent across age classes, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season.
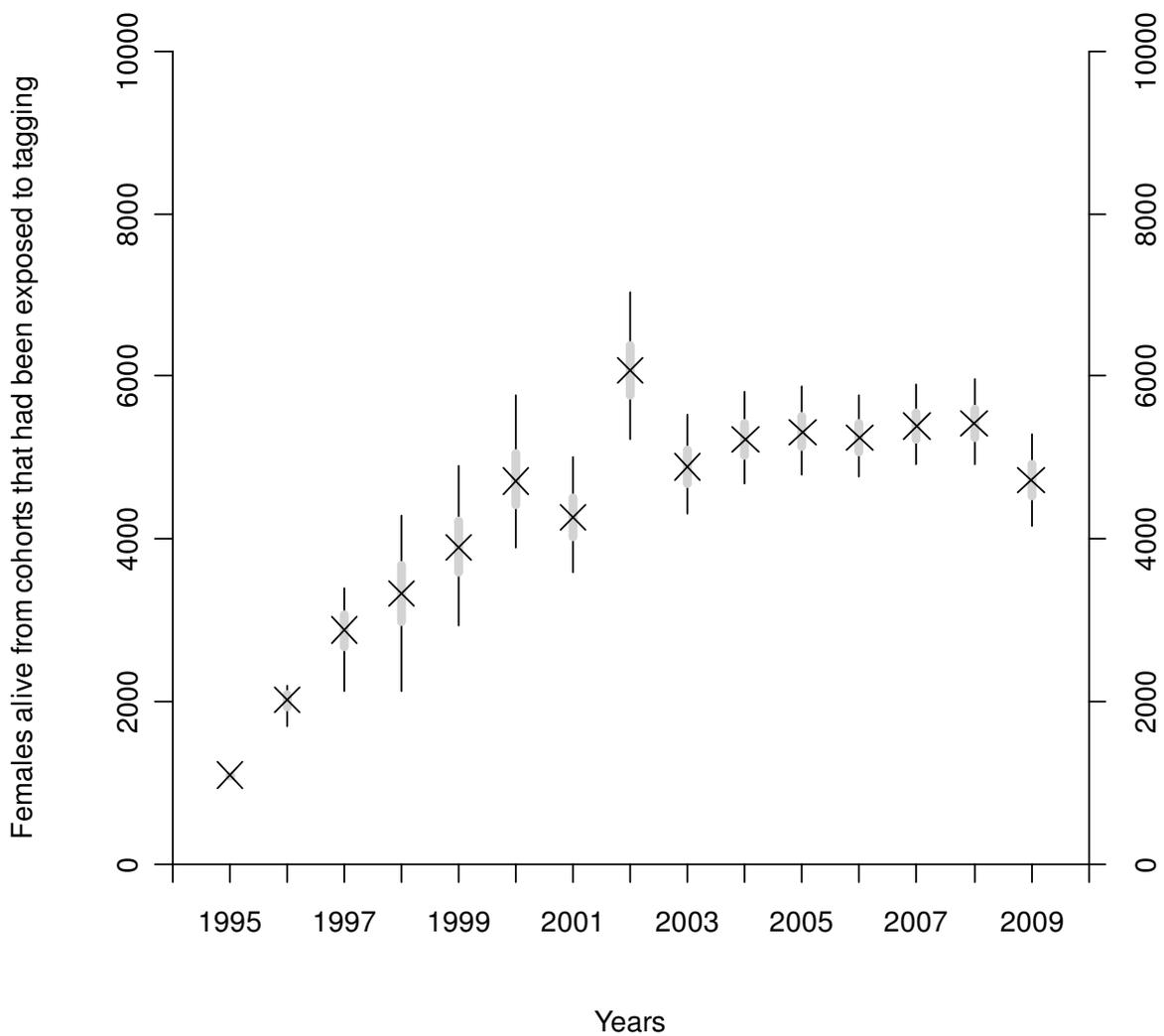
Figure 33: Posterior distribution for estimated number of females alive in year *t* belonging to cohorts that had been exposed to tagging. Model assumed annual variation depending on breeding status and age in