Estimation of Demographic Parameters for New Zealand Sea Lions Breeding on the Auckland Islands
- Final Report: 1997/98-2009/10

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Table of Contents

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 2009/10 field season (MacKenzie 2009, 2010). In addition to the estimation models agreed upon previously, models that allow the number of resights per season to follow a zero-inflated binomial distribution, and logit-linear relationships with age for the 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, **T** because of the multiple potential outcomes (eqn 3).

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

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

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

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 (MacKenzie 2009, 2010), 3 age classes are considered here: 0-3, 4-14, 15+. In addition, logit-linear relationships were also considered for animals aged 4+ (i.e., parameters where equal within the 0-3 age group, then assumed a linear trend on the logistic scale for females aged 4+). 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).

Annual variation in the demographic parameters for the older cohorts was included by assuming variation that was different depending upon breeding status in previous year, but not age. 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:

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

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

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.

In addition, a zero-inflated binomial distribution was also considered for the number of resights per season. That is, some fraction of females will not be sighted in a season, with the number of resights for the rest of the females following a binomial distribution. The fraction of females whose sightings followed a binomial distribution was defined to be $\psi_{a,t,b}$ where a indicates age class (i.e., 0-3, 4-14, and 15+ was used regardless of assumed relationship with age for demographic parameters), t indicates year and b indicates breeding status in that year. Three models were considered with respect to this zero-inflation factor:

1. $\psi_{a,t,b} = 1$, i.e., number of sightings for all females came from a binomial distribution
2. $\psi_{a,b}$, i.e., the zero-inflation factor varied by age classes and breeding status only.
3. $\psi_{a,t,b}$, i.e., as for 2, but with annual variation as well

In all, a total of six models were fit the data. That is, for each of the 3 models for the zero-inflation factor, either the 3 age-classes, or the logit-linear relationship with age was used for the demographic parameters.

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 25,000 iterations were run and checked for convergence and good mixing. Values from the final 20,000 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 used to fit the model to 3 age classes and a time-constant zero-inflation factor to the data has been provided in Appendix 1 as an example.

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-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 and 2009/2010 field seasons, along with all resightings for females tagged as pups in 2003/04 and 2004/5 (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).

The data used has been provided to the Department of Conservation as an Excel spreadsheet and is available on request from the Manager, Marine Conservation Services (e-mail csp@doc.govt.nz).

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.

Posterior distributions of deviance values and deviance-based Bayesian p-values for each model are presented in Figure 8 and 9. Clearly the models that include some zero-inflation parameter for the number of sightings per year have a much lower range of deviance vales (Figure 8), indicating they are much better models for the observed data. The additional number of parameters associated with estimating the zero-inflation parameters is 5 for model where this was assumed to be constant in time or 60 where it varied annually. The Bayesian p-values are very small for the models with no zero-inflation factor indicating those models are not a good fit for the data, but there is no indication of poor model fit for the other models. These results clearly indicate a problem with the models that assume the number of sightings follows a binomial distribution, a result that has not been observed previously in the 2008 and 2009 analyses. There is little to separate the other 4 models and visual inspection of the demographic parameter estimates suggests that inclusion of annual variation in the zero-inflation factor has little effect hence only the results of the 2 simpler models where zero-inflation factor varied by age class and breeding status are presented here.

Figures 10-18 present the posterior distributions for the demographic parameters from the model using the three age classes, while Figures 19-31 present the posterior distributions for the demographic parameters from the model using a logit-linear relationship with age for females aged 4+.

Figures 10-12 present the posterior distributions for the probability of surviving from year *t* to *t*+1 for females that were non-breeders in year *t*. There appears to be a relatively large degree of annual variation with survival in the 4-14 age class appearing to be higher than the other classes. In comparison with females that bred in year *t* (Figures 13-14), survival for non-breeders appears to be generally lower and more variable. Figures 15-16 contain the posterior distribution for the probability of breeding in year *t*+1, given a female was a non-breeder in year *t*. For non-breeders, breeding probability was estimated to be lower in the mid-2000’s compared to other times, with probabilities being slightly lower for non-breeders aged 4-14 compared to those aged 15+. For females that were breeders in year *t*, in Figures 17-18 there is no indication of a temporal pattern with breeding probability being slightly higher for females in the 4-14 age class compare to those aged 15+. Overall, the breeding probabilities are higher for those females that bred the previous year compared to those that did not.

Very similar temporal patterns in demographic parameters were obtained from the model using a logit-linear relationship with age for females age 4+ (Figures 19-23, 26-29) instead of age classes. For comparison with the results from the model that used age classes, the posterior distributions for females age 9 and 18 have been presented. Figure 24 indicates the estimated relationship for the probability of surviving from year *t* to *t*+1 for females that were non-breeders in year *t*, and similarly Figure 25 is for females that bred in year *t*. Again, breeders appear to have higher survival than non-breeders, and in both cases survival appears to decline with age. For females that were non-breeders in year *t*, the probability of breeding in year *t*+1 is estimated to increase with age (Figure 30), but slightly decline with age if a female was a breeder in year *t* (Figure 31).

Tag loss and retention probabilities (per year) rates were very similar for the 2 main models being considered and are given in Table 1. 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., $0.04 \neq 0.11^2$). 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'

The models that used a zero-inflated binomial distribution for the number of resightings each year provided a much better fit to the data than those that did not (Figure 32), and also had less extreme Bayesain p-values (Figure 33).

As has been observed in previous analyses (MacKenzie 2009, 2010), the main appreciable difference on the demographic parameters with using a more liberal definition of breeder is that breeding probabilities are slightly higher compared using a stricter definition (Figure 32-55). There is, however, an apparent anomaly for the estimated breeding probability in 2010 of females that had not bred in the previous year (i.e., Figures 39-40, 50-51), with the estimated rate being unusually low. WinBUGS code and data have been verified as correct, and consistent results are achieved when using alternative starting values for the MCMC analysis. This leads to the conclusion that there is some combination of factors (most likely data-related) causing the MCMC analysis to 'prefer' the unusually low value for 2010, though the exact cause is undetermined at this stage. The addition of data from the 2010/11 field season may shed some light on the cause of this result.

References

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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.

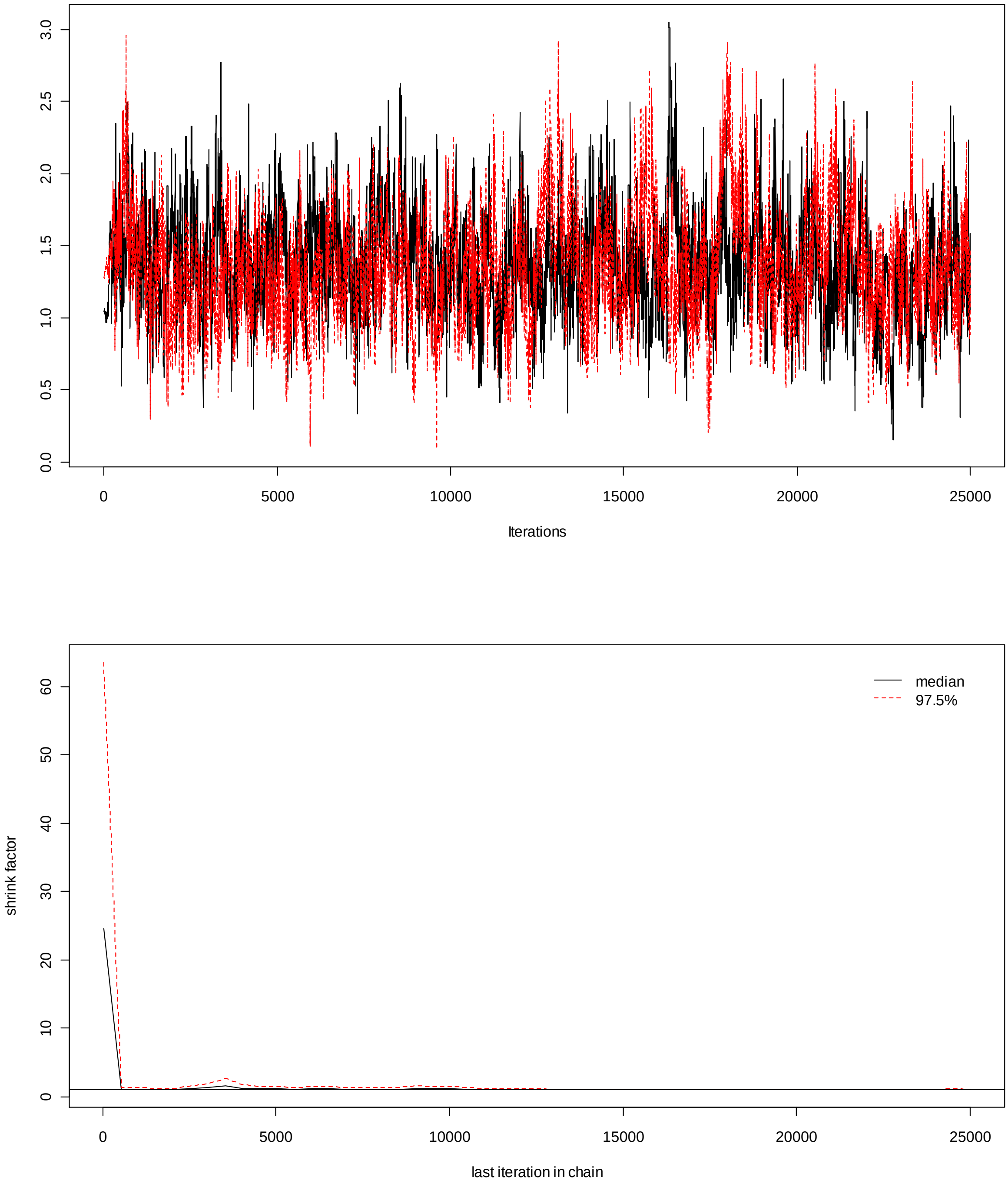


Figure 2: Example diagnostic plots of mean annual breeding probability for females that did bred and were aged 4-14 in previous year. Upper panel is a trace plot of the 2 chains and lower panel is the Gelman-Rubin-Brooks plot for convergence.

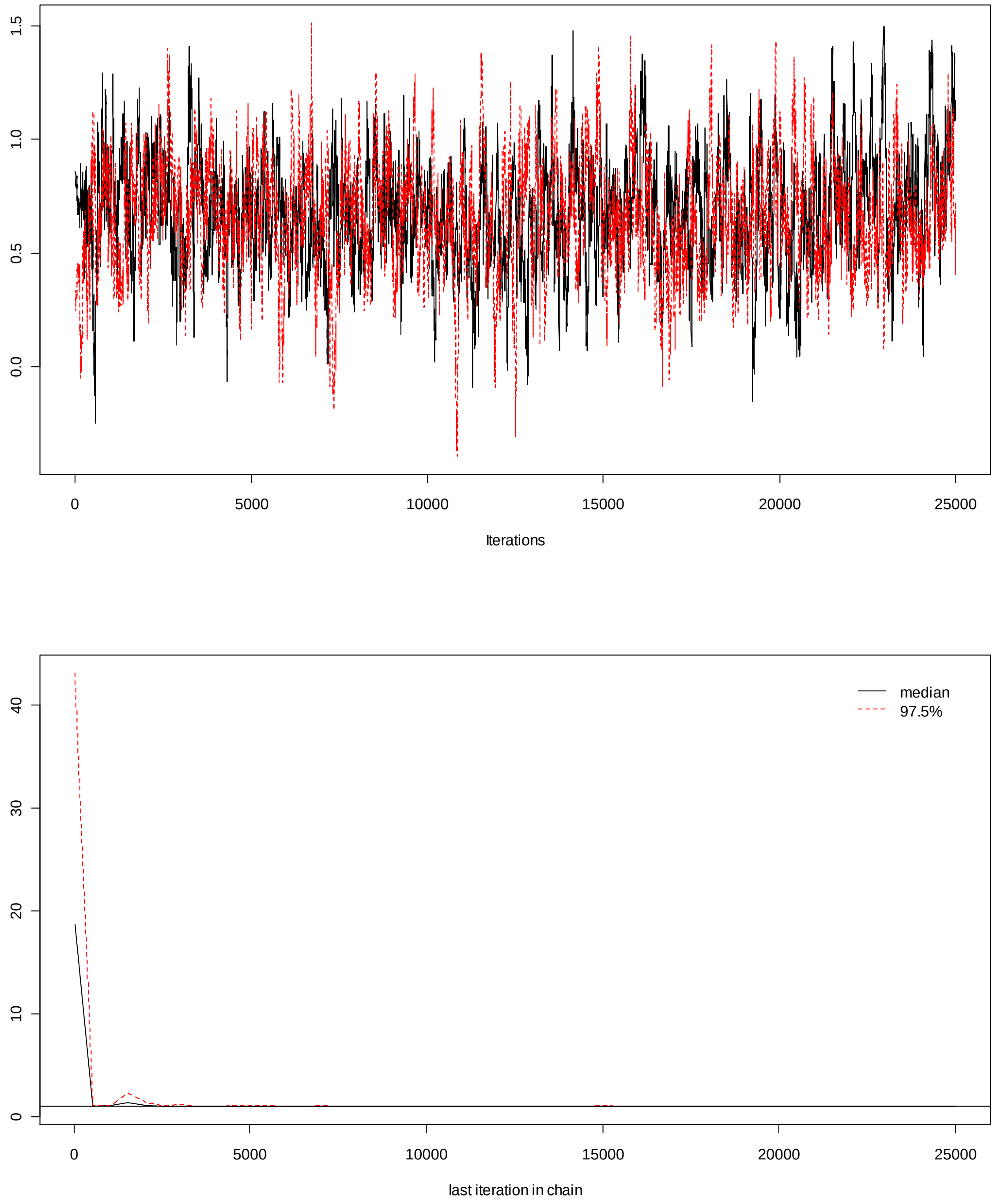


Figure 3: Example diagnostic plots of the standard deviation of annual survival for females that bred in the previous year. Upper panel is a trace plot of the 2 chains and lower panel is the Gelman-Rubin-Brooks plot for convergence.

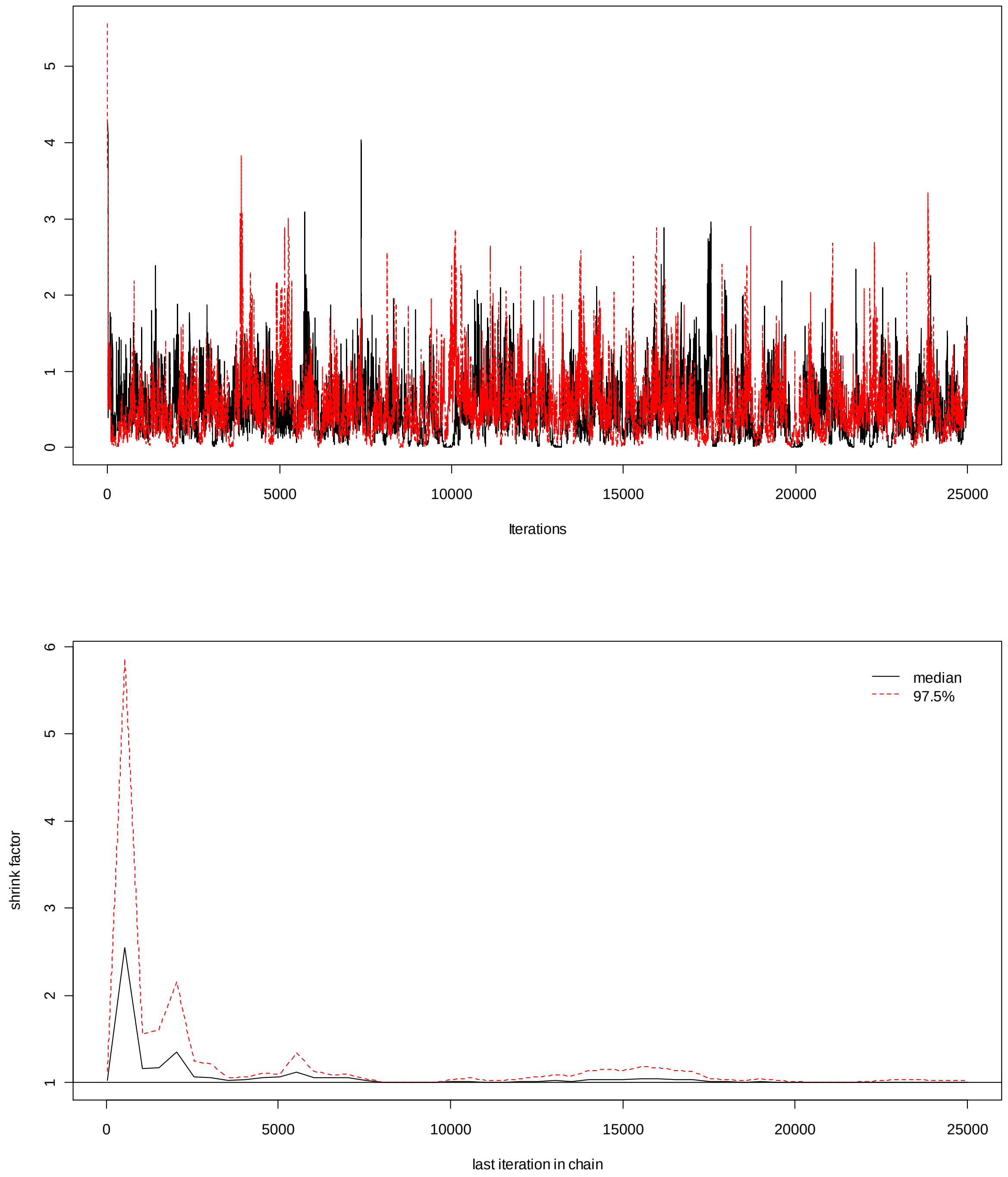


Figure 4: Posterior distribution for the daily probability of sighting a branded individual in each year by age class. Resight probabilities for which there was no information in the data are not indicated. Grey-shaded distributions indicate non-breeders and red-shaded distributions breeders. Years are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

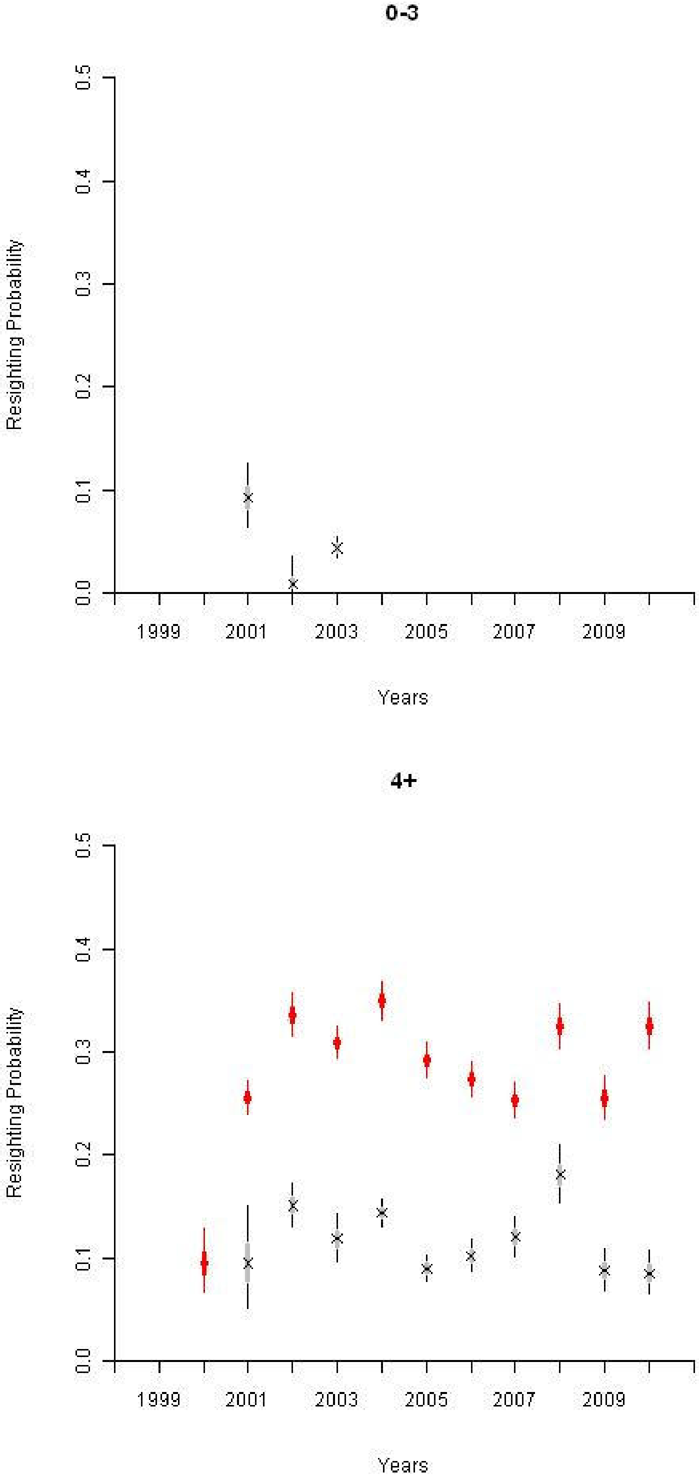


Figure 5: Posterior distribution for the daily probability of sighting a PIT tagged individual with no flipper tags in each year by age class. Resight probabilities for which there was no information in the data are not indicated. Grey-shaded distributions indicate non-breeders and red-shaded distributions breeders. Years are denoted in terms of the calendar year associated with the January portion of the field season.

