Estimation of Demographic Parameters for New Zealand Sea Lions Breeding on the Auckland Islands
- Final Report: 1997/98-2010/11

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Executive Summary

- Tag-resight data from female New Zealand sea lions on Enderby Island, collected between 1997/98-2010/11, was analysed to estimate survival and breeding probabilities.
- Multi-state mark-recapture models were used for the estimation within a Bayesian statistical framework.
- Demographic parameters were presumed to vary annually, and also due to age and breeding status. Females with differing numbers of tags or other markings were presumed to have different daily resighting rates. Daily resighting rates were also presumed to vary annually and by age.
- Two definitions of breeder were used based upon the recorded status of a female; a strict and more liberal definition.
- For each data set, four models were compared to determine which best represented the data. The four models represented combinations of two factors being considered; 1) whether age relationships were best described using 3 age-classes (0-3, 4-14 and 5+) or a linear-logistic relationship; and 2) whether the number of resights per season per females was best described by a binomial or zero-inflated binomial distribution.
- For both data sets, the models with the zero-inflated binomial distribution performed better, though there was little separation between the age-classes and linear-logistic models.
- Average survival probabilities of prime-age females (around 9-years old) was approximately 0.90 for non-breeding females and 0.95 for breeding females, using both data sets. Survival was lower for females that were much older or younger than this. There was no discernible temporal pattern in survival probabilities.
- Average breeding probabilities of prime-age females was approximately 0.30 and 0.65 for females that did not breed and did breed in the previous year respectively, using the stricter definition of breeder. Using the more liberal definition of breeder, average breeding probabilities were, approximately 0.35 and 0.68 for females that did not breed and did breed in the previous year respectively. While there were some apparent temporal patterns in estimated breeding probabilities, these are possibly confounded with a changing age-structure or tagged females.
- An exploratory analysis was conducted using an alternative approach to representing the nature of the relationship between age and demographic parameters that does not require the general parametric form to be defined a priori, allowing the data to have greater influence in determining the general form of the relationship. The exploratory models fit the data better than those used in the primary analysis although a number of issues remain to be fully considered before a full analysis is recommended using this approach. The general method does hold some promise for future analyses.

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 2010/11 field season (MacKenzie 2009, 2010, 2011). The same models as used by MacKenzie (2011) have been fit to the updated data set, with the exception of the models that allowed the zero-inflation factor to vary independtly for each year and age class.

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

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

Number of tags in year t|alive in year t, number of tags in $t-1 \sim multinomial\left(\boldsymbol{T}_{tags},\,1\right)$ (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, 2011), 3 age classes are considered here: 0-3, 4-14, 15+, as was a logit-linear relationship with age 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, i.e., 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:

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

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

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

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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. Two 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.

In all, a total of four models were fit the data. That is, for each of the 2 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 at least 30,000 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 with the resightings from the 2008/09 and 2009/2010 field seasons, along with all resightings for females tagged as pups in 2003/2004 and 2004/2005 respectively (additional data supplied by Louise Chilvers, DOC), for the analyses presented in MacKenzie (2010) and MacKenzie (2011). The data used for this current analysis is the same as that used by MacKenzie (2011), updated with the resighting data from the 2010/2011 field season and includes females tagged as pups in 2005/2006. 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 10,000 minimum burn in period, although in some instances convergence did take longer to achieve. 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 the 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. There are five additional parameters in the models associated with estimating the zero-inflation. 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. There is little to distinguish between the age-class and logit-linear models otherwise, therefore the results of both models with the zero-inflation factor 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 may be some indication of a decline in breeding probability over time, however, any temporal pattern may be confounded somewhat with a changing age profile of tagged females (Appendix 2). 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.

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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, 2011), 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).