year *t*-1, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey lines indicate the central 50% of the distribution and thin black lines indicate the central 95% of the distribution. Years are denoted in terms of the calendar year associated with the January portion of the field season.
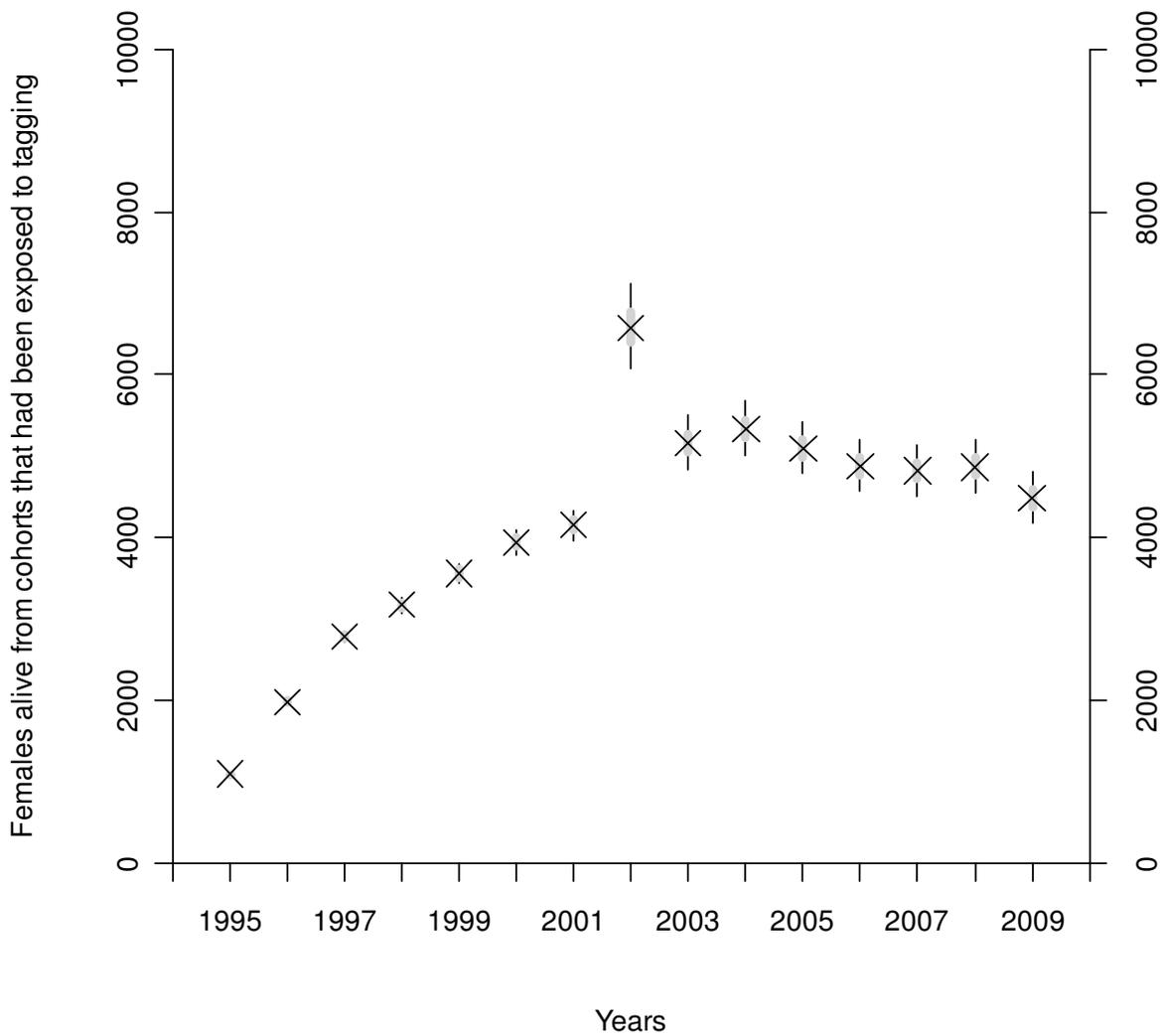
Tables