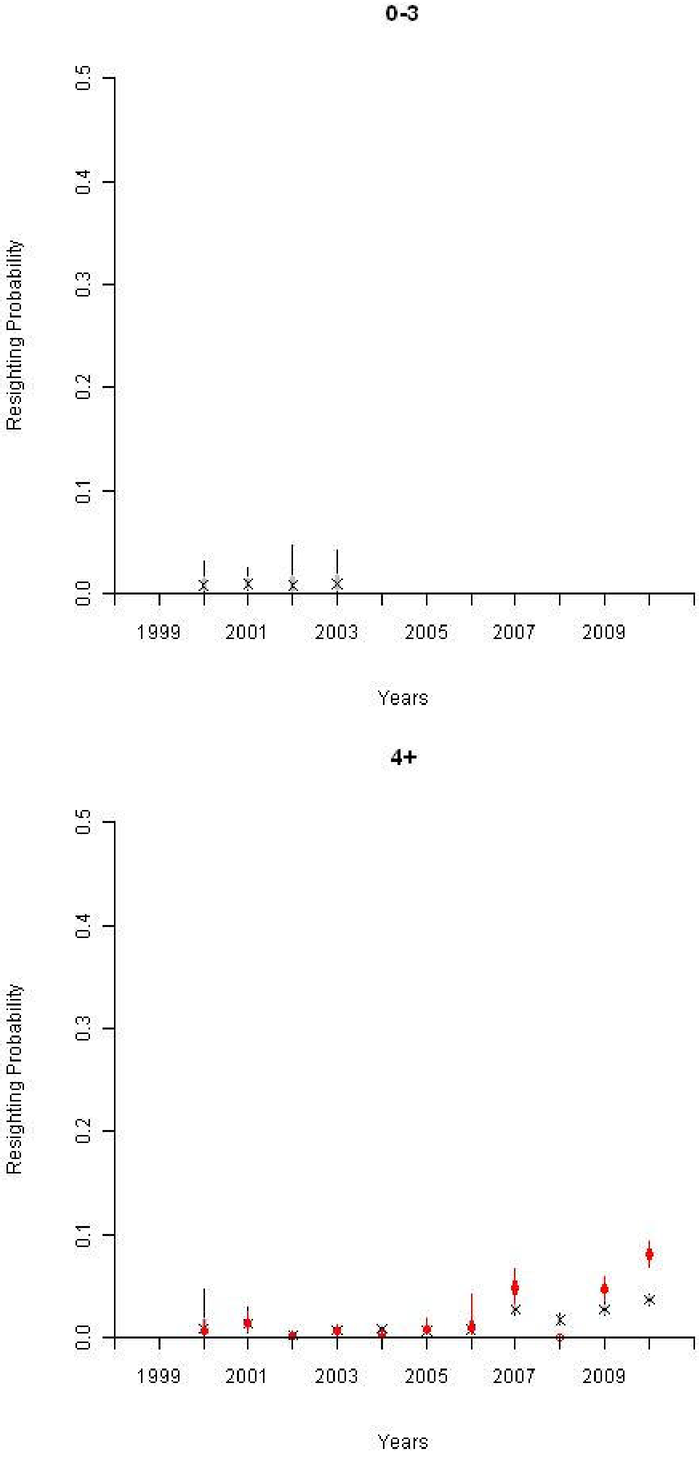


Figure 6: Posterior distribution for the daily probability of sighting an individual with 1 flipper tag in each year by age class. Resight probabilities for which there was no information in the data are not indicated. Grey-shaded distributions indicate non-breeders and red-shaded distributions breeders. Years are denoted in terms of the calendar year associated with the January portion of the field season.

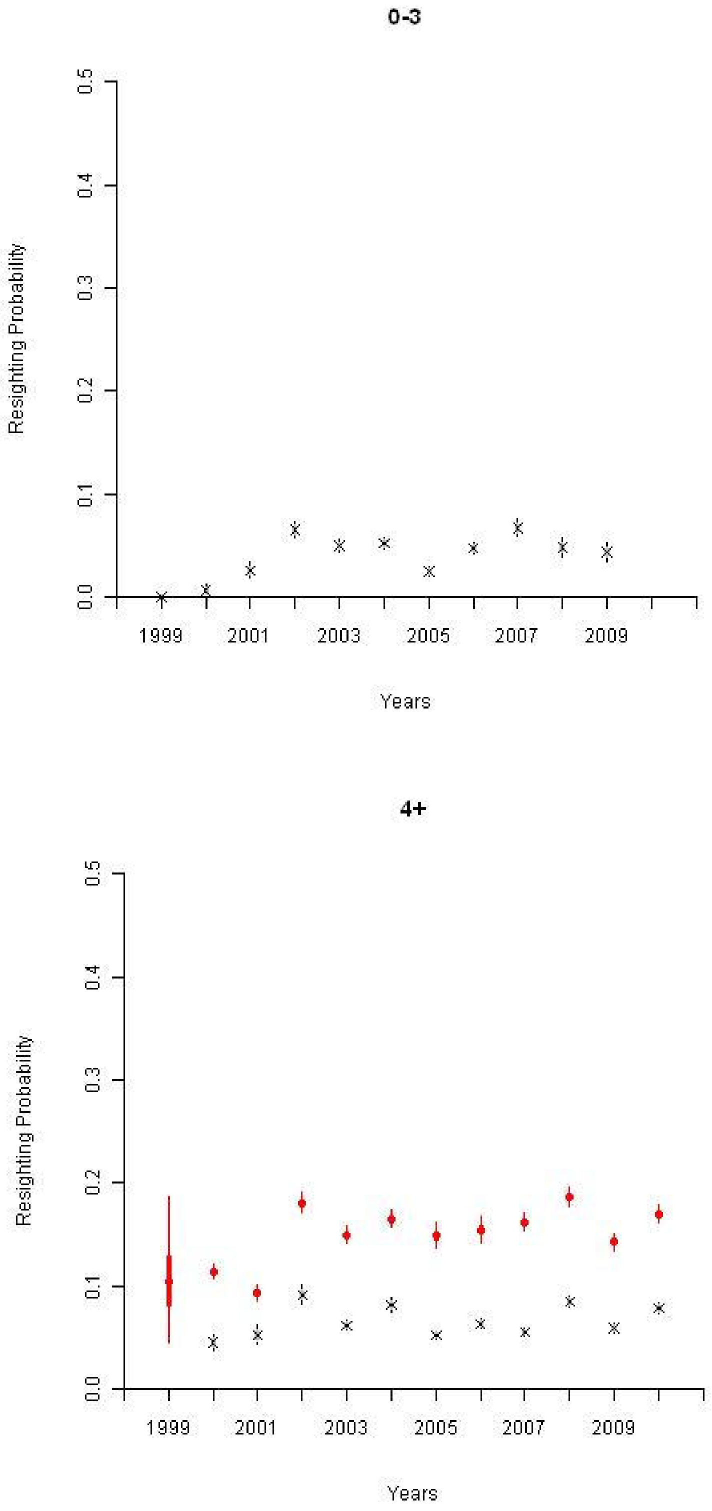


Figure 7: Posterior distribution for the daily probability of sighting an individual with 2 flipper tags in each year by age class. Resight probabilities for which there was no information in the data are not indicated. Grey-shaded distributions indicate non-breeders and red-shaded distributions breeders.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

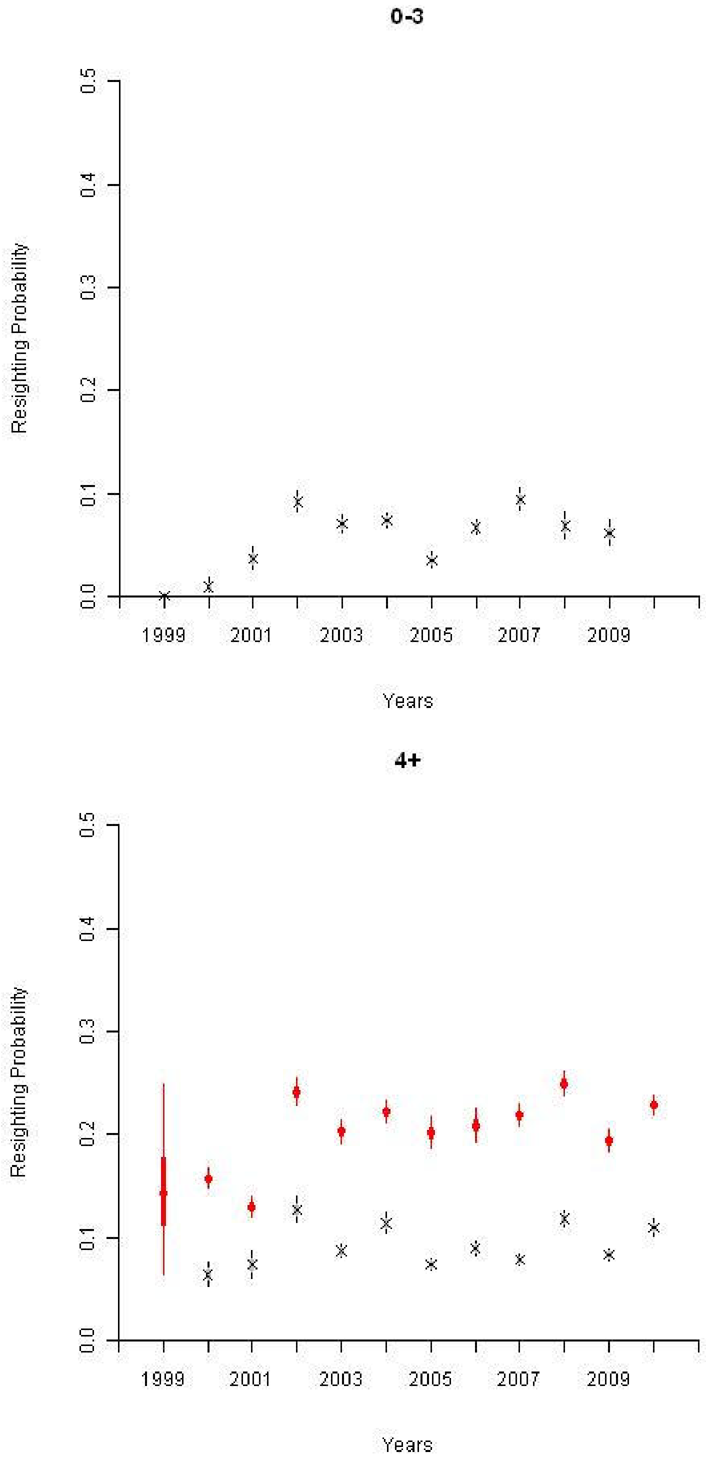


Figure 8: Using the strict definition of breeder, posterior distributions for the deviance value from models with 3 age-classes and; unconstrained zero-inflation (lightest-grey); temporally-constant zero-inflation (black); and no zero-inflation (charcoal; mostly obscured at right of plot). Posterior distributions for the deviance value from models with linear age relationship and; unconstrained zero-inflation (medium-light grey); temporally-constant zero-inflation (medium-dark grey); and no zero-inflation (white). Smaller values indicate a better fit to the data.

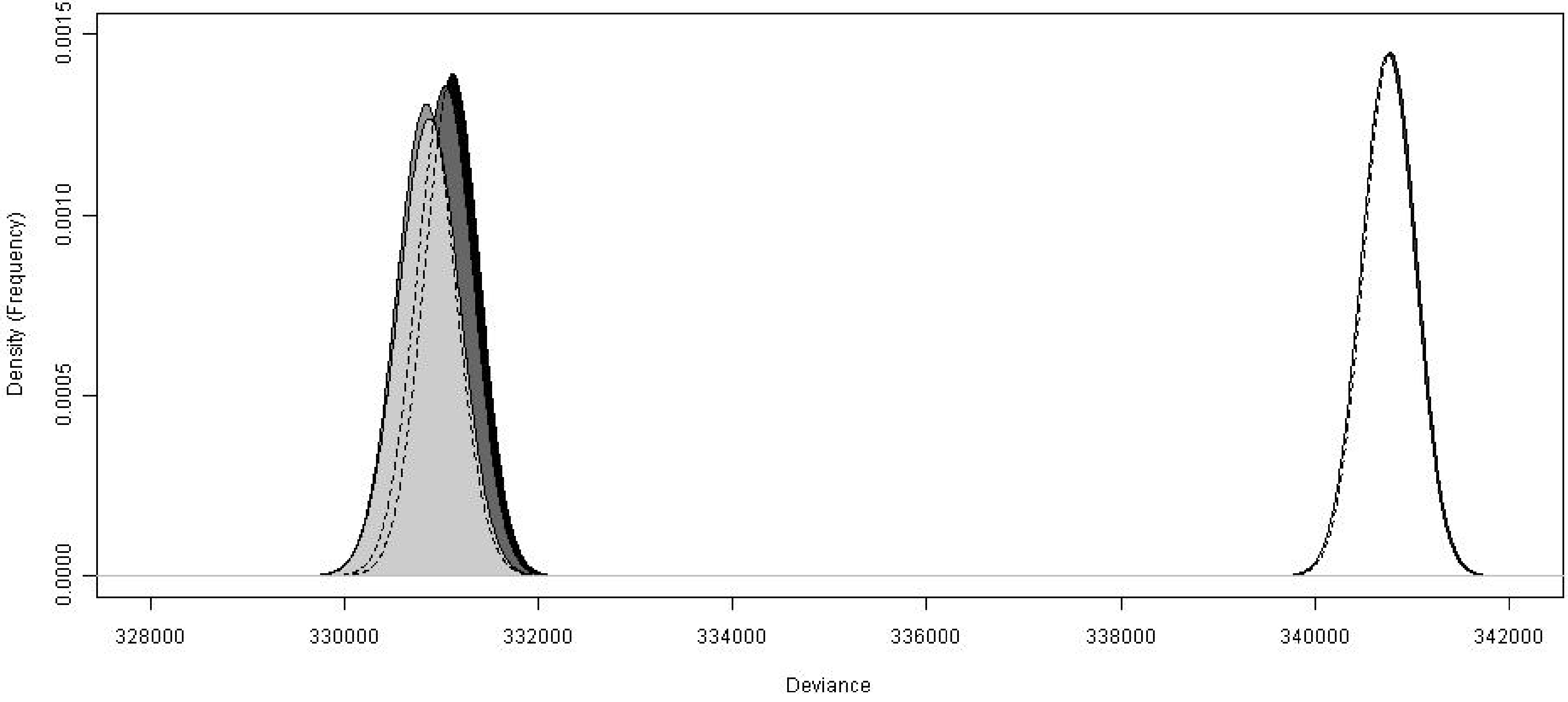


Figure 9: Plots of posterior (light grey) and predicted (dark grey) deviance values from each model with data using the strict definition of breeder. Bayesian p-values are indicated.

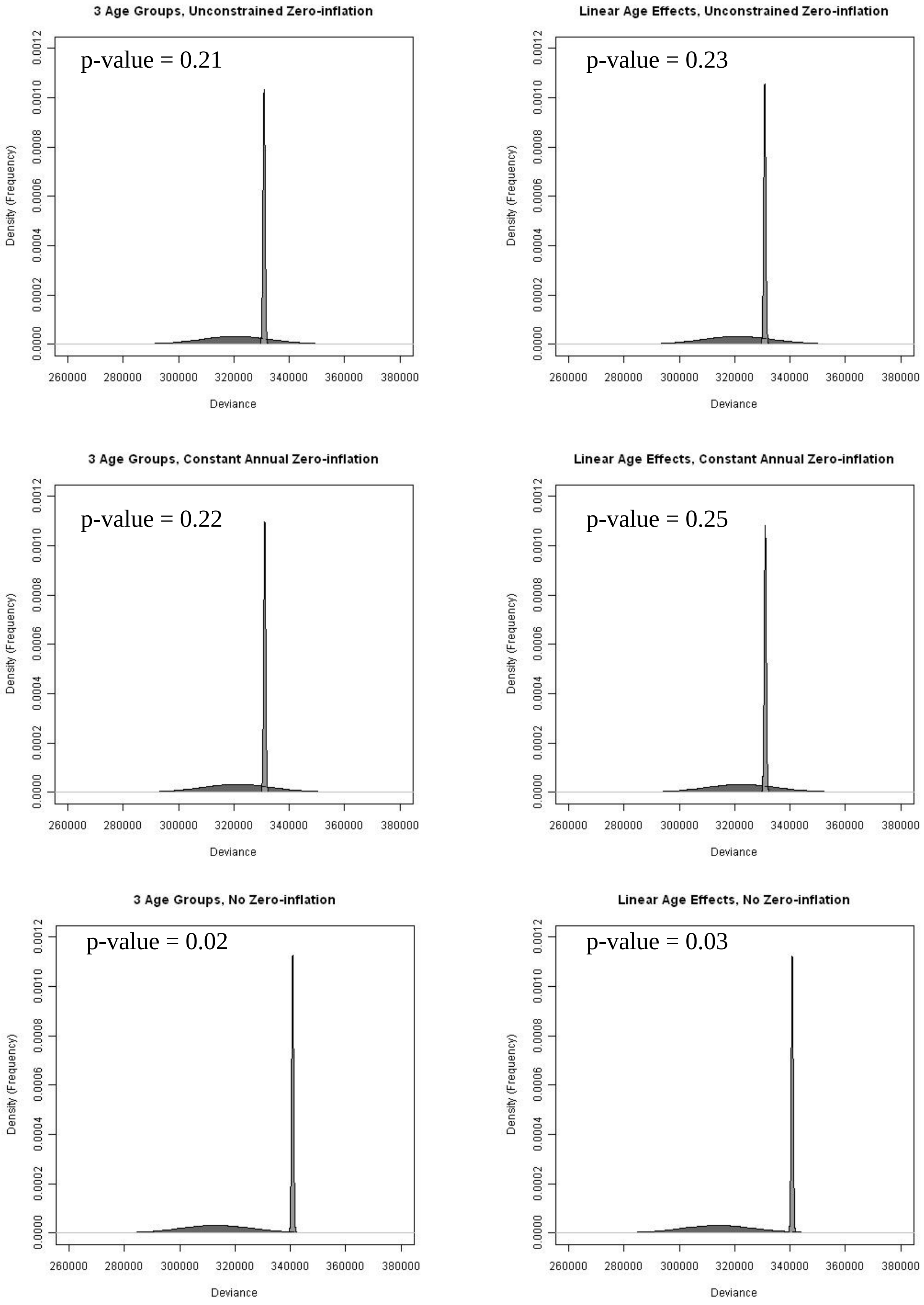


Figure 10: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were non-breeders aged 0-3 in year *t*, from model using age classes and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the median of the distribution, 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*.