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Exploratory Analysis

An exploratory analysis was conducted using a non-parametric, curve-fitting technique (known as splines) to describe the relationship between the demographic parameters and sea-lion age. The spline procedure essentially fits a separate relationship between each successive pair of knots, which are predefined ages at which the relationship is allowed to change. Splines were used to describe the relationship between survival and age either for only those animals aged 4+, or for all animals. Knots of age 8 and 12, or 4, 8 and 12 were used respectively. For breeding probability, the spline relationship was only used for animals aged 4+, and it was assumed to be constant (and expected to be near zero) for younger females. The types of spline relationships considered were either linear or quadratic (on the logistic scale; eqns 6 and 7), where increasing the degree of the spline used results in a smoother overall curve.

$$\text{logit}(\theta_{a,t,b}) = \alpha_{0,b} + \alpha_{1,b}(a-4) + \sum_{k=1}^{K} [\beta_{k,b}(a-\kappa_k) I(a \geq \kappa_k)] + \varepsilon_{t,b} \tag{6}$$

$$\text{logit}(\theta_{a,t,b}) = \alpha_{0,b} + \sum_{j=1}^{2} \alpha_{j,b}(a-4)^j + \sum_{k=1}^{K} [\beta_{k,b}(a-\kappa_k)^2 I(a \geq \kappa_k)] + \varepsilon_{t,b} \tag{7}$$

In eqns 6 and 7, a is sea-lion age, K is the number of knots, κ_k is the knot value, $I(a \geq \kappa_k)$ is an indicator function that equals 1 if the sea-lion age is greater than a particular knot value and equals 0 otherwise. The parameters to be estimated are α which is a typical fixed-effect regression coefficient, and the β parameters are random values from a normal distribution with mean = 0 and standard deviation = σ_θ. The methods of Crainiceanu et al. (2005) and Gimenez et al. (2006) were used to apply the spline procedure in WinBUGS.

Only the data using the stricter definition of breeder was considered here, and all models included a zero-inflation factor for the detection of sea-lions each year. A comparison of the four exploratory models fit to the data, along with the two best models fit in the primary analysis, is presented in Figure 56. The two exploratory models that used a spline relationship only for sea-lions aged 4+ are better fits to the data than the two models from the primary analysis, whereas the best fitting models are those that use the spline relationship for all ages. The resulting relationships between the demographic parameters and age are illustrated in Figures 57-60. Generally, the linear and quadratic splines give similar results, except for the older ages, where there is very little data, hence the curve is this region may be more prone to

the vagaries of small samples. Survival probabilities (Figures 57-58) remain higher for medium-aged females, before decreasing more sharply for older individuals, compared to the results from the logit-linear model. When the spline approach is extended back to the 0-3 age group, survival probabilities appear to increase for younger animals, although resighting rates for younger individuals is low. Breeding probabilities for females that did not breed in the previous year (Figure 59) initially increase rapidly from age 4 to age 9, after which they then decrease then slowly raise again from age 12, although as before this is an area in which data is relatively sparse. Breeding probabilities for females that had bred in the previous year (Figure 60) are surprisingly consistent with age. It is noted that using the spline approach, the annual breeding probabilities for females that did not breed in the previous year do not exhibit a dip in the mid 2000's as when using the age-class or logit-linear relationship between age and demographic parameters. It has been suggested previously that this dip may be the result of the changing age distribution within the 'non-breeder' cohort given that tagging has only been of primarily pups since the late 1990's.

From this exploratory analysis, the spline approach holds some promise for future analyses as it avoids the need to specify a general parametric form for the nature of any relationship, enabling the nature of the relationship to be driven by the data itself. This can also be viewed as a disadvantage, however, as it precludes scientific reasoning to define what type of relationship would be biologically reasonable (although that could be accomplished by careful thought and the use of informative prior distributions in a Bayesian analysis). There remain a number of technical considerations that would need to be addressed more thoroughly in a full analysis that used the spline approach considered here, including (but not limited to) the appropriate number and positioning of knots, convergence of the MCMC chains. Nonetheless, this exploratory analysis just suggest the spline approach may be generally feasible.