Table 1: Number of female New Zealand sea lions tagged or resighted each year, by age, from which resighting data was analysed. Percentages indicate percentage that were breeders in that year using the strict definition of breeder.

Age	1997/98	1998/99	1999/00	2000/01	2001/02	2002/03	2003/04	2004/05	2005/06	2006/07	2007/08	2008/09
Pup	256 (0%)	211 (0%)	239 (0%)	268 (0%)	160 (0%)	204 (0%)	224 (0%)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)
1	0 (-)	0 (-)	8 (0%)	8 (0%)	19 (0%)	9 (0%)	12 (0%)	6 (0%)	0 (-)	0 (-)	0 (-)	0 (-)
2	0 (-)	0 (-)	3 (0%)	10 (0%)	3 (0%)	14 (0%)	8 (0%)	17 (0%)	15 (0%)	0 (-)	0 (-)	0 (-)
3	0 (-)	0 (-)	0 (-)	16 (0%)	28 (0%)	23 (0%)	48 (0%)	18 (0%)	54 (0%)	18 (0%)	0 (-)	0 (-)
4	0 (-)	0 (-)	0 (-)	0 (-)	19 (5%)	52 (0%)	40 (8%)	58 (12%)	29 (0%)	66 (8%)	43 (0%)	0 (-)
5	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	35 (9%)	48 (29%)	41 (24%)	52 (25%)	31 (26%)	61 (44%)	41 (27%)
6	1 (100%)	62 (44%)	0 (-)	0 (-)	0 (-)	0 (-)	35 (14%)	42 (33%)	35 (49%)	56 (50%)	22 (77%)	59 (37%)
7	5 (100%)	68 (59%)	69 (74%)	0 (-)	0 (-)	0 (-)	0 (-)	17 (12%)	39 (33%)	37 (59%)	39 (67%)	23 (61%)
8	0 (-)	43 (65%)	74 (69%)	61 (84%)	0 (-)	0 (-)	0 (-)	0 (-)	19 (26%)	39 (41%)	27 (70%)	38 (42%)
9	0 (-)	23 (43%)	57 (82%)	70 (77%)	53 (60%)	0 (-)	0 (-)	0 (-)	0 (-)	26 (8%)	32 (38%)	29 (59%)
10	0 (-)	0 (-)	30 (73%)	40 (80%)	62 (53%)	50 (74%)	0 (-)	0 (-)	0 (-)	0 (-)	20 (5%)	32 (47%)
11	0 (-)	0 (-)	0 (-)	25 (68%)	27 (59%)	53 (55%)	51 (65%)	0 (-)	0 (-)	0 (-)	0 (-)	27 (26%)
12	0 (-)	0 (-)	0 (-)	0 (-)	15 (87%)	29 (76%)	45 (73%)	35 (46%)	0 (-)	0 (-)	0 (-)	0 (-)
13	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	17 (76%)	27 (63%)	35 (54%)	27 (41%)	0 (-)	0 (-)	0 (-)
14	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	13 (69%)	21 (29%)	25 (28%)	21 (43%)	0 (-)	0 (-)
15	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	9 (44%)	14 (50%)	25 (40%)	21 (52%)	0 (-)
16	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	9 (33%)	17 (53%)	20 (45%)	11 (36%)
17	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	4 (50%)	11 (36%)	11 (73%)
18	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	2 (50%)	10 (60%)
19	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	1 (0%)

Table 2: Median and central 95% credible interval for the mean and standard deviation (SD) of annual survival probabilities calculated on the logistic scale, by age-class and breeding status, using the strict definition of breeder.

	Age Class	Breeder	Non-breeder
Mean	0-3	-	1.11 (0.75, 1.52)
	4-14	2.54 (2.12, 3.1)	2.01 (1.62, 2.42)
	15+	1.10 (0.38, 1.95)	0.77 (0.19, 1.41)
SD	All	0.50 (0.09, 1.22)	0.54 (0.30, 1.10)

Table 3: Median and central 95% credible interval for the mean and standard deviation (SD) of annual breeding probabilities calculated on the logistic scale, by age-class and breeding status, using the strict definition of breeder. No annual variation is assumed for non-breeders aged 0-3.