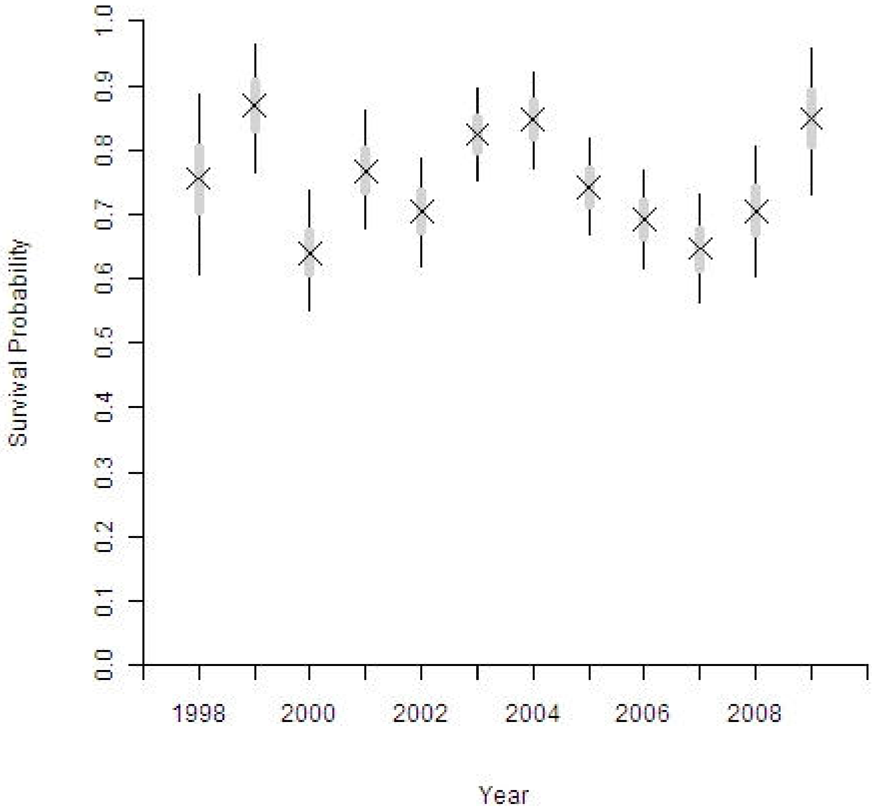


Figure 11: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were non-breeders aged 4-14 in year *t*, from model with age classes and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the median of the distribution, 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*.

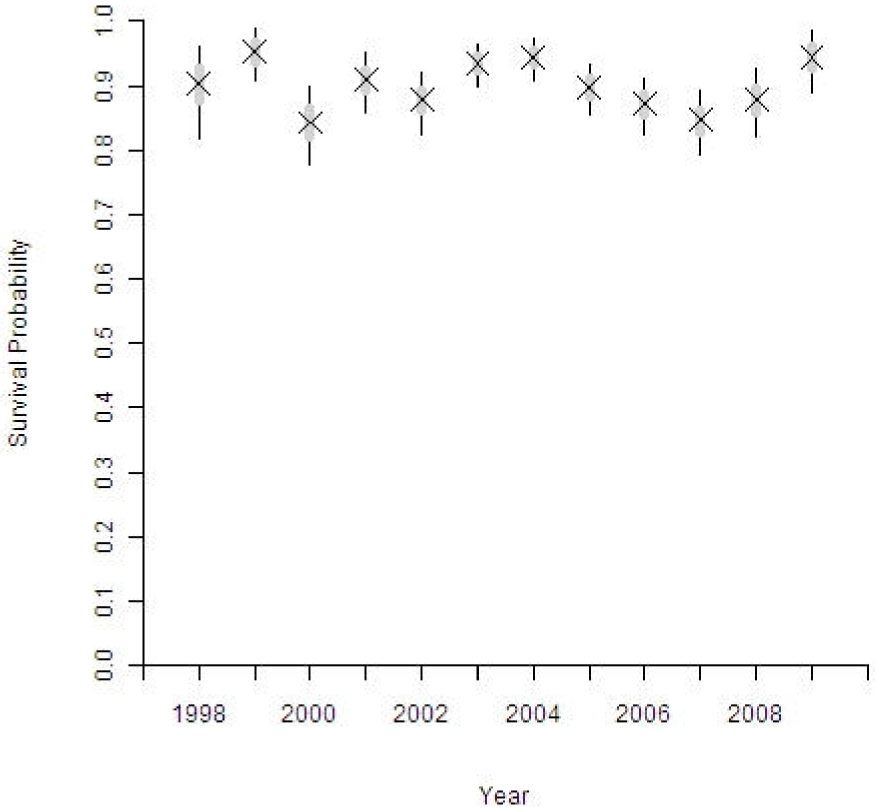


Figure 12: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were non-breeders aged 15+ in year *t*, from model with age classes and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the median of the distribution, 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*.

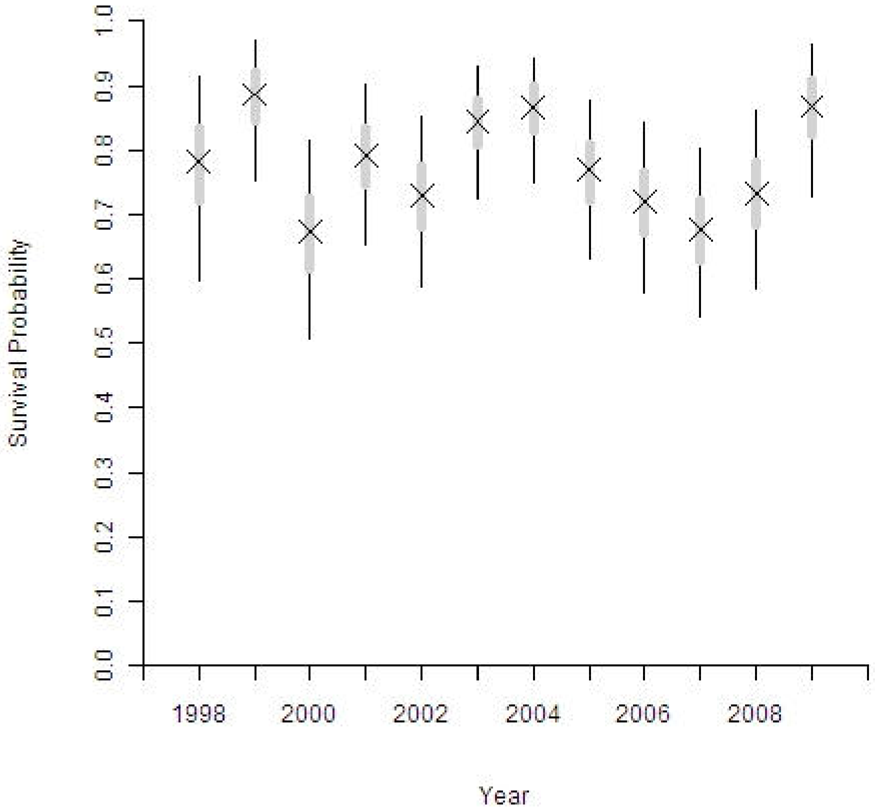


Figure 13: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were breeders aged 4-14 in year *t*, from model with age classes and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the median of the distribution, 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*.

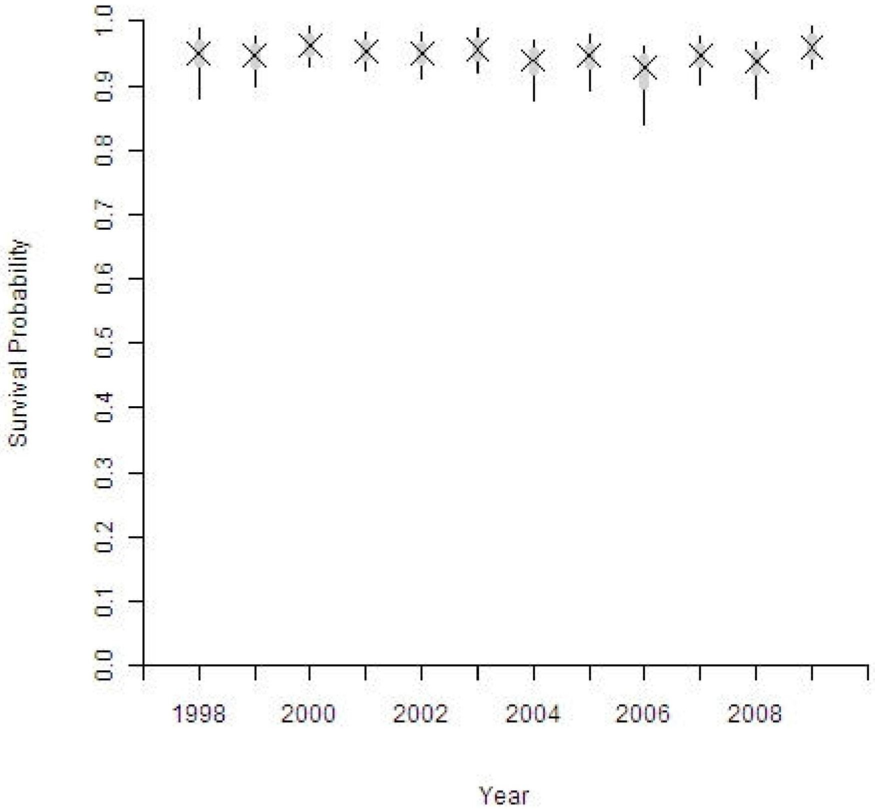


Figure 14: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were breeders aged 15+ in year *t*, from model with age classes and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the median of the distribution, thick 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*.

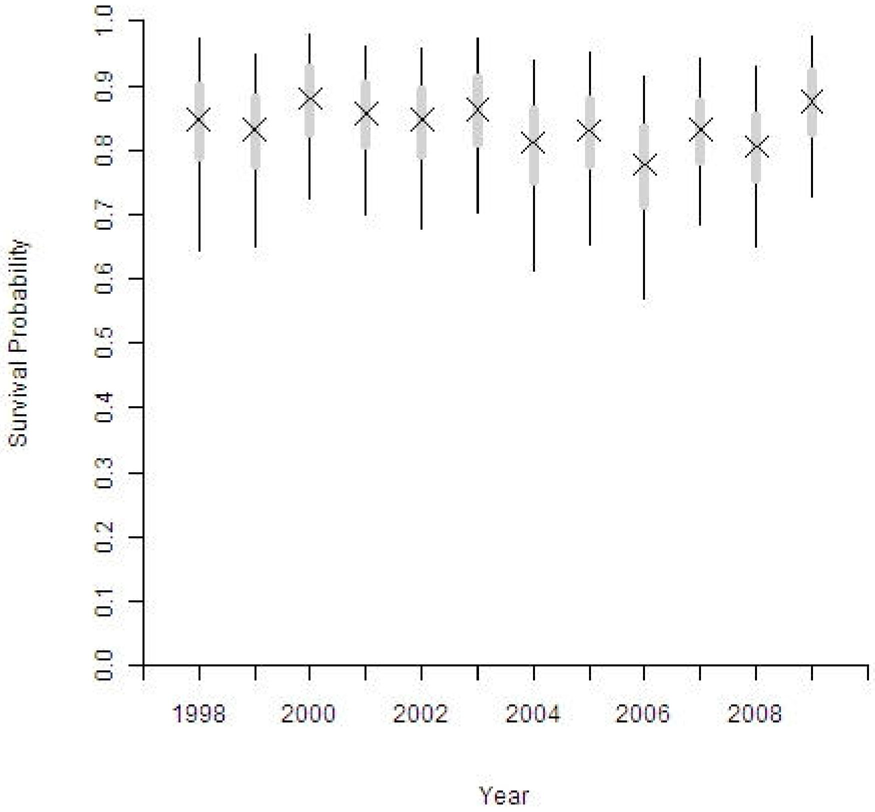


Figure 15: Posterior distribution for probability of breeding in year *t*+1 for individuals that were non-breeders aged 4-14 in year *t*, from model with age classes and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the median of the distribution, thick 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.

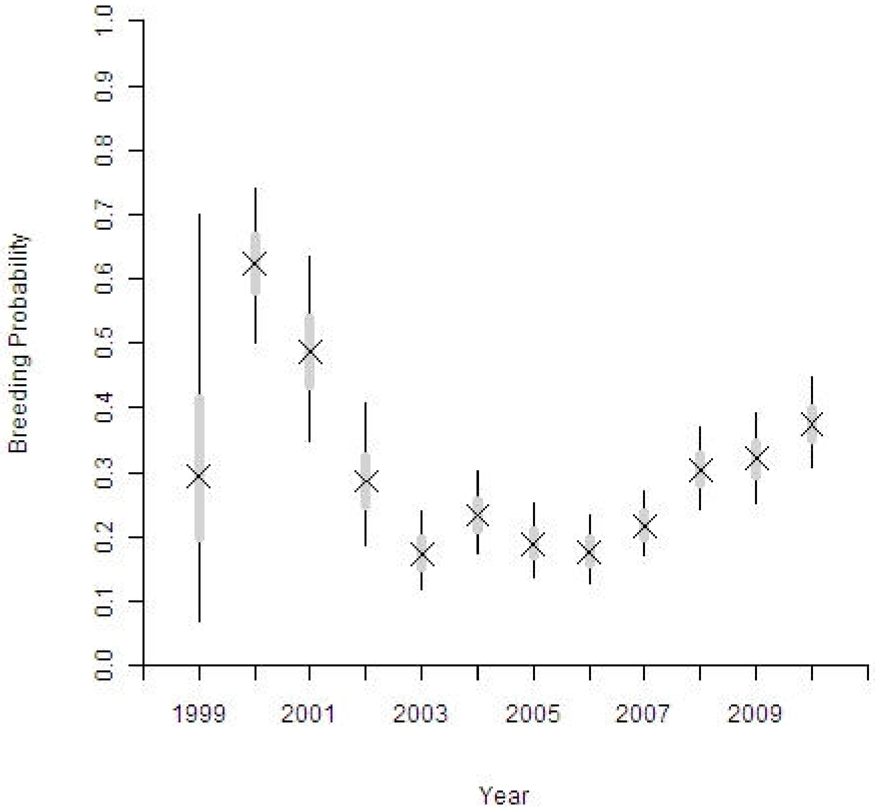


Figure 16: Posterior distribution for probability of breeding in year *t*+1 for individuals that were non-breeders aged 15+ in year *t*, from model with age classes and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the median of the distribution, thick 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.

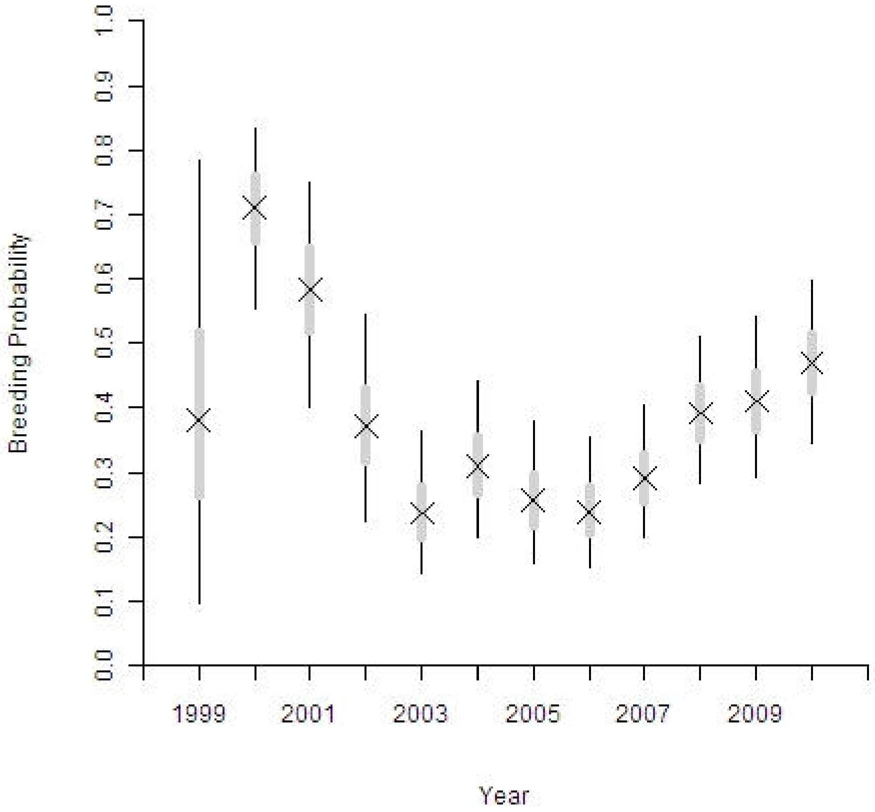


Figure 17: Posterior distribution for probability of breeding in year *t*+1 for individuals that were breeders aged 4-14 in year *t*, from model with age classes and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey 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.

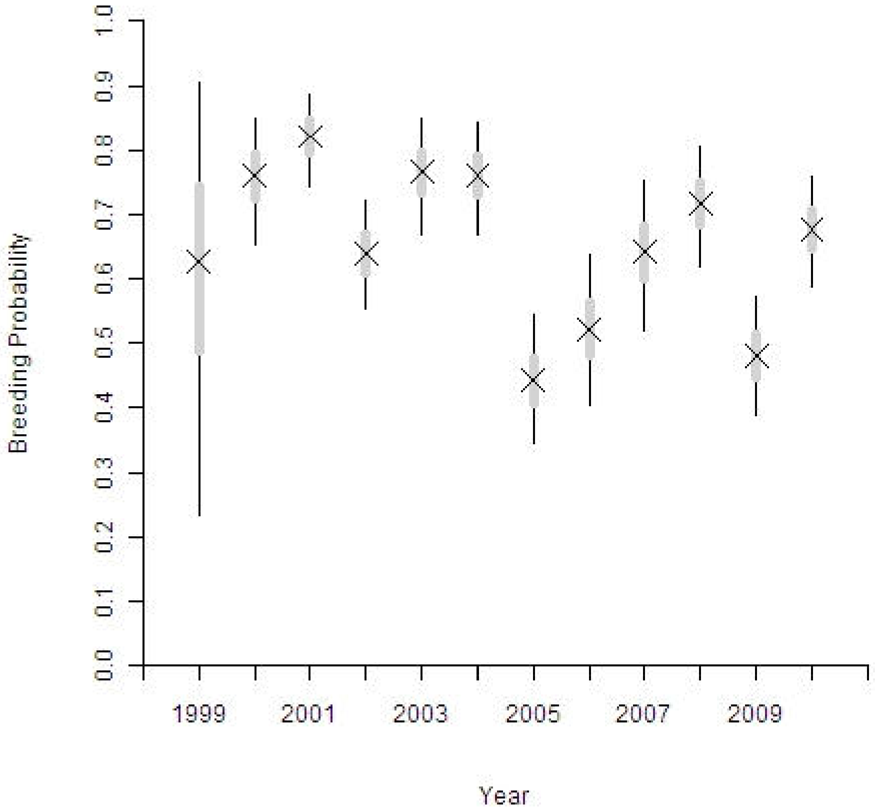


Figure 18: Posterior distribution for probability of breeding in year *t*+1 for individuals that were breeders aged 15+ in year *t*, from model with age classes and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey 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.