Discussion

Broadly similar conclusions are reached about the demographic parameters for female New Zealand sea lions from all of the primary analyses conducted. For prime-age females, average annual survival appears to be (approximately) 0.90 for females that did not breed and approximately 0.95 for females that did breed. There is no indication of a systematic change

in survival during the period 1997/98 – 2010/11 regardless of whether the stricter, or more liberal, definition of breeder is used. Average breeding probabilities for prime-age females that did not breed or did breed in the previous year was approximately 0.30 and 0.65 respectively using the stricter definition of breeder. While there is some evidence of temporal patterns in breeding probabilities, any systematic temporal change may be (at least) partially confounded with a changing age profile of tagged females, particularly for individuals that did not breed in the previous year. Using the more liberal definition of breeder, average breeding probabilities are higher, approximately 0.35 and 0.68 for females that did not breed and did breed in the previous year respectively.

The exploratory analysis of using splines to enable the data to determine the nature of the relationship between age and demographic parameters provided some promising results. It has greater flexibility than when using more parametrically-defined relationships that have to be specified a priori. The results suggested biologically plausible relationships that were a better fit to the data than the models considered in the primary analysis. However, there are a number of technical issues that would need further consideration prior to a full analysis using these methods, such as determination of the number and position of knots that do have to be defined a priori.

At the Conservation Services Programme Technical Working Group meeting of 21 October 2011 it was enquired whether it would be possible to track specific cohorts of sea lions to determine the impact of events such as disease outbreaks on their survival and reproductive output later in life. Theoretically it would be relatively straight forward to do so in a manner similar to that used to allow branded females to have a different resighting probability to unbranded individuals. A factor could be defined that indicates whether each females using born during a year of a disease event or not, with the effect of that factor then be estimated during the analysis. How reliable the results from such an approach would be in practice will depend upon potential confounding of other factors, but at this point I think the consequences of any confounding would be minimal.

Integrated modelling was also suggested as an analysis approach to estimate demographic parameters for New Zealand sea lions. The basic idea is to combine multiple data sources that

each provide some information of the population demographics in a single analysis with the intent that the combined analysis will yield better results than analyses of the individual data sets. Here the potential data sources that could be combined would be (presumably) pup counts and the tag-resight data. Such an approach was initially considered in the proposal for an earlier piece of related work (POP 2007/01, Objective 3), however it was not pursued due to time and budgetary constraints of the project. Integrated modelling approaches have some appeal, although they do require careful consideration and parametrisation to ensure that a demographic parameter common to both components of the integrated model as the exact same biological interpretation in the context of the individual data sets, and how those data sets were collected. There can also be issues of data quality versus quantity to consider and appropriately address. When combining data sets into a single analysis it is possible that a poor quality, large data set could overwhelm the more accurate information contained within a smaller, better quality data set leading to less reliable conclusions than what would have been reached from analysing the smaller data set alone. The concept of large and small data sets applies to the effective sample size and not necessarily how the data is represented within the analysis as a notionally smaller aggregated data set may have an effective sample size that is greater than a notionally larger finer-scale data set. In short, an integrated modelling approach will not necessarily provide more reliable inferences than a single-data set analysis.