	Age Class	Breeder	Non-breeder
Mean	0-3	-	-4.98 (-5.51, -4.52)
	4-14	0.50 (-0.04, 0.99)	-0.71 (-1.17, -0.24)
	15+	0.66 (-0.17, 1.53)	-0.61 (-1.33, 0.11)
SD	4+	0.65 (0.37, 1.28)	0.60 (0.35, 1.15)

Table 4: Median and central 95% credible interval from each model for the probability of number of tags in year t given the number of tags in year $t-1$, using the strict definition of breeder.

Tags at t-1	Tags at t	Probability
1	0	0.09 (0.08, 0.11)
	1	0.91 (0.89, 0.92)
2	0	0.07 (0.05, 0.09)
	1	0.15 (0.13, 0.17)
	2	0.78 (0.76, 0.80)

Table 5: Median and central 95% credible interval for the mean and standard deviation (SD) of annual survival probabilities calculated on the logistic scale, by age-class and breeding status, using the liberal definition of breeder.

	Age Class	Breeder	Non-breeder
Mean	0-3	-	1.14 (0.78, 1.60)
	4-14	2.50 (2.06, 3.10)	1.97 (1.58, 2.42)
	15+	1.00 (0.32, 1.86)	0.82 (0.19, 1.49)
SD	All	0.54 (0.17, 1.28)	0.57 (0.32, 1.15)

Table 6: Median and central 95% credible interval for the mean and standard deviation (SD) of annual breeding probabilities calculated on the logistic scale, by age-class and breeding status, using the liberal definition of breeder. No annual variation is assumed for non-breeders aged 0-3.

	Age Class	Breeder	Non-breeder
Mean	0-3	-	-4.98 (-5.53, -4.51)
	4-14	0.66 (0.20, 1.03)	-0.47 (-0.99, 0.01)
	15+	0.73 (-0.05, 1.50)	-0.32 (-1.04, 0.39)
SD	4+	0.54 (0.29, 1.07)	0.68 (0.40, 1.29)

Table 7: Median and central 95% credible interval from each model for the probability of number of tags in year t given the number of tags in year $t-1$, using the liberal definition of breeder.

Tags at t-1	Tags at t	Probability
1	0	0.09 (0.08, 0.11)
	1	0.91 (0.89, 0.92)
2	0	0.08 (0.06, 0.09)
	1	0.15 (0.13, 0.17)
	2	0.78 (0.76, 0.79)

Table 8: Assumed number of female pups that survived >8 weeks and number of older (pre-1998 cohorts) and younger females aged 4+ that were observed each year. This values were used to obtain ballpark estimate of population size.

Year	Pup Counts	Cohorts	
		<1998	≥1998
1995	1103		
1996	1195		
1997	1365		
1998	1175		
1999	1286		
2000	1345		
2001	1234		
2002	913	157	19
2003	1039	149	87
2004	1174	136	123
2005	1017	100	158
2006	904	75	174
2007	1044	67	255
2008	1011	54	244
2009	705	33	270

Appendix 1

Annual pup production for the Auckland Islands 1996/97 to 2008/09. Arrows indicate the years mass mortality events occurred.
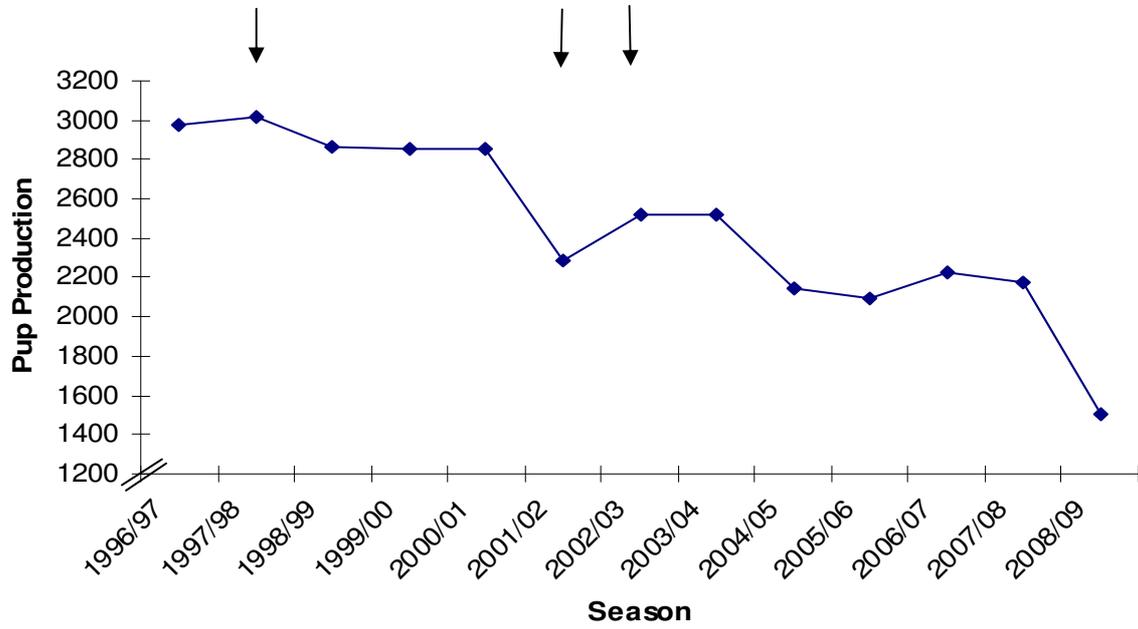
Appendix 2