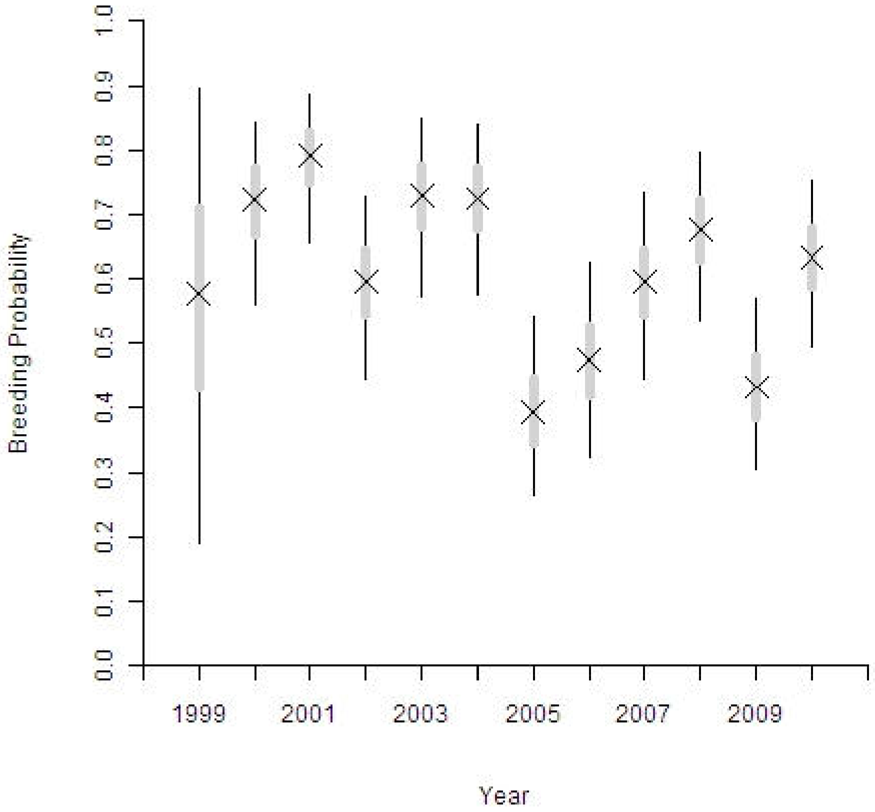


Figure 19: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were non-breeders aged 0-3 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses 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*.

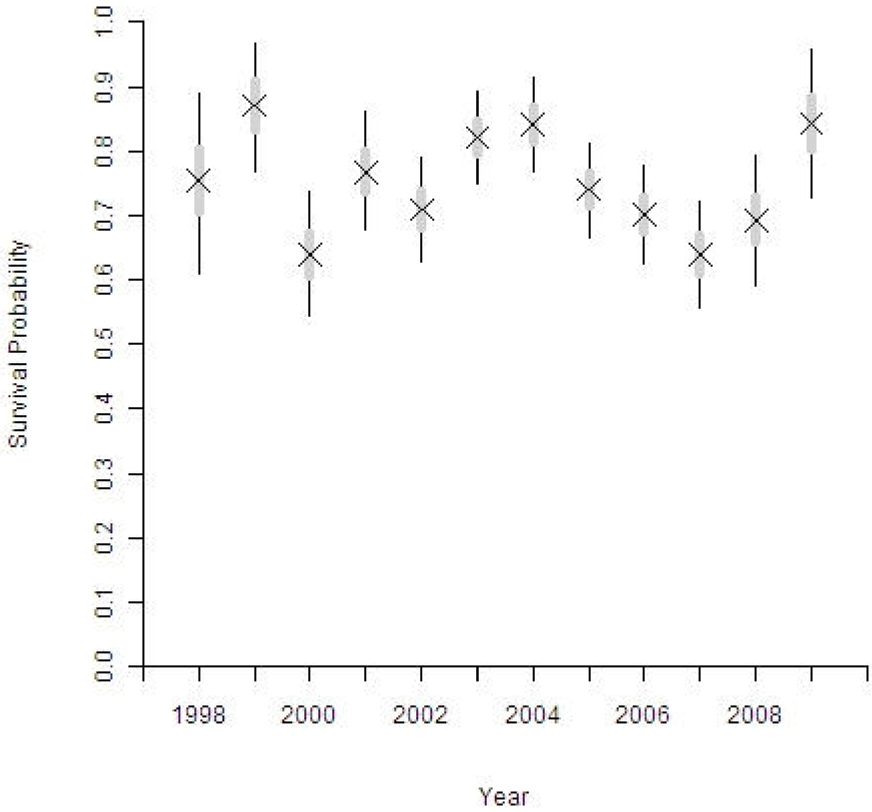


Figure 20: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were non-breeders aged 9 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses 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*.

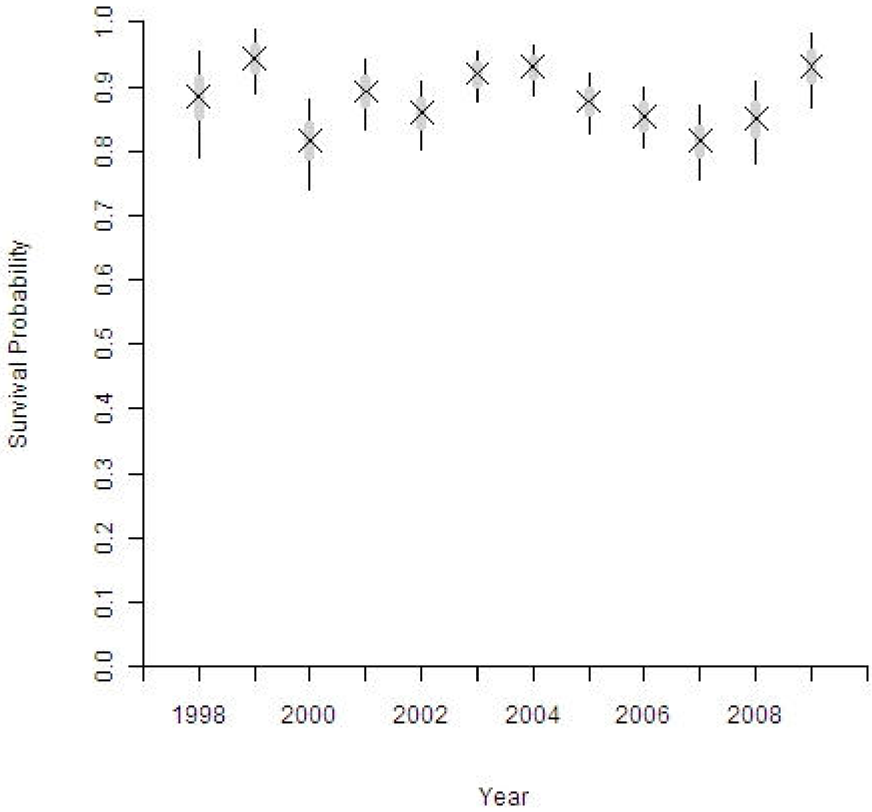


Figure 21: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were non-breeders aged 18 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses 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*.

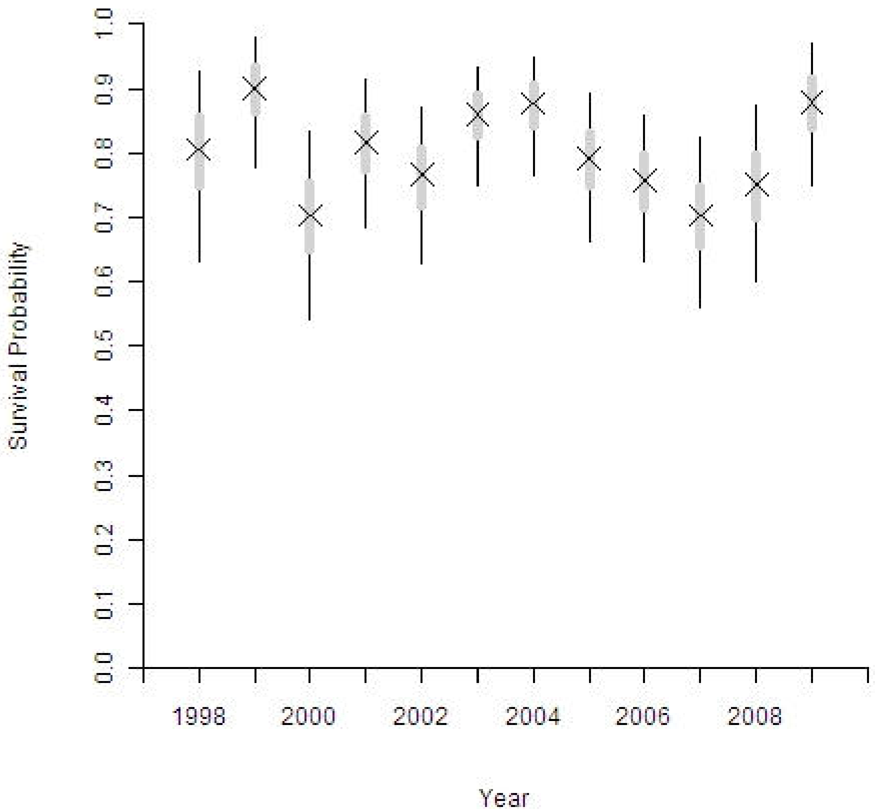


Figure 22: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were breeders aged 9 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses 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*.

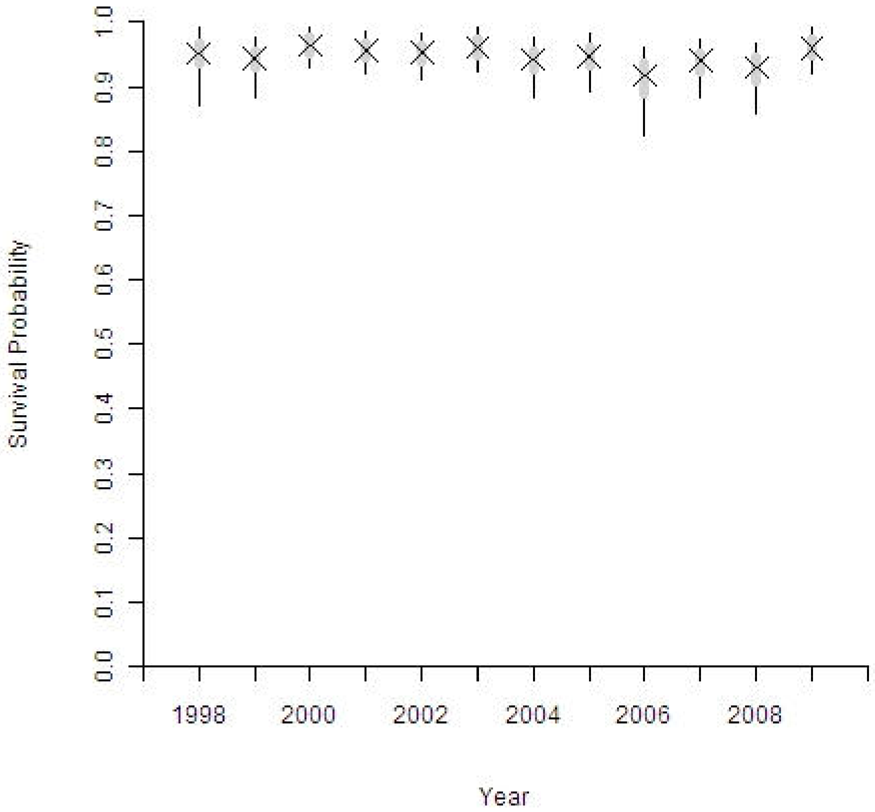


Figure 23: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were breeders aged 18 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses 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*.

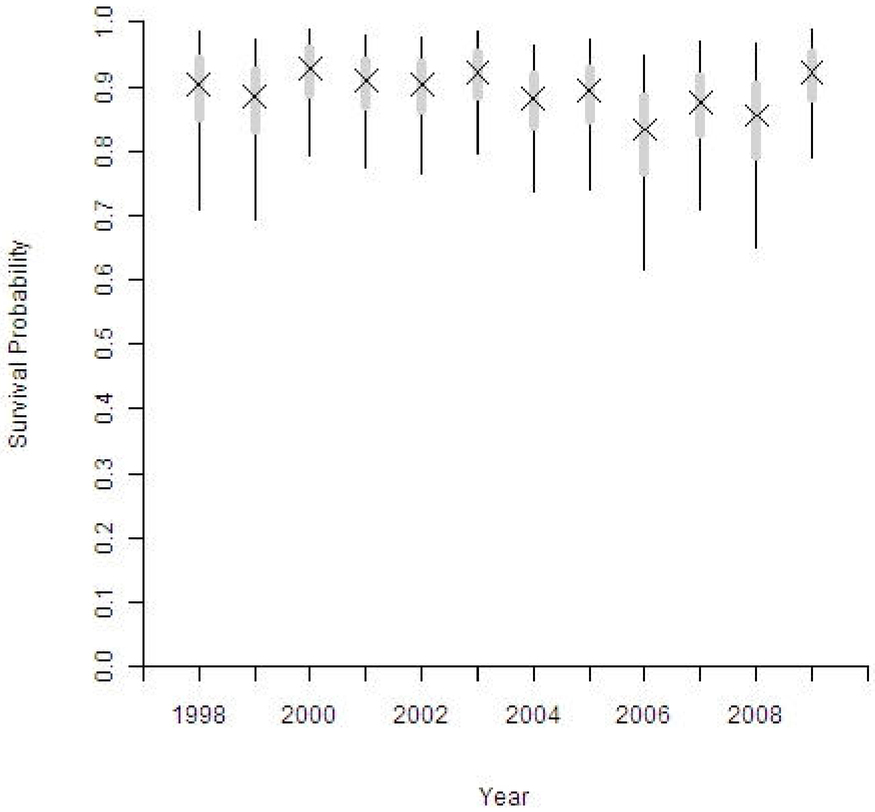


Figure 24: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were non-breeders of age in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses 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*. Note the width of the posterior distributions incorporate both annual variation and estimation uncertainty.

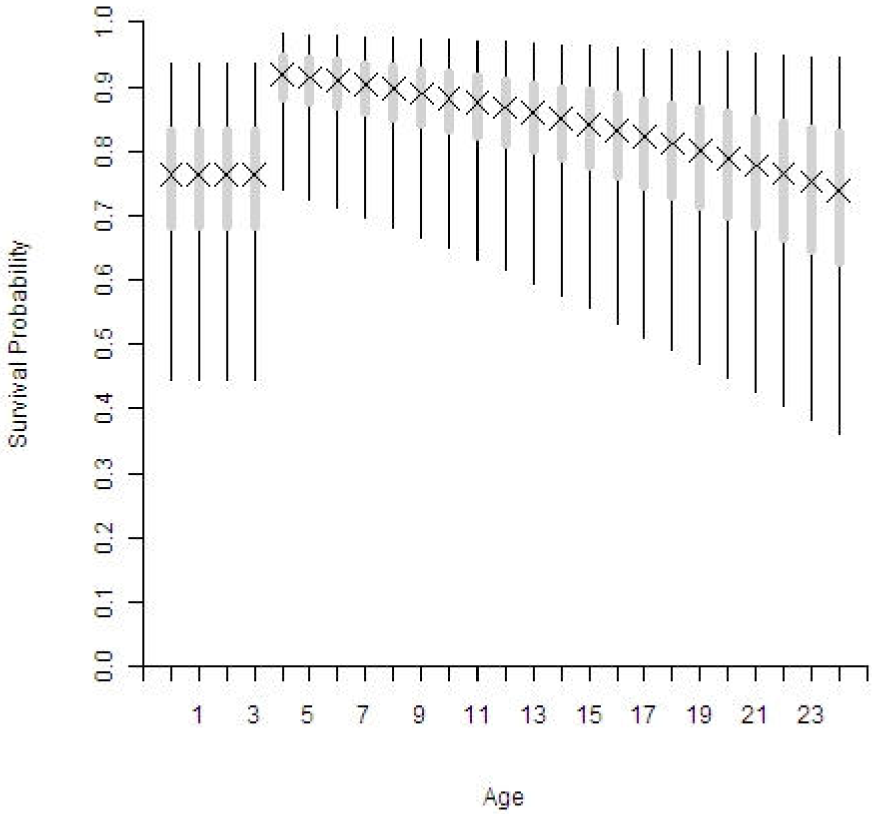


Figure 25: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were breeders of age in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses 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*. Note the width of the posterior distributions incorporate both annual variation and estimation uncertainty.

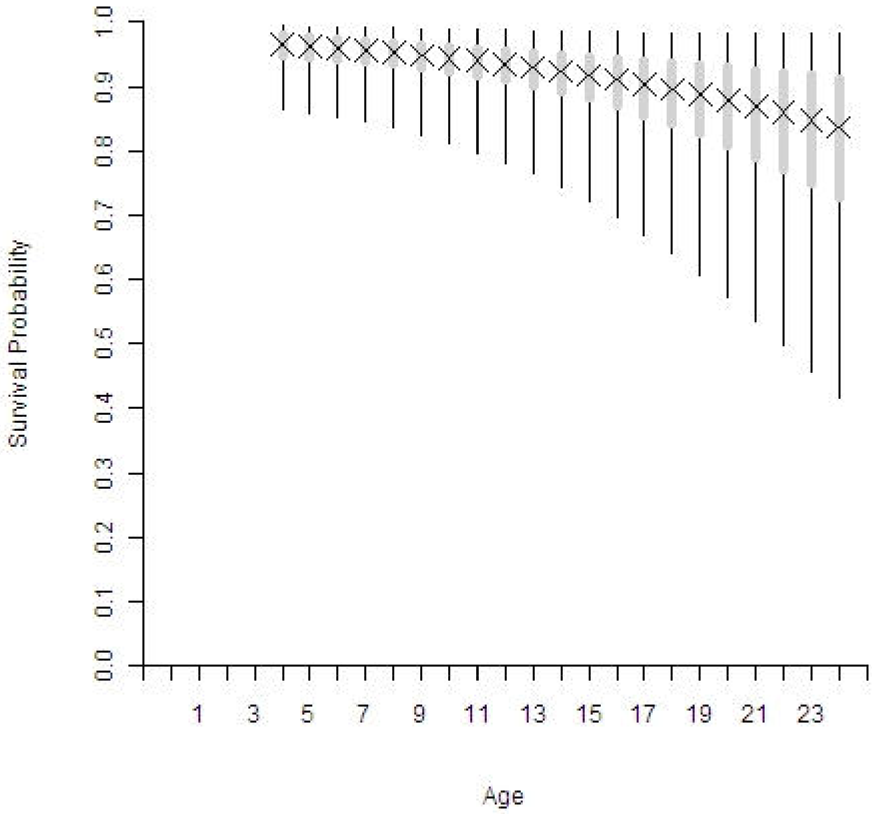


Figure 26: Posterior distribution for probability of breeding in year *t*+1 for individuals that were non-breeders aged 9 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate 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.