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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.
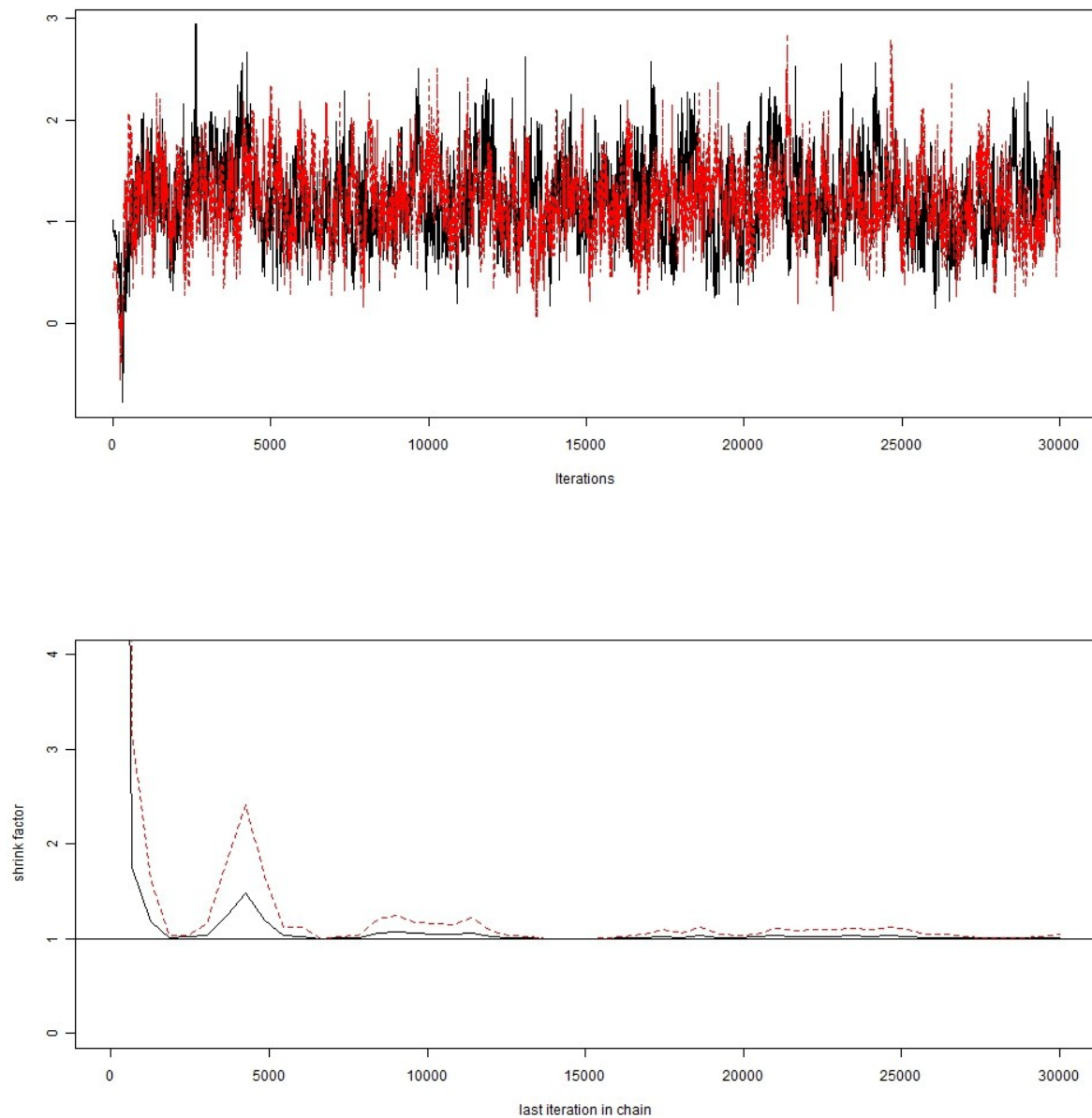
Figure 2: Example diagnostic plots of mean annual breeding probability for females that did bred and were aged 4-14 in previous year. Upper panel