WinBUGS code for fitting model to the tag-resight data. Comments in WinBUGS are indicated by hashes.

PBreed is an array that contains the probability of breeding/not breeding in the current year, indexed by year, age, breeding status in the previous year (1=no, 2=yes), currently alive (1=no, 2=yes), breeding outcome in current year (1=no, 2=yes).

bBreed is an array containing the probability of breeding in the current year, indexed by year, breeding status in the previous year (1=no, 2=yes) and age group (1=0-3, 2=4-14, 3=15+).

S is an array that contains the probability of surviving/dying in the current year, indexed by year, age, breeding status in the previous year (1=no, 2=yes), currently alive (1=no, 2=yes), survival outcome in current year (1=no, 2=yes).

bS is an array containing the probability of surviving the current year, indexed by year, breeding status in the previous year (1=no, 2=yes) and age group (1=0-3, 2=4-14, 3=15+).

```
model {
### define parameters for model
        for (jj in 1:14) {              ## jj is indexing year
                for (aa in 1:4) {       ## aa is indexing age
                        PBreed[jj,aa,1,1,2] <- 0                        ##PBreed[Bred(t-1),Alive(t),Bred(t)]
                        PBreed[jj,aa,1,2,2] <- bBreed[jj,1,1]
                        PBreed[jj,aa,2,1,2] <- 0
                        PBreed[jj,aa,2,2,2] <- 0

                        PBreed[jj,aa,1,1,1] <- 1-PBreed[jj,aa,1,1,2]
                        PBreed[jj,aa,1,2,1] <- 1-PBreed[jj,aa,1,2,2]
                        PBreed[jj,aa,2,1,1] <- 1-PBreed[jj,aa,2,1,2]
```

```
        PBreed[jj,aa,2,2,1] <- 1-PBreed[jj,aa,2,2,2]

        S[jj,aa,1,1,2] <- 0                              ##S[Bred(t-1),Alive(t-1),Alive(t)]
        S[jj,aa,1,2,2] <- bS[jj,1,1]
        S[jj,aa,2,1,2] <- 0
        S[jj,aa,2,2,2] <- 0

        S[jj,aa,1,1,1] <-1-S[jj,aa,1,1,2]
        S[jj,aa,1,2,1] <-1-S[jj,aa,1,2,2]
        S[jj,aa,2,1,1] <-1-S[jj,aa,2,1,2]
        S[jj,aa,2,2,1] <-1-S[jj,aa,2,2,2]
}

for (aa in 5:15) {
        PBreed[jj,aa,1,1,2] <- 0                         ##PBreed[Bred(t-1),Alive(t),Bred(t)]
        PBreed[jj,aa,1,2,2] <- bBreed[jj,1,2]
        PBreed[jj,aa,2,1,2] <- 0
        PBreed[jj,aa,2,2,2] <- bBreed[jj,2,2]

        PBreed[jj,aa,1,1,1] <- 1-PBreed[jj,aa,1,1,2]
        PBreed[jj,aa,1,2,1] <- 1-PBreed[jj,aa,1,2,2]
        PBreed[jj,aa,2,1,1] <- 1-PBreed[jj,aa,2,1,2]
        PBreed[jj,aa,2,2,1] <- 1-PBreed[jj,aa,2,2,2]

        S[jj,aa,1,1,2] <- 0                              ##S[Bred(t-1),Alive(t-1),Alive(t)]
        S[jj,aa,1,2,2] <- bS[jj,1,2]
        S[jj,aa,2,1,2] <- 0
        S[jj,aa,2,2,2] <- bS[jj,2,2]

        S[jj,aa,1,1,1] <-1-S[jj,aa,1,1,2]
        S[jj,aa,1,2,1] <-1-S[jj,aa,1,2,2]
        S[jj,aa,2,1,1] <-1-S[jj,aa,2,1,2]
        S[jj,aa,2,2,1] <-1-S[jj,aa,2,2,2]
}


for (aa in 16:20) {
        PBreed[jj,aa,1,1,2] <- 0                         ##PBreed[Bred(t-1),Alive(t),Bred(t)]
        PBreed[jj,aa,1,2,2] <- bBreed[jj,1,3]
```

```