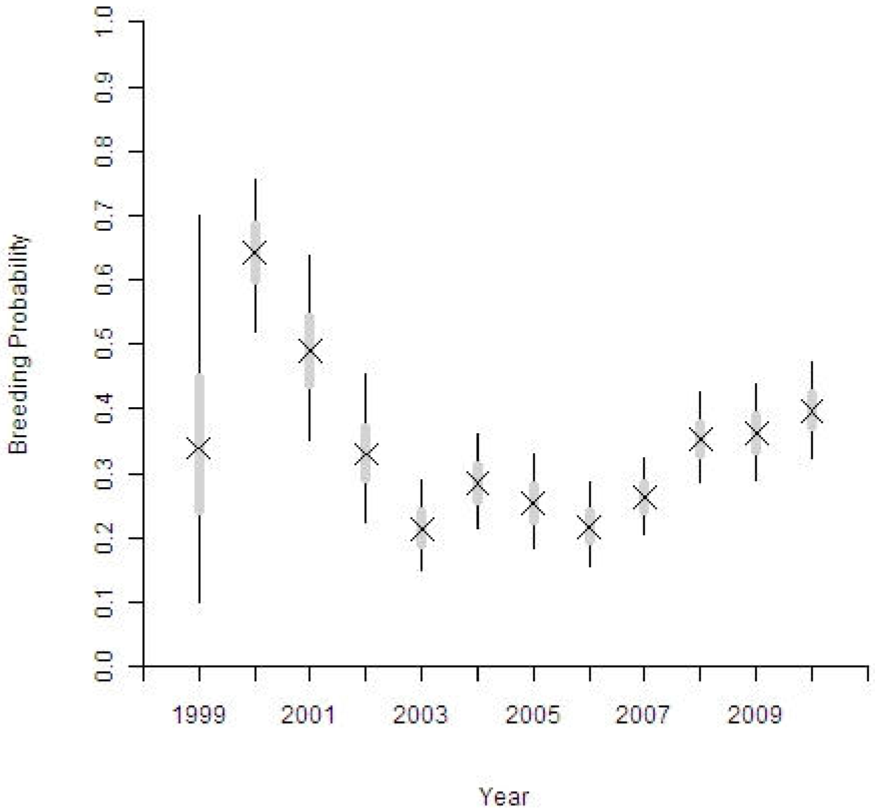


Figure 27: Posterior distribution for probability of breeding in year *t*+1 for individuals that were non-breeders aged 18 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate 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.

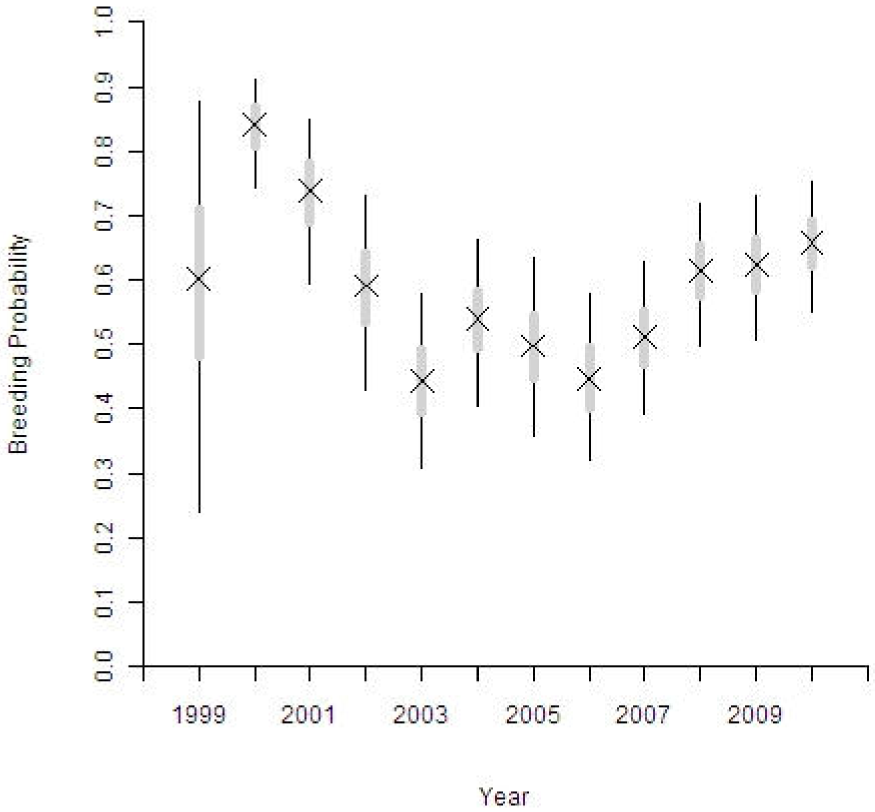


Figure 28: Posterior distribution for probability of breeding in year *t*+1 for individuals that were breeders aged 9 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate 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.

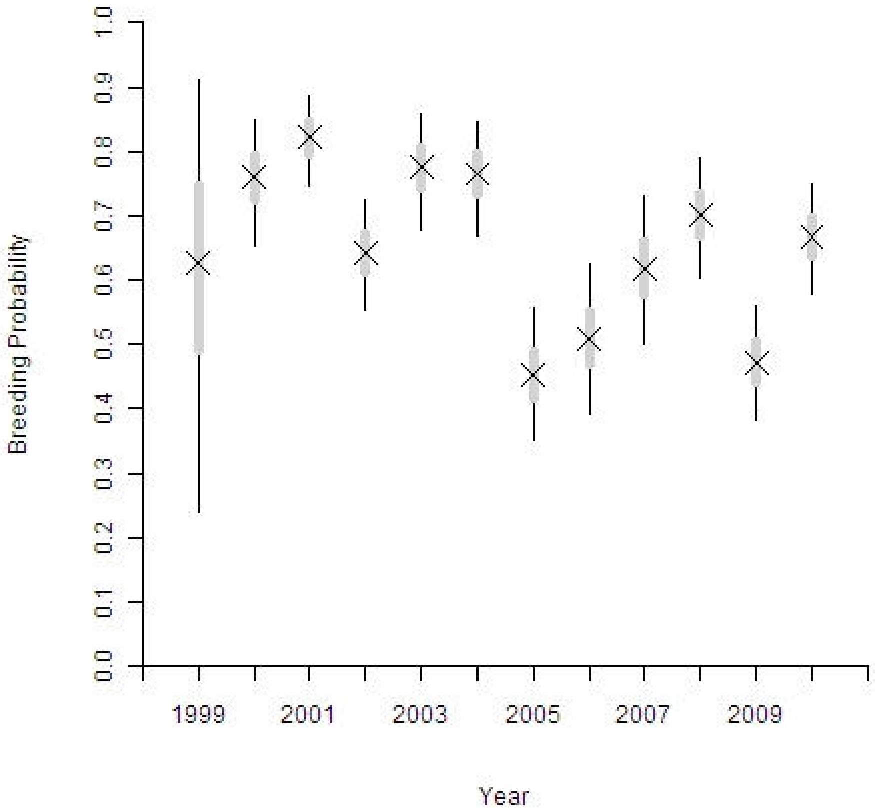


Figure 29: Posterior distribution for probability of breeding in year *t*+1 for individuals that were breeders aged 18 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate 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.

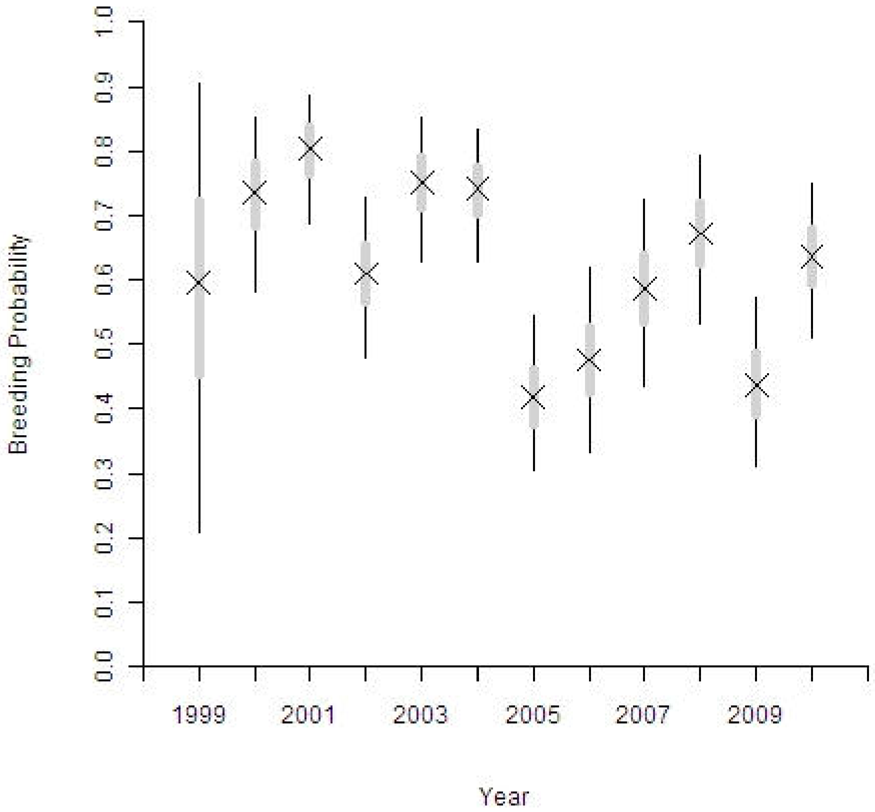


Figure 30: Posterior distribution for probability of breeding in year *t*+1 for individuals that were non-breeders of age in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate 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. Note the width of the posterior distributions incorporate both annual variation and estimation uncertainty.

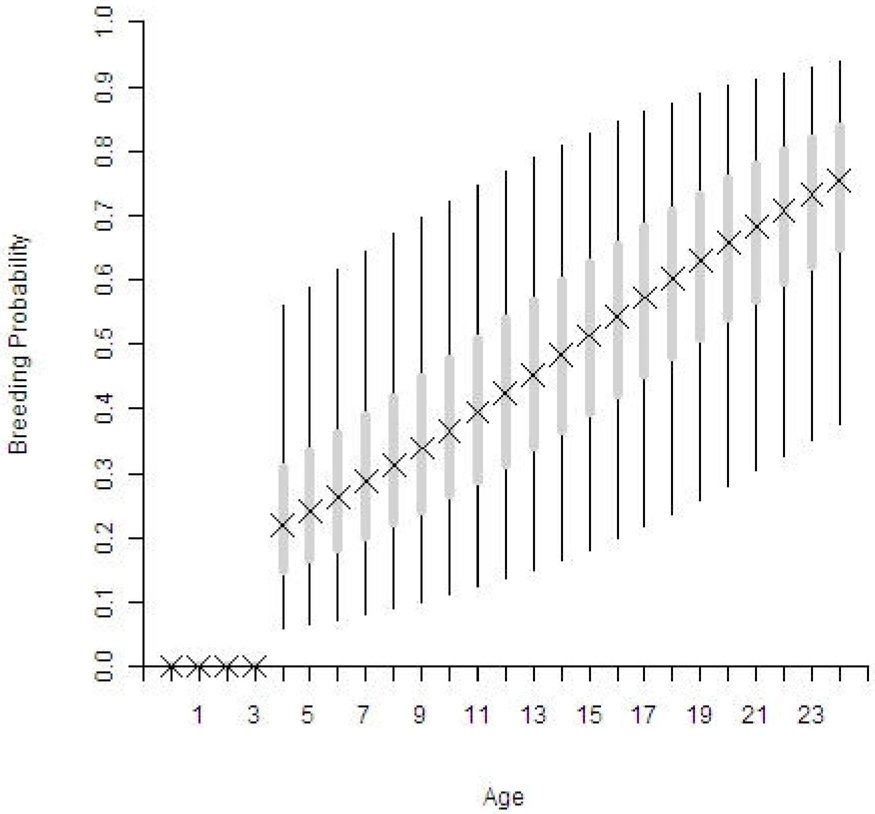


Figure 31: Posterior distribution for probability of breeding in year *t*+1 for individuals that were breeders of age in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate 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. Note the width of the posterior distributions incorporate both annual variation and estimation uncertainty.

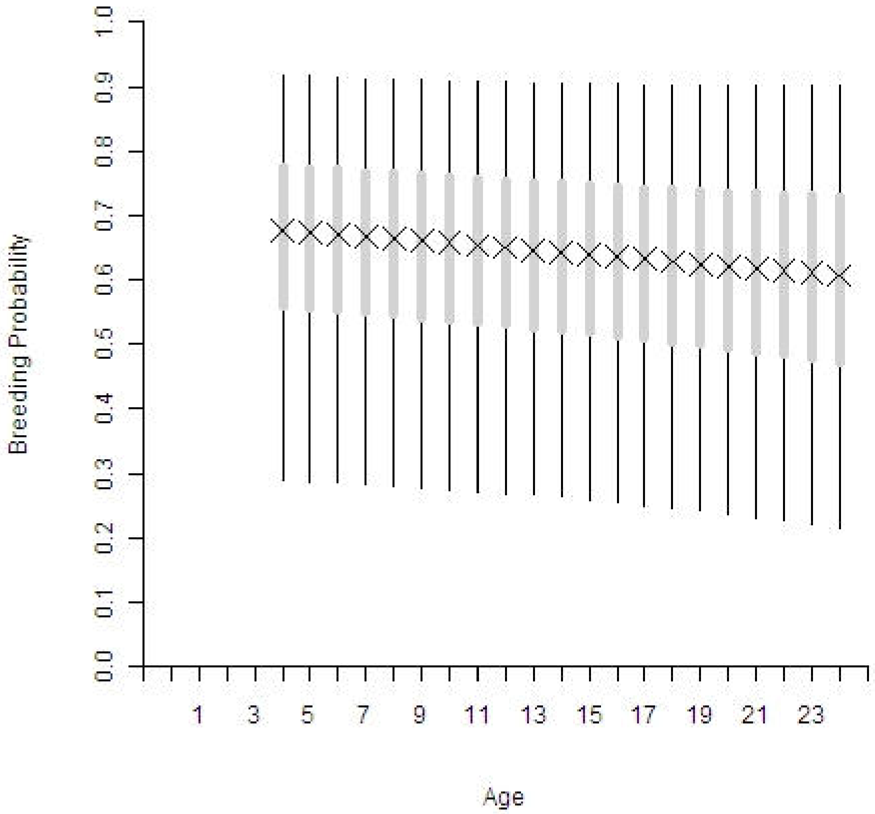


Figure 32: Using the liberal definition of breeder, posterior distributions for the deviance value from models with 3 age-classes and; unconstrained zero-inflation (lightest-grey); temporally-constant zero-inflation (black); and no zero-inflation (charcoal; mostly obscured at right of plot). Posterior distributions for the deviance value from models with linear age relationship and; unconstrained zero-inflation (medium-light grey); temporally-constant zero-inflation (medium-dark grey); and no zero-inflation (white). Smaller values indicate a better fit to the data.

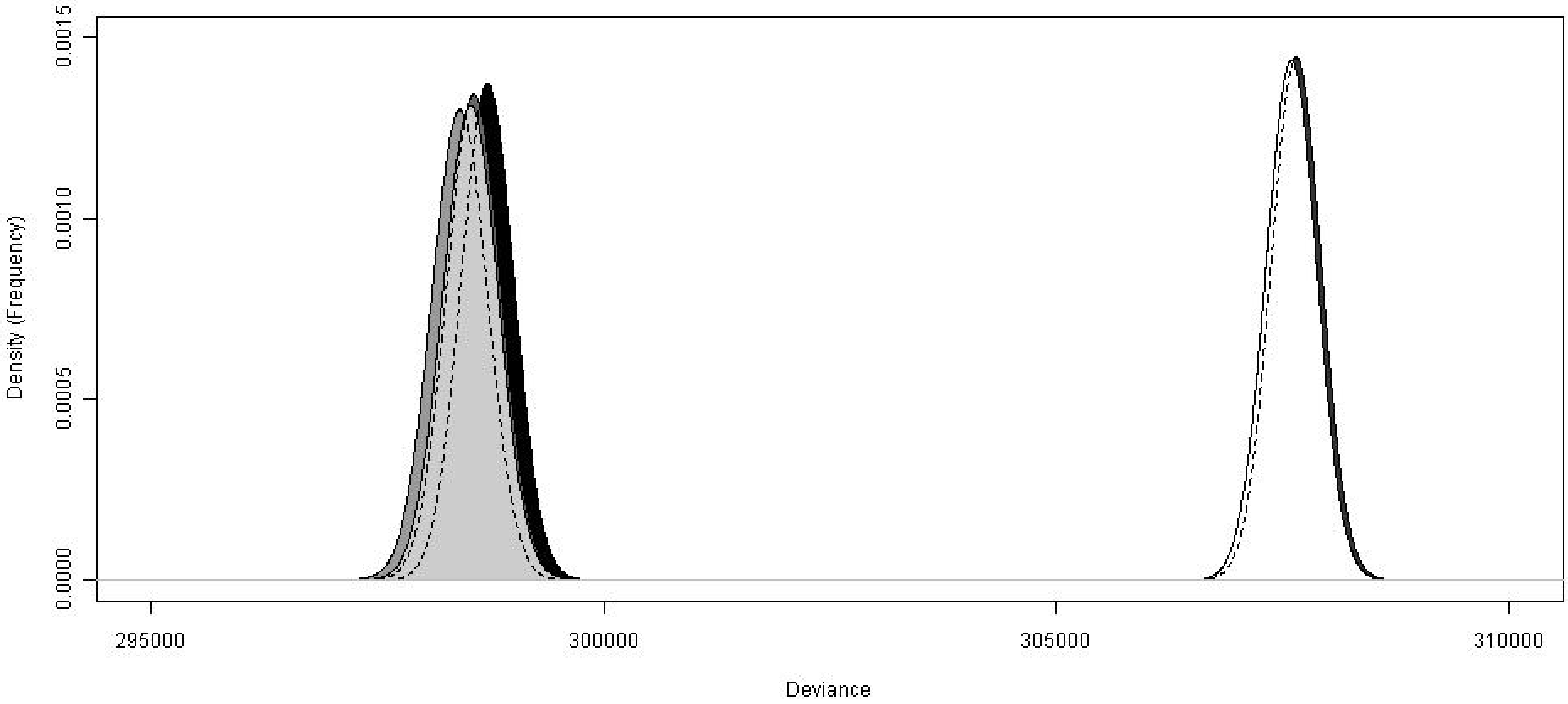


Figure 33: Plots of posterior (light grey) and predicted (dark grey) deviance values from each model with data using the liberal definition of breeder. Bayesian p-values are indicated.