is a trace plot of the 2 chains and lower panel is the Gelman-Rubin-Brooks plot for convergence.
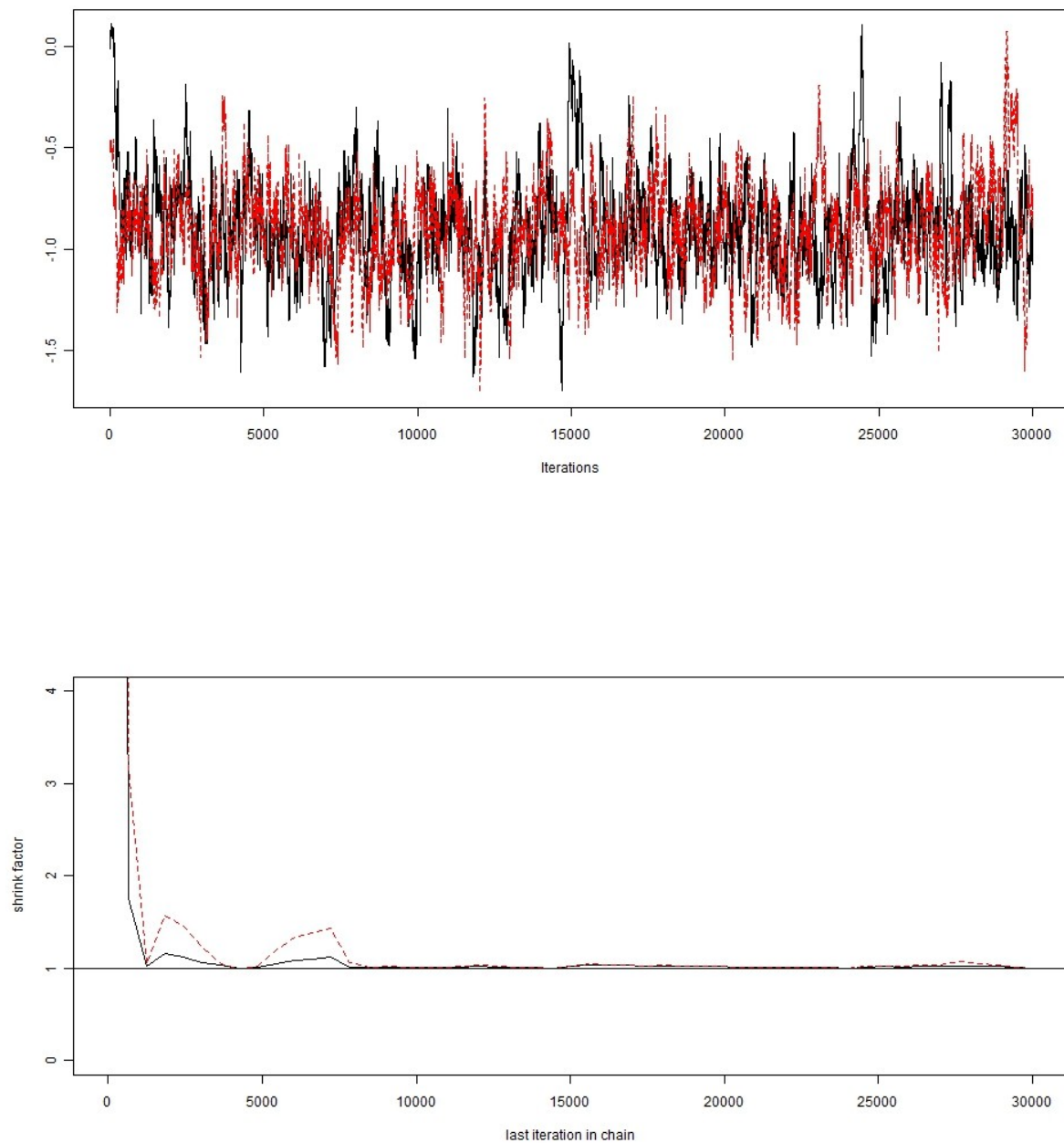
Figure 3: Example diagnostic plots of the standard deviation of annual survival for females that bred in the previous year. Upper panel is a trace plot of the 