                    PBreed[jj,aa,2,1,2] <- 0
                    PBreed[jj,aa,2,2,2] <- bBreed[jj,2,3]

                    PBreed[jj,aa,1,1,1] <- 1-PBreed[jj,aa,1,1,2]
                    PBreed[jj,aa,1,2,1] <- 1-PBreed[jj,aa,1,2,2]
                    PBreed[jj,aa,2,1,1] <- 1-PBreed[jj,aa,2,1,2]
                    PBreed[jj,aa,2,2,1] <- 1-PBreed[jj,aa,2,2,2]

                    S[jj,aa,1,1,2] <- 0                              ##S[Bred(t-1),Alive(t-1),Alive(t)]
                    S[jj,aa,1,2,2] <- bS[jj,1,3]
                    S[jj,aa,2,1,2] <- 0
                    S[jj,aa,2,2,2] <- bS[jj,2,3]

                    S[jj,aa,1,1,1] <-1-S[jj,aa,1,1,2]
                    S[jj,aa,1,2,1] <-1-S[jj,aa,1,2,2]
                    S[jj,aa,2,1,1] <-1-S[jj,aa,2,1,2]
                    S[jj,aa,2,2,1] <-1-S[jj,aa,2,2,2]
            }


## juvenile survival and breeding probs
            for (aa in 1:2) {
                    logit(bBreed[jj,aa,1]) <- muBreed[aa,1]
                    logit(bS[jj,aa,1]) <- muS[aa,1] + eS[jj,aa,1]

                    eS[jj,aa,1]~dnorm(0,tauS[aa,1])I(-12,12)
                    eBreed[jj,aa,1]~dnorm(0,tauBreed[aa,1])I(-12,12)
            }
## adult survival and breeding probs
            for (ii in 2:3) {
                    for (aa in 1:2) {
                            logit(bBreed[jj,aa,ii]) <- muBreed[aa,ii] + eBreed[jj,aa,1]
                            logit(bS[jj,aa,ii]) <- muS[aa,ii] + eS[jj,aa,1]

                            eBreed[jj,aa,ii]~dnorm(0,tauBreed[aa,ii])
                            eS[jj,aa,ii]~dnorm(0,tauS[aa,ii])
                    }
            }
        } #### end year loop
```

```
### specify survival and breeding related priors
    for (aa in 1:2) {
        muBreed[aa,1] ~ dnorm(0, 0.07)
        muS[aa,1] ~ dnorm(0, 0.07)

        sdS[aa,1] ~ dunif(0,10)
        tauS[aa,1] <- 1/(sdS[aa,1]*sdS[aa,1])

        sdBreed[aa,1] ~ dunif(0,10)
        tauBreed[aa,1] <- 1/(sdBreed[aa,1]*sdBreed[aa,1])

    }


    for (ii in 2:3) {
        for (aa in 1:2) {
            muBreed[aa,ii] ~ dnorm(0, 0.07)
            muS[aa,ii] ~ dnorm(0, 0.07)

            sdBreed[aa,ii] ~ dunif(0,10)
            sdS[aa,ii] ~ dunif(0,10)
            tauBreed[aa,ii] <- 1/(sdBreed[aa,ii]*sdBreed[aa,ii])
            tauS[aa,ii] <- 1/(sdS[aa,ii]*sdS[aa,ii])
        }
    }


### Probability of tag loss, PTag. Indexed by number of tags (+1) in t-1 and t
    PTag[1,1] <- 1
    PTag[1,2] <- 0
    PTag[1,3] <- 0

    PTag[2,1] <- 1 - PTag[2,2]
    PTag[2,2] ~ dunif(0,1)
    PTag[2,3] <- 0

    PTag[3,1:3] ~ ddirch(alpha3[])
```

```
### resighting probabilities
      ## p[ind,tags,bred,alive,time]
      for (ii in 1:2133) {
            for(jj in (FirstCap[ii]+1):LastCap[ii]) {
                  p[ii,1,1,1,jj] <- 0
                  p[ii,1,2,1,jj] <- 0
                  p[ii,2,1,1,jj] <- 0
                  p[ii,2,2,1,jj] <- 0
                  p[ii,3,1,1,jj] <- 0
                  p[ii,3,2,1,jj] <- 0