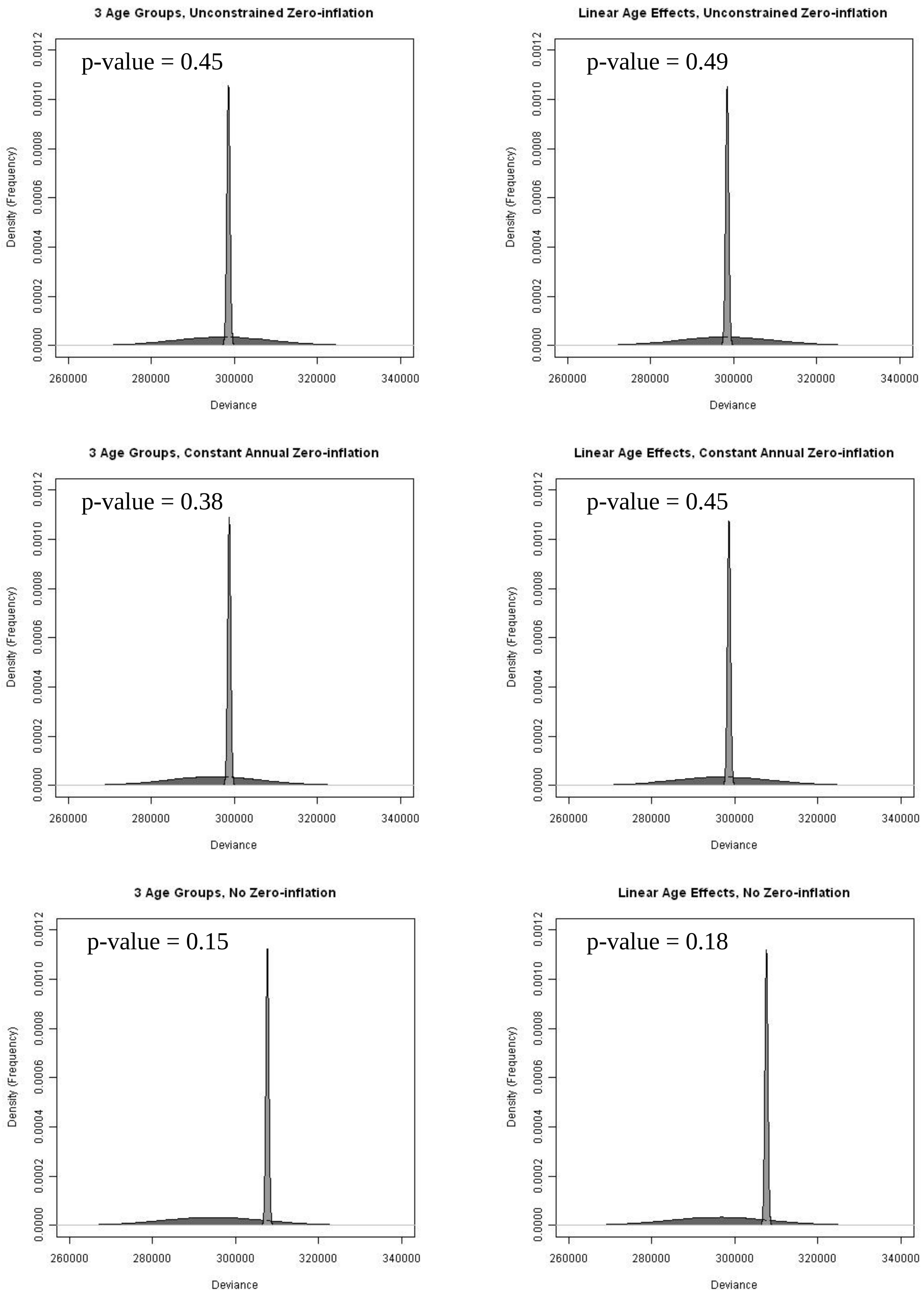


Figure 34: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were non-breeders aged 0-3 in year *t*, from model using age classes and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate the median of the distribution, 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*.

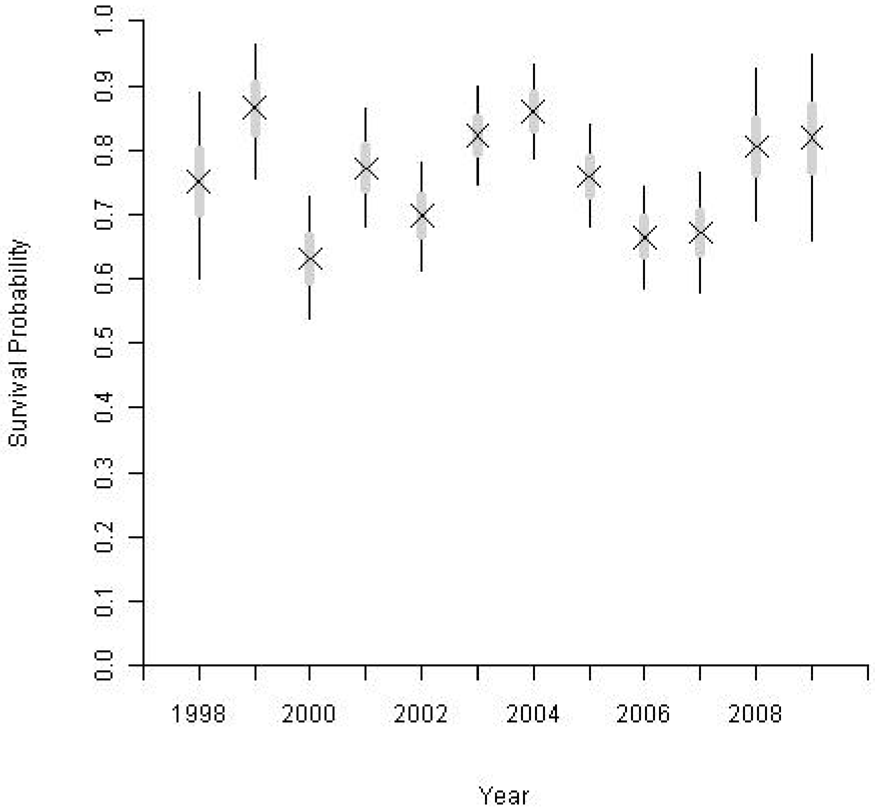


Figure 35: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were non-breeders aged 4-14 in year *t*, from model with age classes and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate the median of the distribution, 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*.

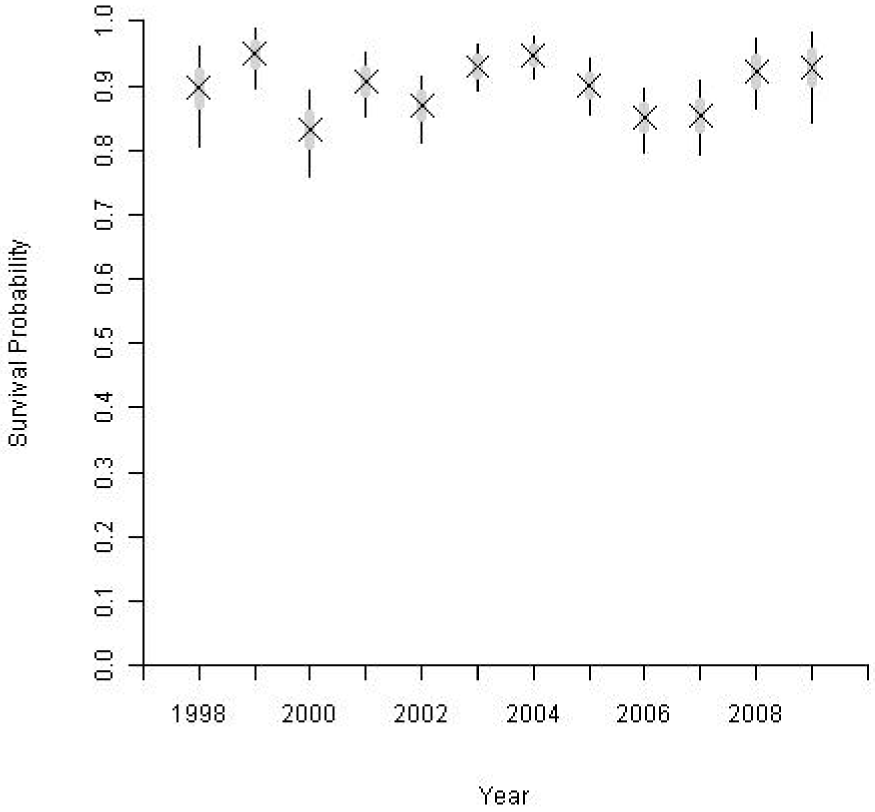


Figure 36: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were non-breeders aged 15+ in year *t*, from model with age classes and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate the median of the distribution, 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*.

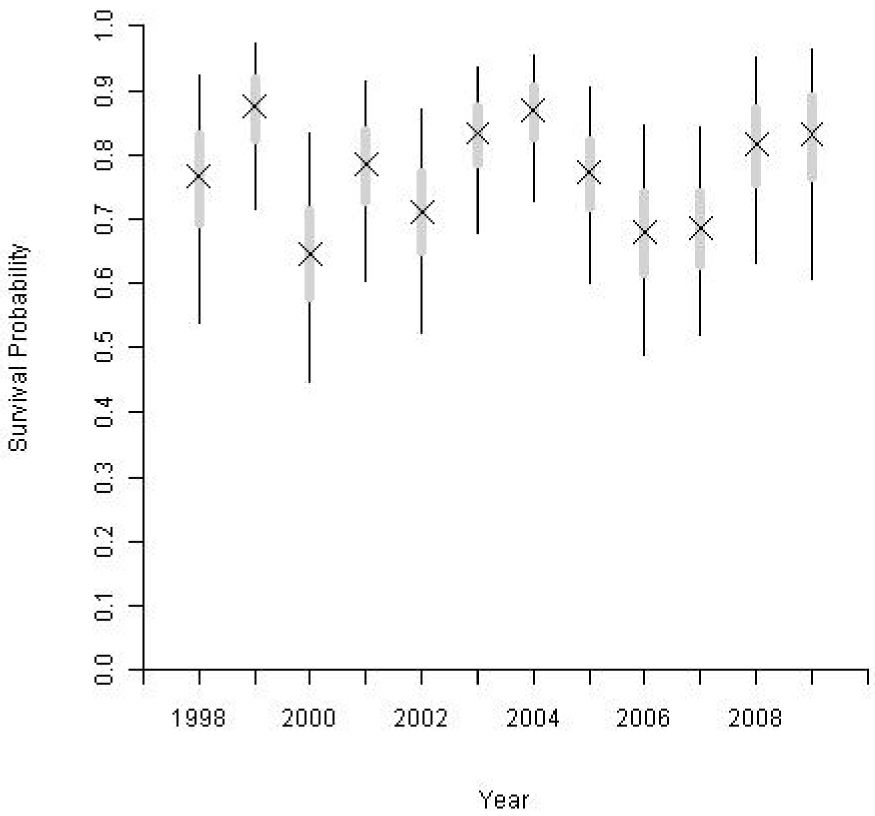


Figure 37: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were breeders aged 4-14 in year *t*, from model with age classes and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate the median of the distribution, 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*.

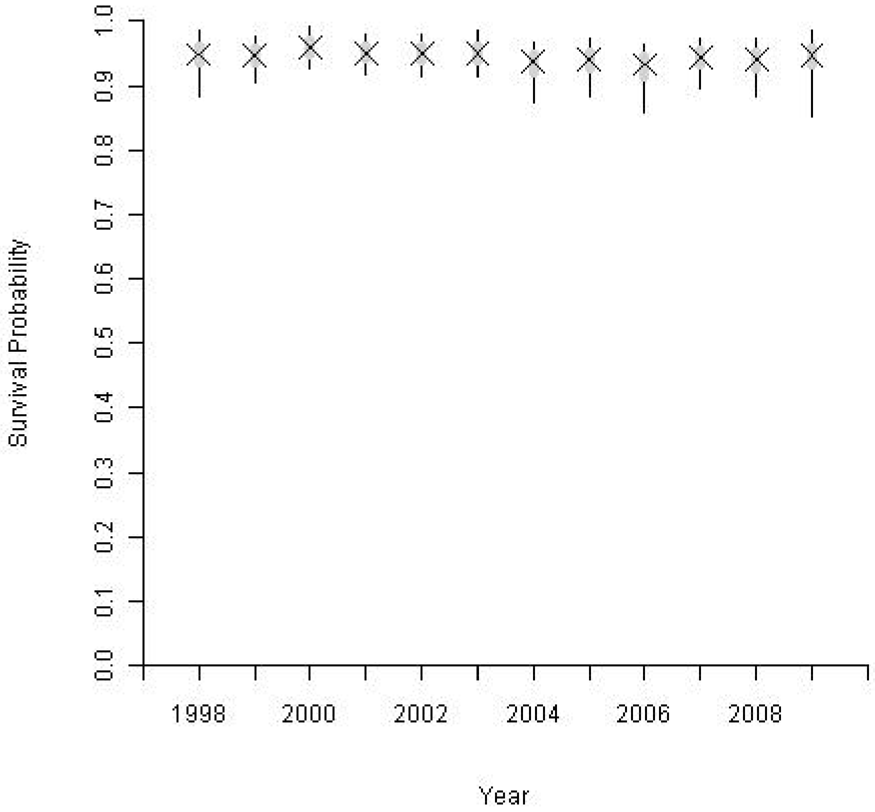


Figure 38: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were breeders aged 15+ in year *t*, from model with age classes and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate the median of the distribution, 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*.

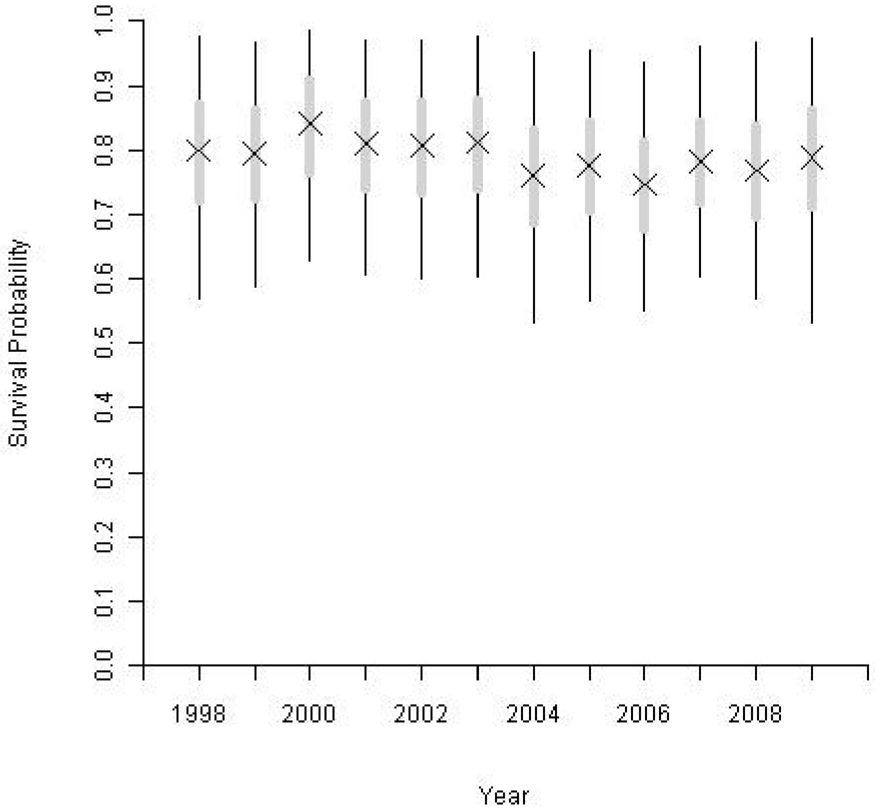


Figure 39: Posterior distribution for probability of breeding in year *t*+1 for individuals that were non-breeders aged 4-14 in year *t*, from model with age classes and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick 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.

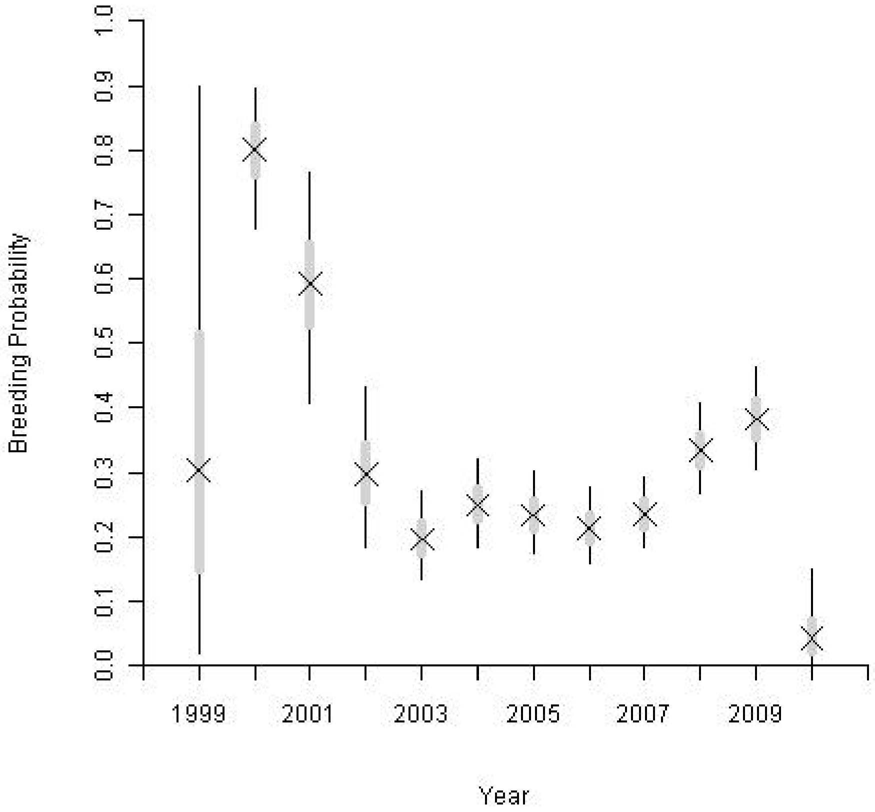


Figure 40: Posterior distribution for probability of breeding in year *t*+1 for individuals that were non-breeders aged 15+ in year *t*, from model with age classes and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick 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.

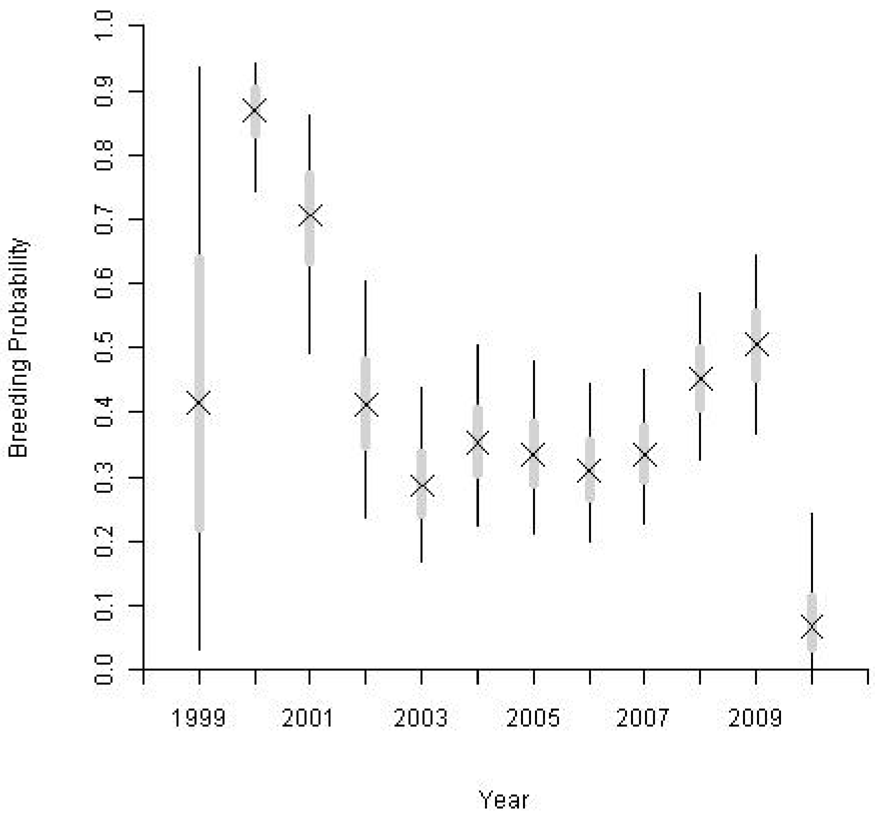


Figure 41: Posterior distribution for probability of breeding in year *t*+1 for individuals that were breeders aged 4-14 in year *t*, from model with age classes and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick grey 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.