2 chains and lower panel is the Gelman-Rubin-Brooks plot for convergence.
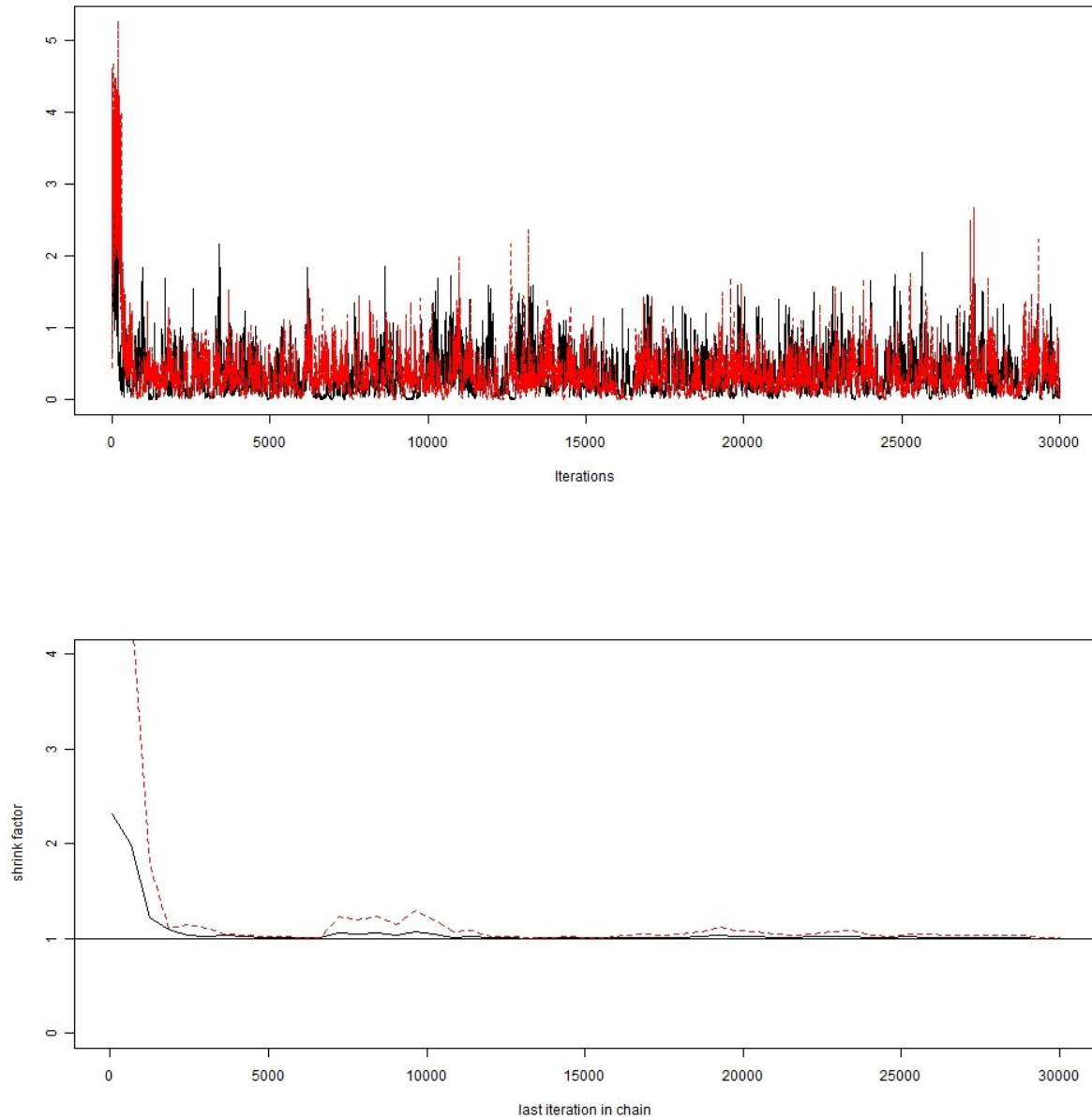
Figure 4: Posterior distribution for the daily probability of sighting a branded individual in each year by age class. Resight probabilities for which there was no information in the