                  p[ii,1,1,2,jj] <- Brand[ii]*pBrand[AgeCat[Age98[ii]+jj],1,jj] + (1-Brand[ii])*Chip[ii]*pChip[AgeCat[Age98[ii]+jj],1,jj]
                  p[ii,1,2,2,jj] <- Brand[ii]*pBrand[AgeCat[Age98[ii]+jj],2,jj] + (1-Brand[ii])*Chip[ii]*pChip[AgeCat[Age98[ii]+jj],2,jj]
                  p[ii,2,1,2,jj] <- Brand[ii]*pBrand[AgeCat[Age98[ii]+jj],1,jj] + (1-Brand[ii])*pT1[AgeCat[Age98[ii]+jj],1,jj]
                  p[ii,2,2,2,jj] <- Brand[ii]*pBrand[AgeCat[Age98[ii]+jj],2,jj] + (1-Brand[ii])*pT1[AgeCat[Age98[ii]+jj],2,jj]
                  p[ii,3,1,2,jj] <- Brand[ii]*pBrand[AgeCat[Age98[ii]+jj],1,jj] + (1-Brand[ii])*pT2[AgeCat[Age98[ii]+jj],1,jj]
                  p[ii,3,2,2,jj] <- Brand[ii]*pBrand[AgeCat[Age98[ii]+jj],2,jj] + (1-Brand[ii])*pT2[AgeCat[Age98[ii]+jj],2,jj]


            }
      }

## priors for resighting probabilities
      for (aa in 1:3) {
            for (ii in 1:2) {
                  for (jj in 1:12) {
                        pBrand[aa,ii,jj] ~ dunif(0,1)
                        pChip[aa,ii,jj] ~ dunif(0,1)
                        pT1[aa,ii,jj] ~ dunif(0,1)
                        logit(pT2[aa,ii,jj]) <- logit(pT1[aa,ii,jj]) + a
                  }
            }
      }


      a ~ dnorm(0,0.01) ## increase in sightability with second tag
```

```
####################################################################################################
### actual model fitting

    for (ii in 1:2133) {           ### individuals loop
        for(jj in 1:(FirstCap[ii]-1)) {
            Alive[ii,jj] <- 1
            for (kk in 1:12){
                C_Alive[ii,jj,kk] <- 0
            }
            Cap.Pred[ii,jj] <- 0
        }

        Alive[ii,FirstCap[ii]] <- 2

        for (kk in 1:12){
            C_Alive[ii,FirstCap[ii],kk] <- equals(kk,FirstCap[ii])
        }

        logLike[ii, FirstCap[ii]] <- 0;

        Alive.Pred[ii,FirstCap[ii]] <- Alive[ii,FirstCap[ii]]
        Bred.Pred[ii,FirstCap[ii]] <- Bred[ii,FirstCap[ii]]
        Tags.Pred[ii,FirstCap[ii]] <- Tags[ii,FirstCap[ii]]
        Cap.Pred[ii,FirstCap[ii]] <- Cap[ii,FirstCap[ii]]

        logLike.Pred[ii, FirstCap[ii]] <- 0;


        for (jj in (FirstCap[ii]+1):LastCap[ii]) {
            Alive[ii,jj] ~ dcat(S[jj-1,(Age98[ii]+jj-1),Bred[ii,jj-1], Alive[ii,jj-1], ])
            Bred[ii,jj] ~ dcat(PBreed[jj-1,(Age98[ii]+jj-1),Bred[ii,jj-1], Alive[ii,jj], ])
            Tags[ii,jj] ~ dcat(PTag[Tags[ii,jj-1], ])
            Cap[ii,jj] ~ dbin(p[ii,Tags[ii,jj], Bred[ii,jj], Alive[ii,jj],jj], T[jj])

            logLike[ii,jj] <- logLike[ii,jj-1] + max(-99999, log(S[jj-1,(Age98[ii]+jj-1),Bred[ii,jj-1], Alive[ii,jj-1], Alive[ii,jj]]) )+
                            max(-99999, log(PBreed[jj-1,(Age98[ii]+jj-1),Bred[ii,jj-1], Alive[ii,jj], Bred[ii,jj]]) )+
                            max(-99999, log(PTag[Tags[ii,jj-1], Tags[ii,jj]]) )+
                            logfact(Cap[ii,jj]) + logfact(T[jj]-Cap[ii,jj]) - logfact(T[jj]) +
                            Cap[ii,jj]*max(-99999, log(p[ii,Tags[ii,jj], Bred[ii,jj], Alive[ii,jj],jj]) )+
```