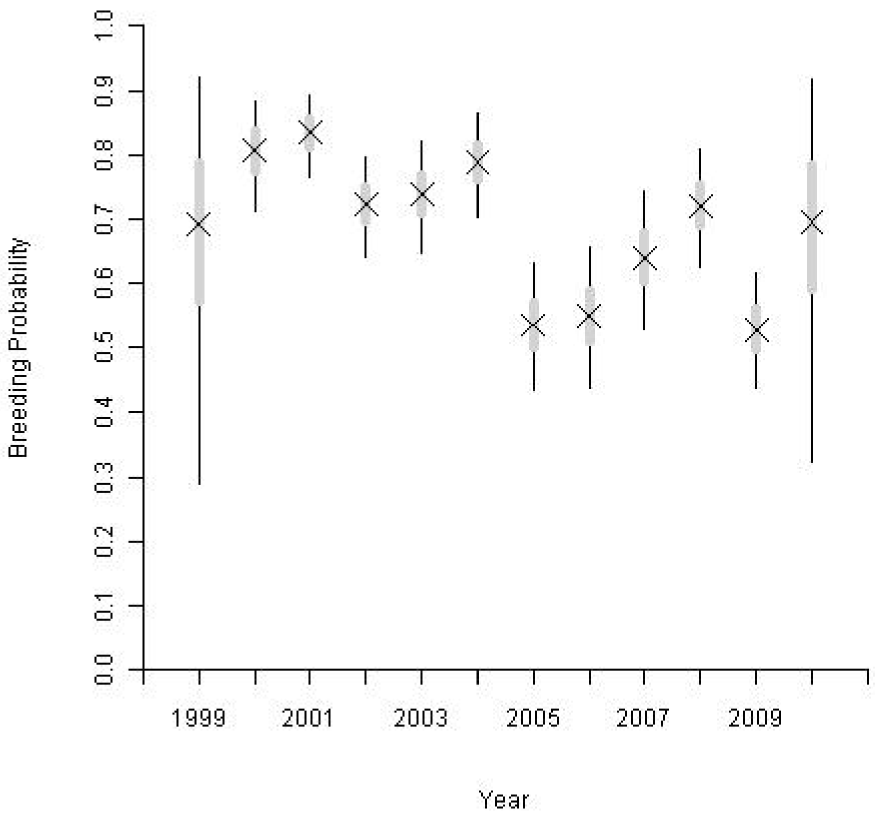


Figure 42: Posterior distribution for probability of breeding in year *t*+1 for individuals that were breeders aged 15+ in year *t*, from model with age classes and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick grey 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.

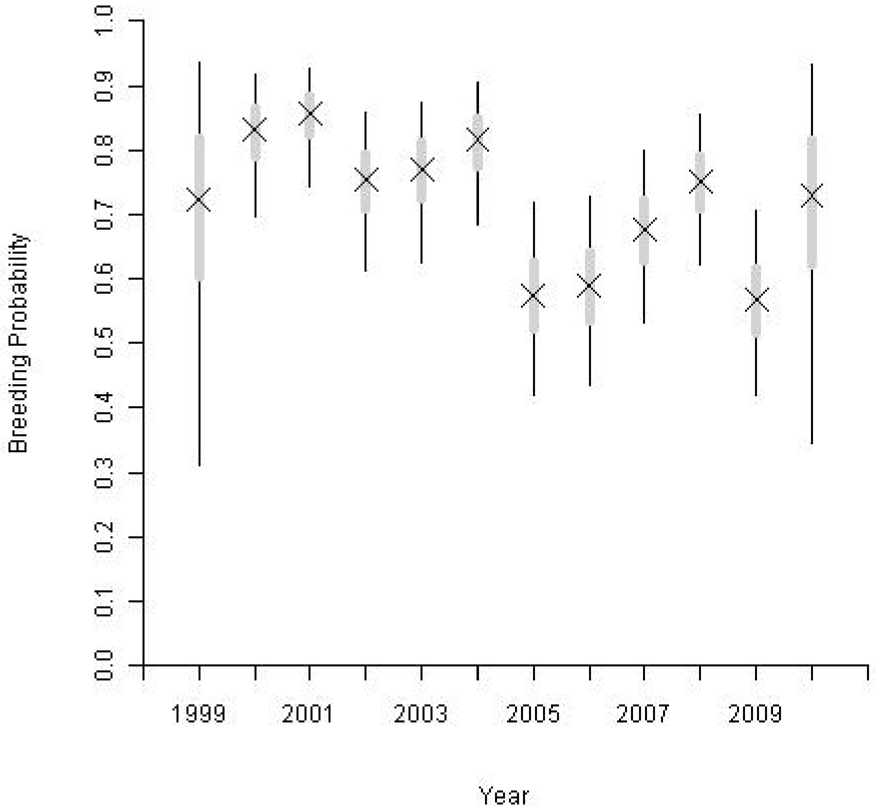


Figure 43: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were non-breeders aged 0-3 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses 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*.

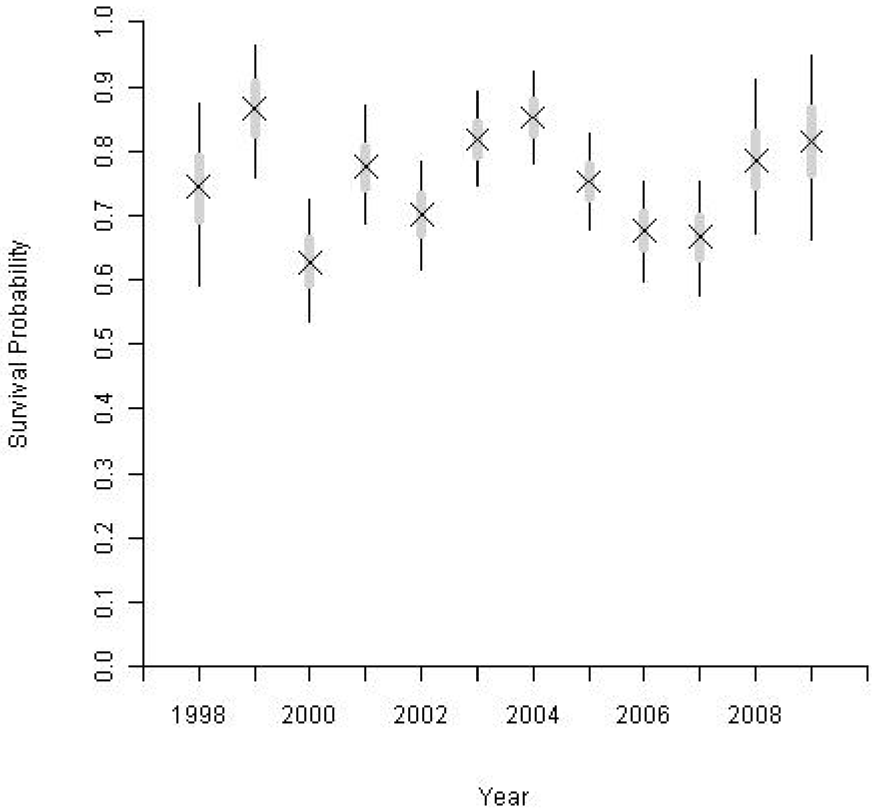


Figure 44: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were non-breeders aged 9 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses 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*.

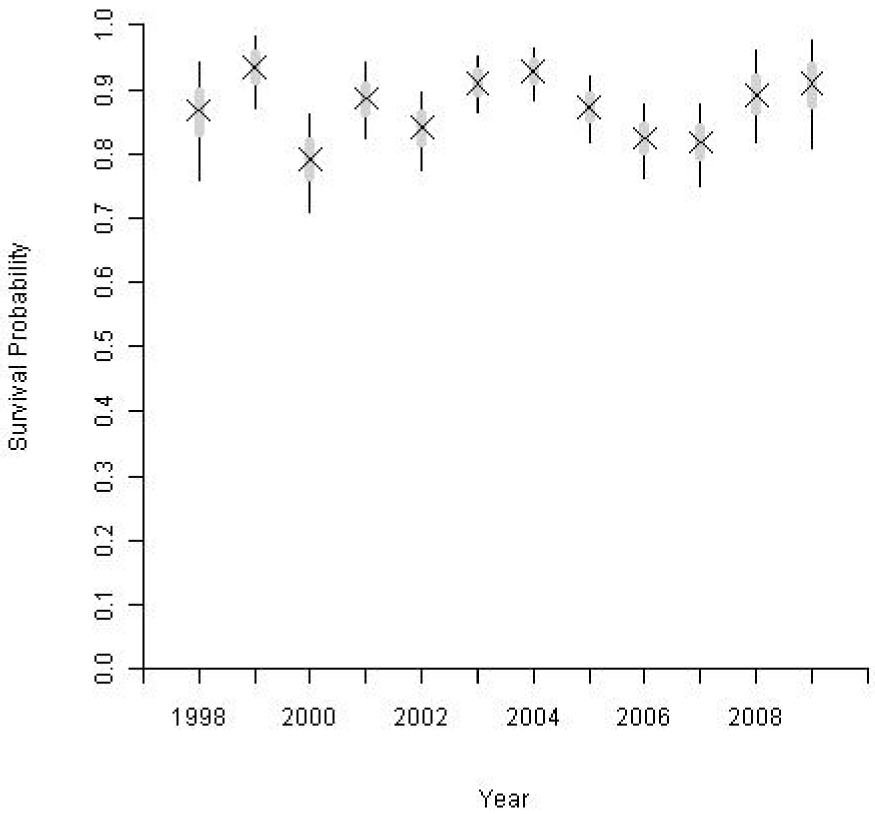


Figure 45: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were non-breeders aged 18 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses 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*.

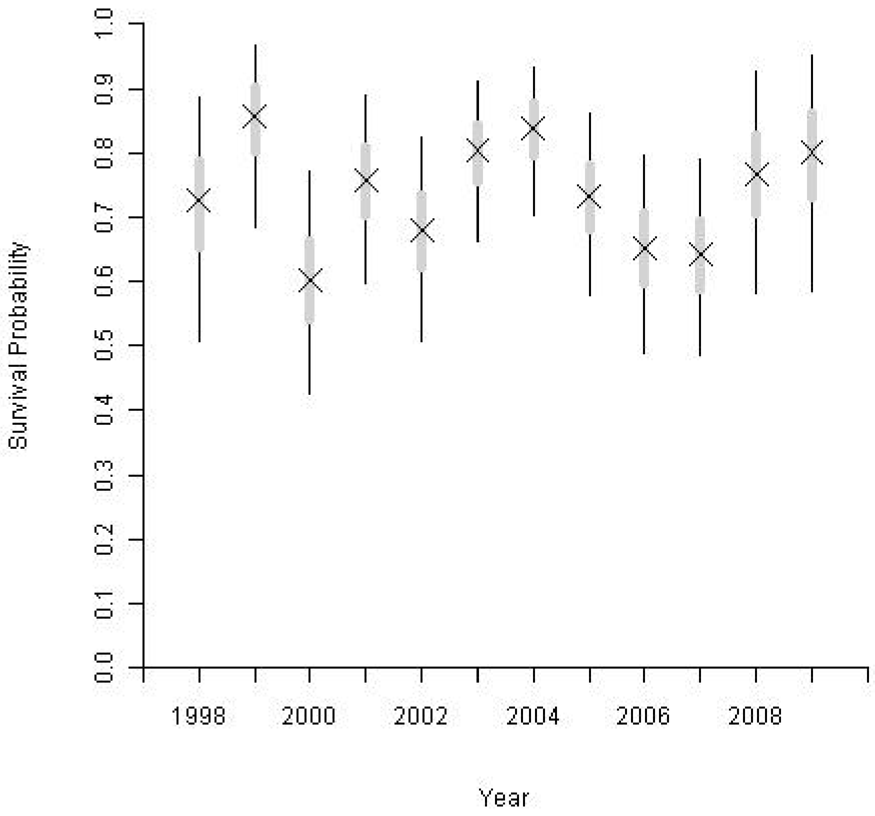


Figure 46: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were breeders aged 9 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses 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*.

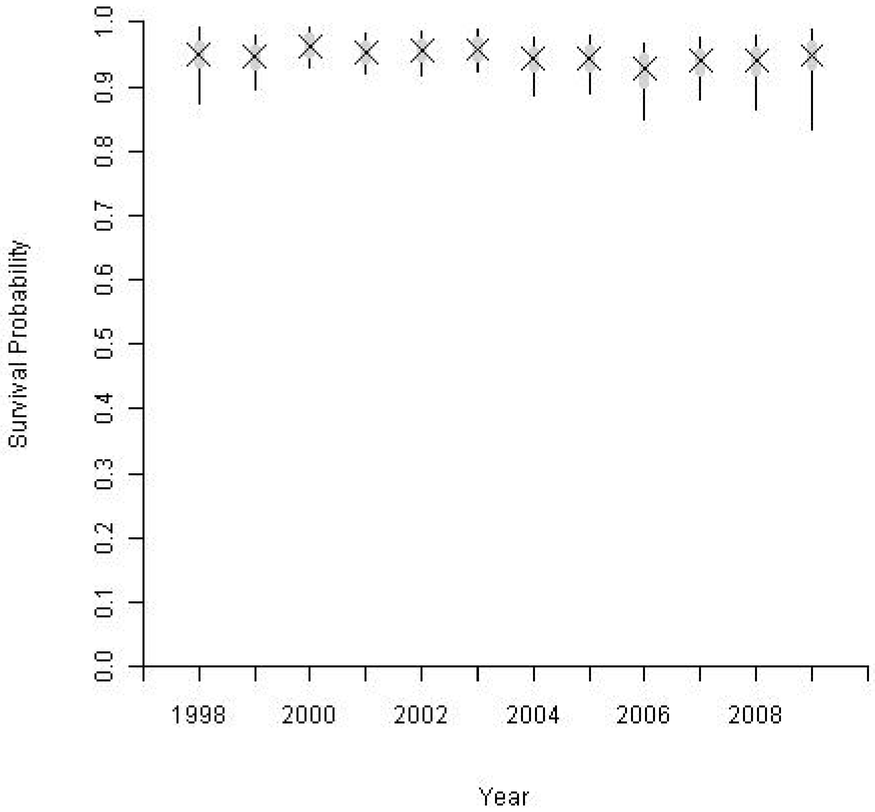


Figure 47: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were breeders aged 18 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses 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*.

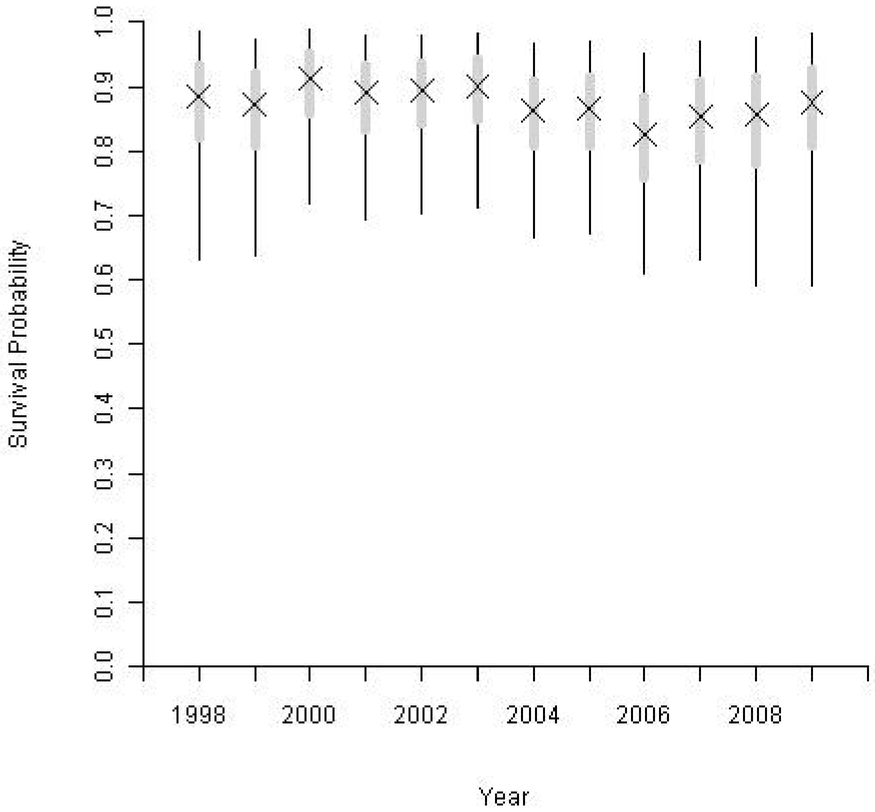


Figure 48: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were non-breeders of age in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses 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*. Note the width of the posterior distributions incorporate both annual variation and estimation uncertainty.

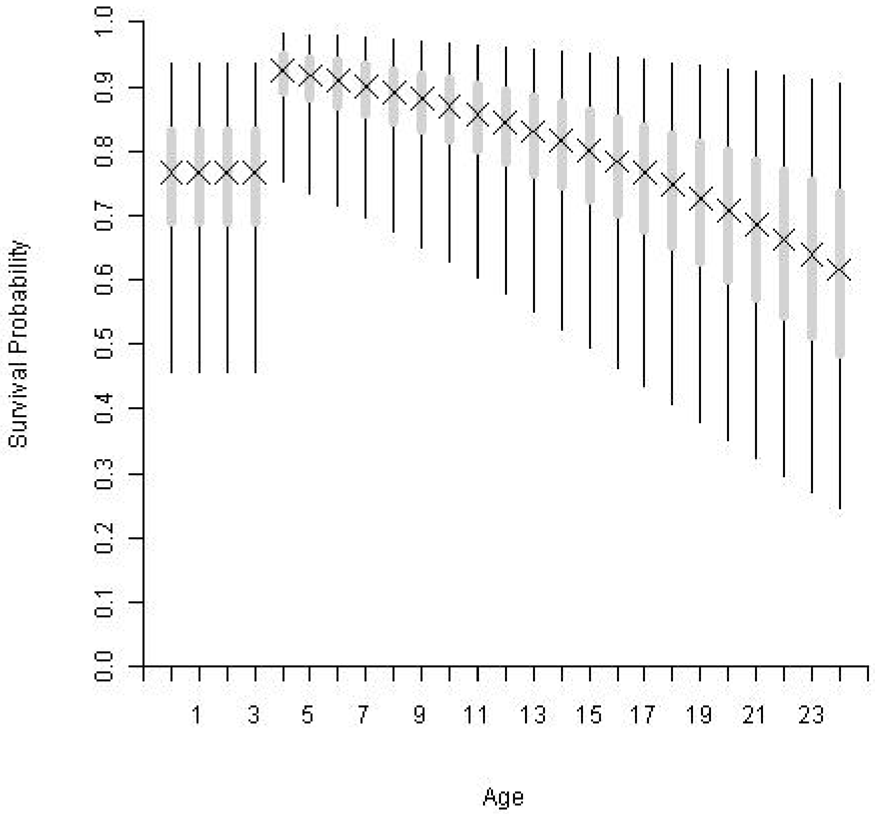


Figure 49: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were breeders of age in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses 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*. Note the width of the posterior distributions incorporate both annual variation and estimation uncertainty.