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```
                                    (T[jj]-Cap[ii,jj])*max(-99999, log(1-p[ii,Tags[ii,jj], Bred[ii,jj], Alive[ii,jj],jj]) )


### generating alternative data
        Alive.Pred[ii,jj] ~ dcat(S[jj-1,(Age98[ii]+jj-1),Bred.Pred[ii,jj-1], Alive.Pred[ii,jj-1], ])
        Bred.Pred[ii,jj] ~ dcat(PBreed[jj-1,(Age98[ii]+jj-1),Bred.Pred[ii,jj-1], Alive.Pred[ii,jj], ])
        Tags.Pred[ii,jj] ~ dcat(PTag[Tags.Pred[ii,jj-1], ])
        Cap.Pred[ii,jj] ~ dbin(p[ii,Tags.Pred[ii,jj], Bred.Pred[ii,jj], Alive.Pred[ii,jj],jj], T[jj])

        logLike.Pred[ii,jj] <- logLike.Pred[ii,jj-1] + max(-99999, log(S[jj-1,(Age98[ii]+jj-1),Bred.Pred[ii,jj-1], Alive.Pred[ii,jj-1], Alive.Pred[ii,jj]])) +
                               max(-99999, log(PBreed[jj-1,(Age98[ii]+jj-1),Bred.Pred[ii,jj-1], Alive.Pred[ii,jj], Bred.Pred[ii,jj]]) )+
                               max(-99999, log(PTag[Tags.Pred[ii,jj-1], Tags.Pred[ii,jj]]) )+
                               logfact(Cap.Pred[ii,jj]) + logfact(T[jj]-Cap.Pred[ii,jj]) - logfact(T[jj]) +
                               Cap.Pred[ii,jj]*max(-99999, log(p[ii,Tags.Pred[ii,jj], Bred.Pred[ii,jj], Alive.Pred[ii,jj],jj]) )+
                               (T[jj]-Cap.Pred[ii,jj])*max(-99999, log(1-p[ii,Tags.Pred[ii,jj], Bred.Pred[ii,jj], Alive.Pred[ii,jj],jj]) )


        }

        for (jj in (LastCap[ii]+1):12) {
                logLike[ii,jj] <- logLike[ii,jj-1]
                logLike.Pred[ii,jj] <- logLike.Pred[ii,jj-1]
        }

    }  ## end individual loop

    Dev <- -2*sum(logLike[, 12])
    Dev.Pred <- -2*sum(logLike.Pred[, 12])
    p.value <- step(Dev.Pred-Dev)

}  ### end model
```