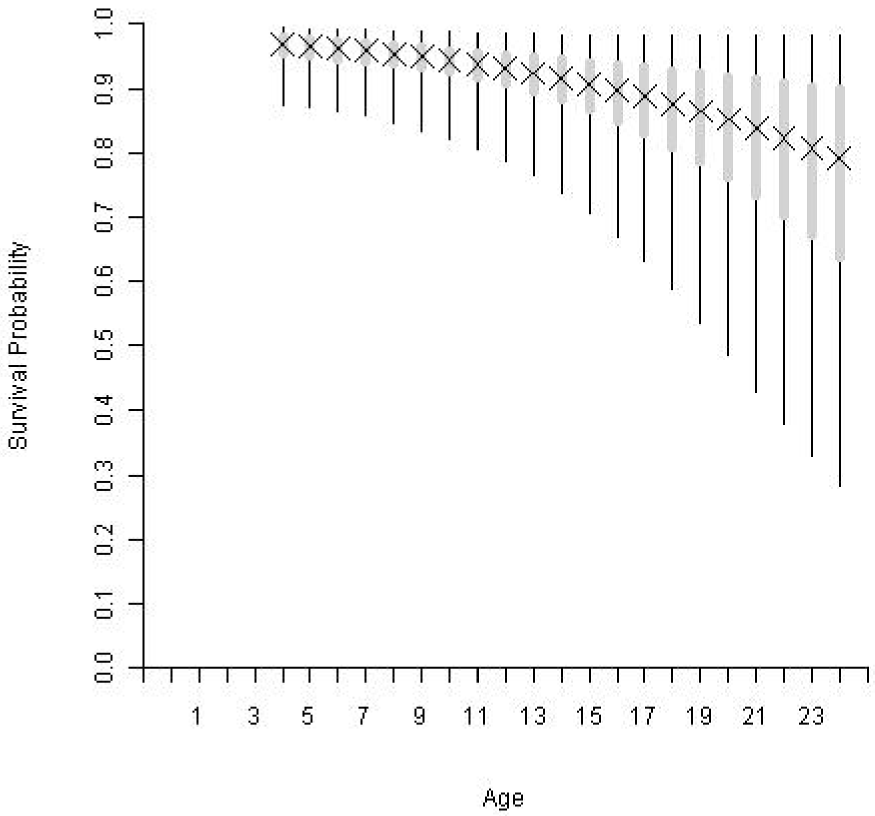


Figure 50: Posterior distribution for probability of breeding in year *t*+1 for individuals that were non-breeders aged 9 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate 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.

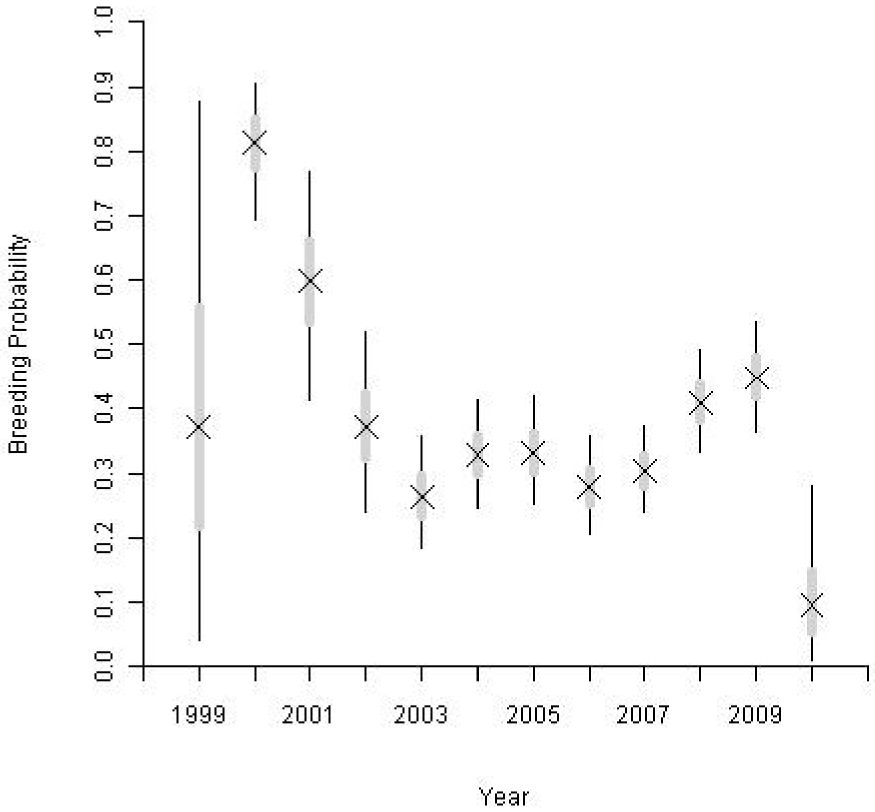


Figure 51: Posterior distribution for probability of breeding in year *t*+1 for individuals that were non-breeders aged 18 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate 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.

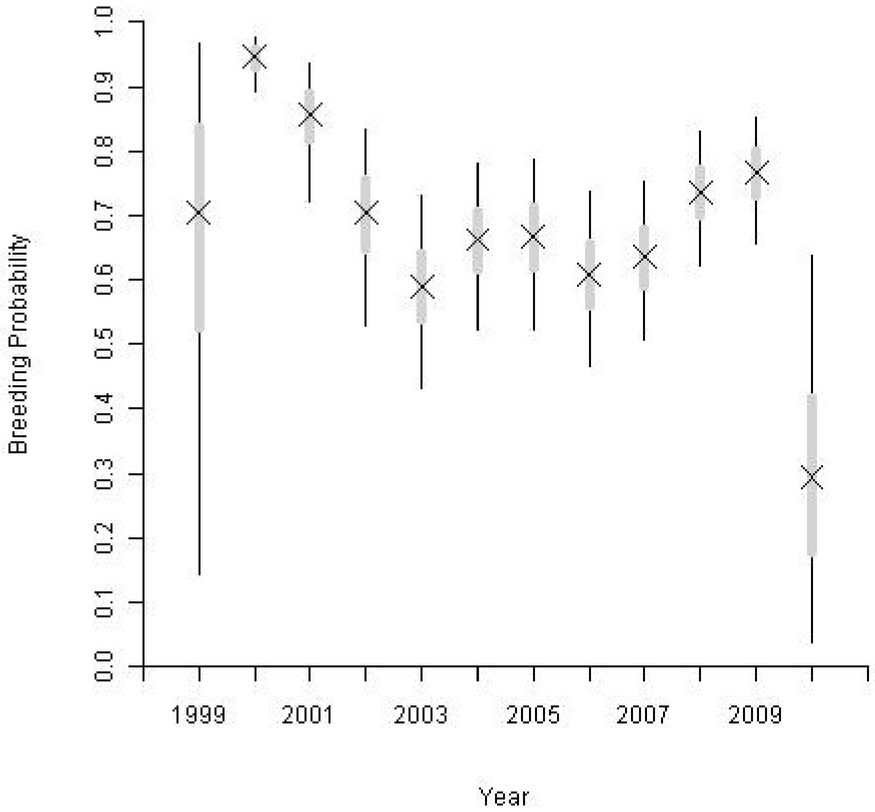


Figure 52: Posterior distribution for probability of breeding in year *t*+1 for individuals that were breeders aged 9 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate 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.

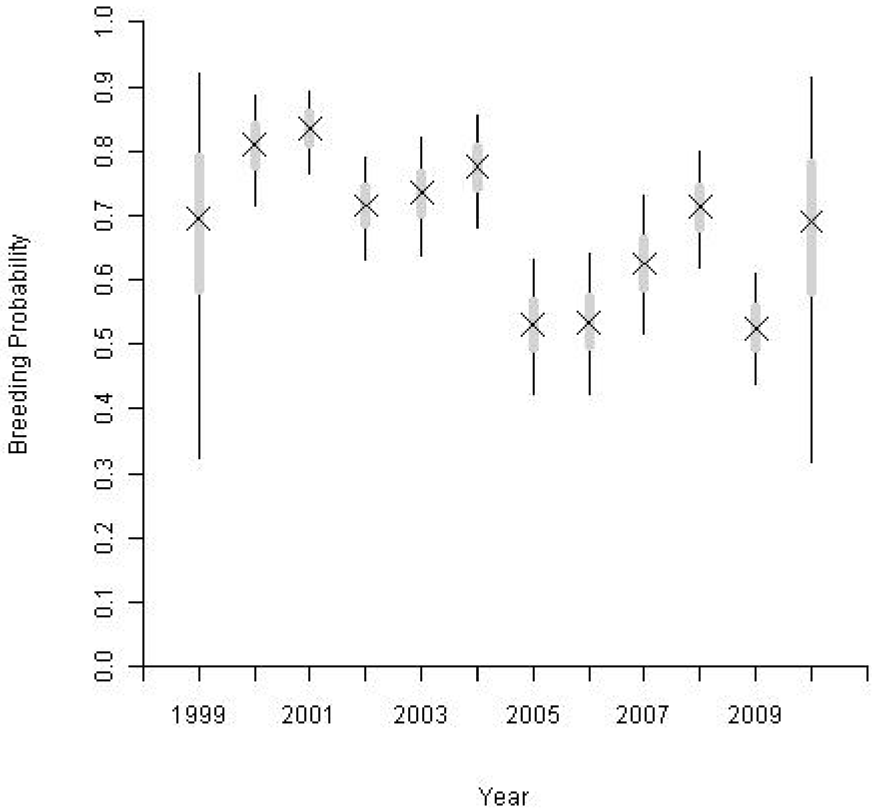


Figure 53: Posterior distribution for probability of breeding in year *t*+1 for individuals that were breeders aged 18 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate 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.

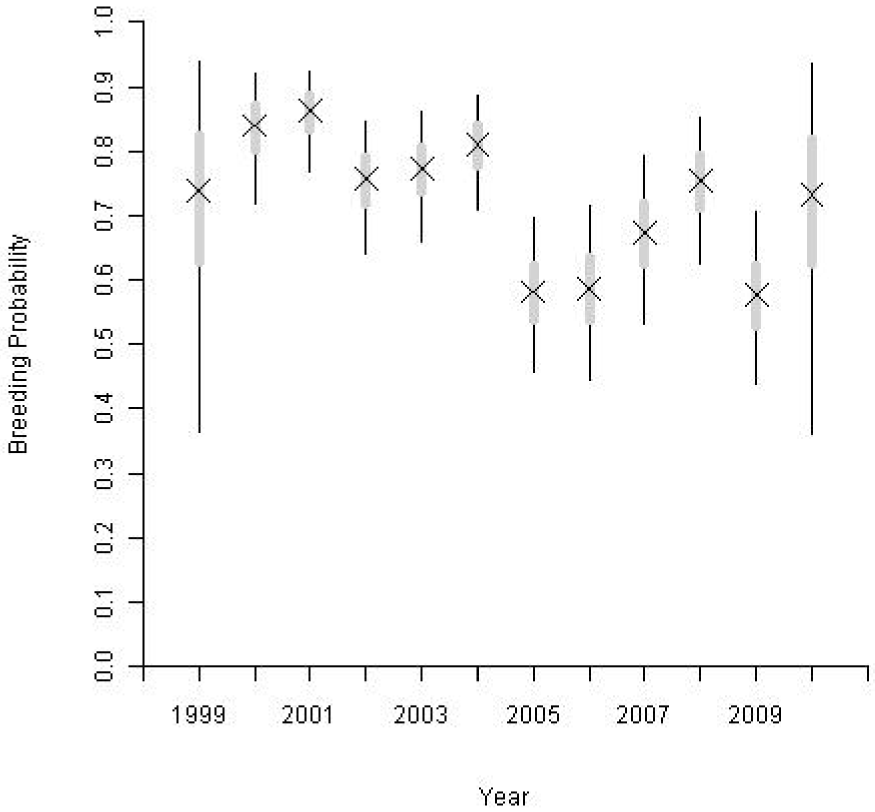


Figure 54: Posterior distribution for probability of breeding in year *t*+1 for individuals that were non-breeders of age in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate 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. Note the width of the posterior distributions incorporate both annual variation and estimation uncertainty.

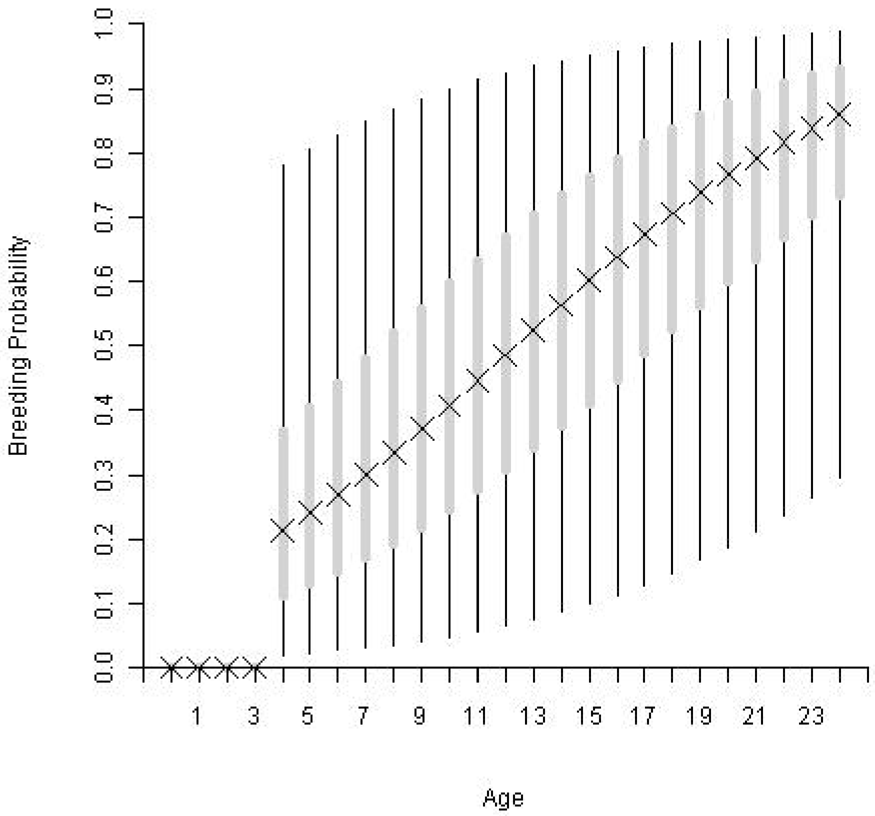
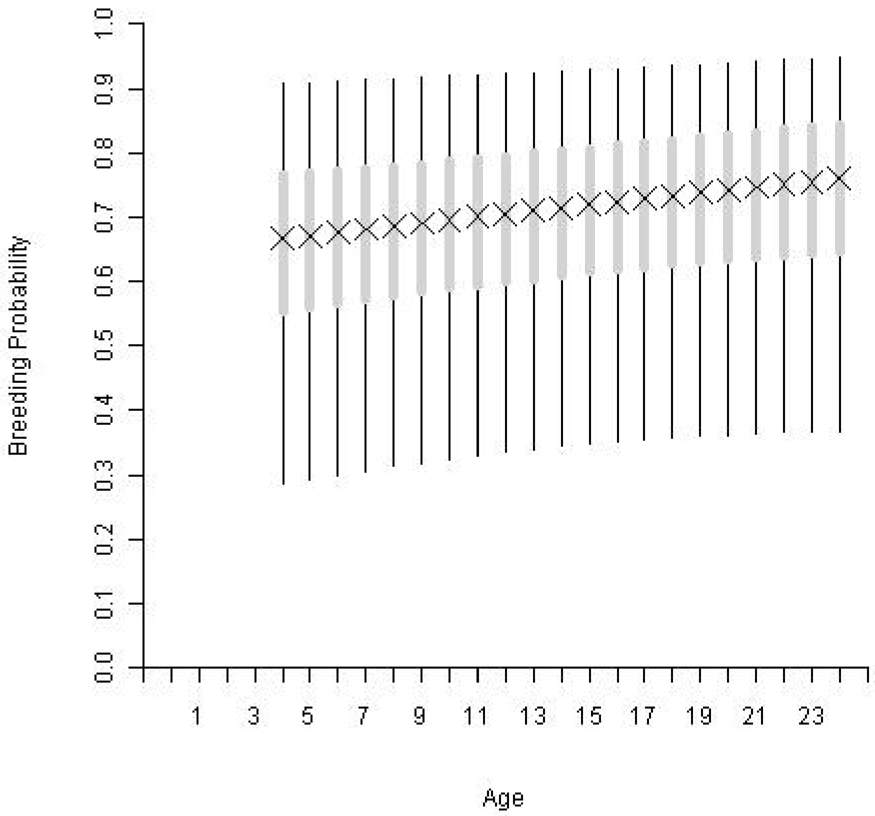


Figure 55: Posterior distribution for probability of breeding in year *t*+1 for individuals that were breeders of age in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate 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. Note the width of the posterior distributions incorporate both annual variation and estimation uncertainty.



Tables

Table 1: 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	0.11 (0.10, 0.13)
	1	0.89 (0.87, 0.90)
2	0	0.04 (0.03, 0.06)
	1	0.14 (0.13, 0.16)
	2	0.81 (0.80, 0.83)

Appendix 1

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])

		psi[aa,1] ~ dunif(0,1)		### zero-inflation factor

	}


	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])

			psi[aa, ii] ~ dunif(0,1)	### zero-inflation factor

		}
	}


### 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
    for (aa in 1:3) {           ## age group
        for (ii in 1:2) {       ## breeding status
            for (jj in 1:13) {  ## year
                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

                ## p[Brand+1,Chip+1,age group,tags,bred,alive,time]
                for (zz in 1:3) {                                   ## tags
                    for (yy in 1:2) {                               ## chipped
                        p[2,yy,aa,zz,ii,2,jj] <- pBrand[aa,ii,jj]   ## alive branded animals; tags have no effect
                        p[2,yy,aa,zz,ii,1,jj] <- 0                  ## dead branded animals
                        p[1,yy,aa,zz,ii,1,jj] <- 0                  ## dead unbranded animals
                    }
                }

                ## alive unbranded animals
                p[1,2,aa,1,ii,2,jj] <- pChip[aa,ii,jj]      ## unbranded, chipped, no tags
                p[1,1,aa,1,ii,2,jj] <- 0                    ## unbranded, unchipped, no tags

                for (yy in 1:2) {                           ## chipped
                    p[1,yy,aa,2,ii,2,jj] <- pT1[aa,ii,jj]   ## unbranded, 1 tag
                    p[1,yy,aa,3,ii,2,jj] <- pT2[aa,ii,jj]   ## unbranded, 2 tags
                }

            }
        }
    }
    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], ])

            temp[ii,jj] ~ dbern(psi[Bred[ii,jj-1],AgeCat2[Age98[ii]+jj]])
            tempp[ii,jj] <- temp[ii,jj]*p[Brand[ii]+1, Chip[ii]+1, AgeCat[Age98[ii]+jj],Tags[ii,jj], Bred[ii,jj], Alive[ii,jj],jj]
            Cap[ii,jj] ~ dbin(tempp[ii,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(tempp[ii,jj] ))+
                                                                    (T[jj]-Cap[ii,jj])*max(-99999, log(1-tempp[ii,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], ])

            temp.Pred[ii,jj] ~ dbern(psi[Bred.Pred[ii,jj-1],AgeCat2[Age98[ii]+jj]])
            tempp.Pred[ii,jj] <- temp[ii,jj]*p[Brand[ii]+1, Chip[ii]+1, AgeCat[Age98[ii]+jj],Tags.Pred[ii,jj], Bred.Pred[ii,jj], Alive.Pred[ii,jj],jj]
            Cap.Pred[ii,jj] ~ dbin(tempp.Pred[ii,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(tempp.Pred[ii,jj] ))+
                                                           (T[jj]-Cap.Pred[ii,jj])*max(-99999, log(1-tempp.Pred[ii,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
```