data are not indicated. Grey-shaded distributions indicate non-breeders and red-shaded distributions breeders. Years are denoted in terms of the calendar year associated with the January portion of the field season.
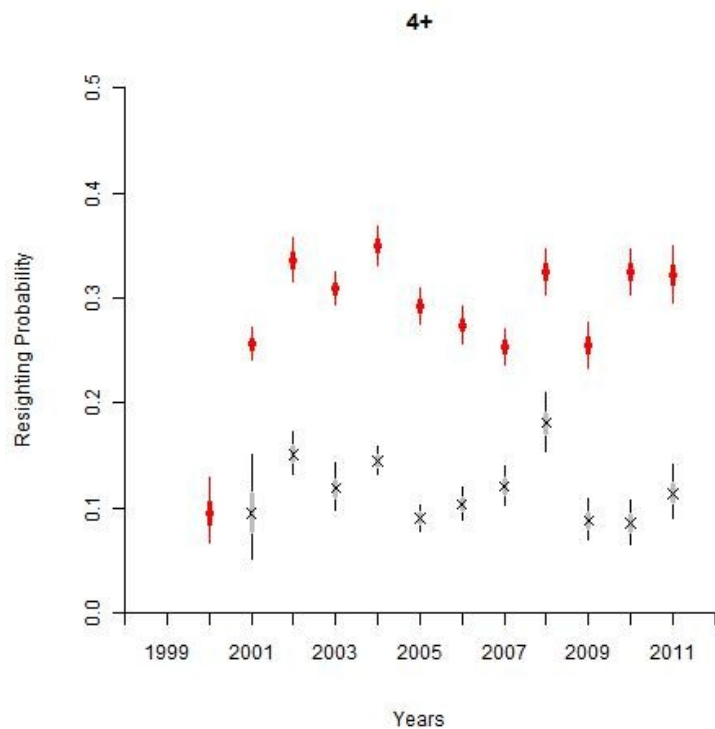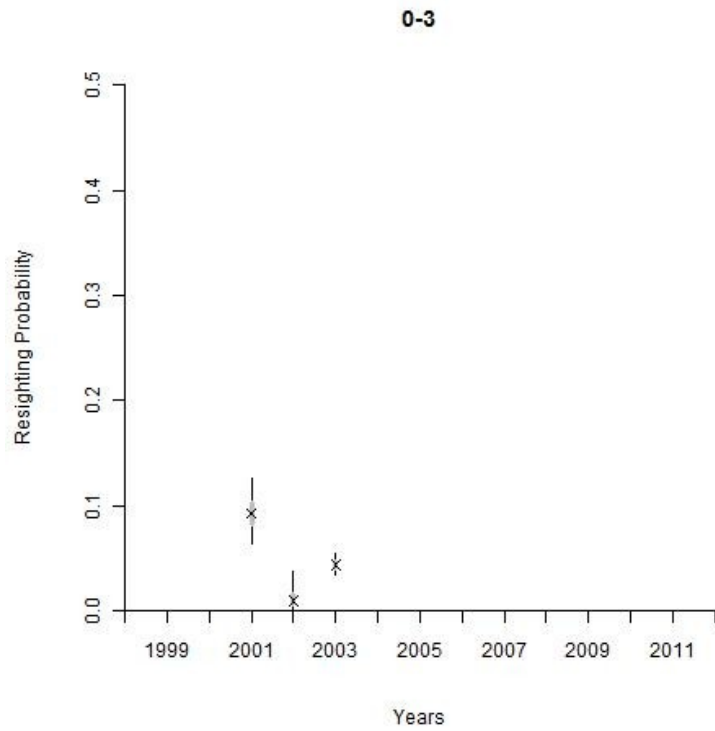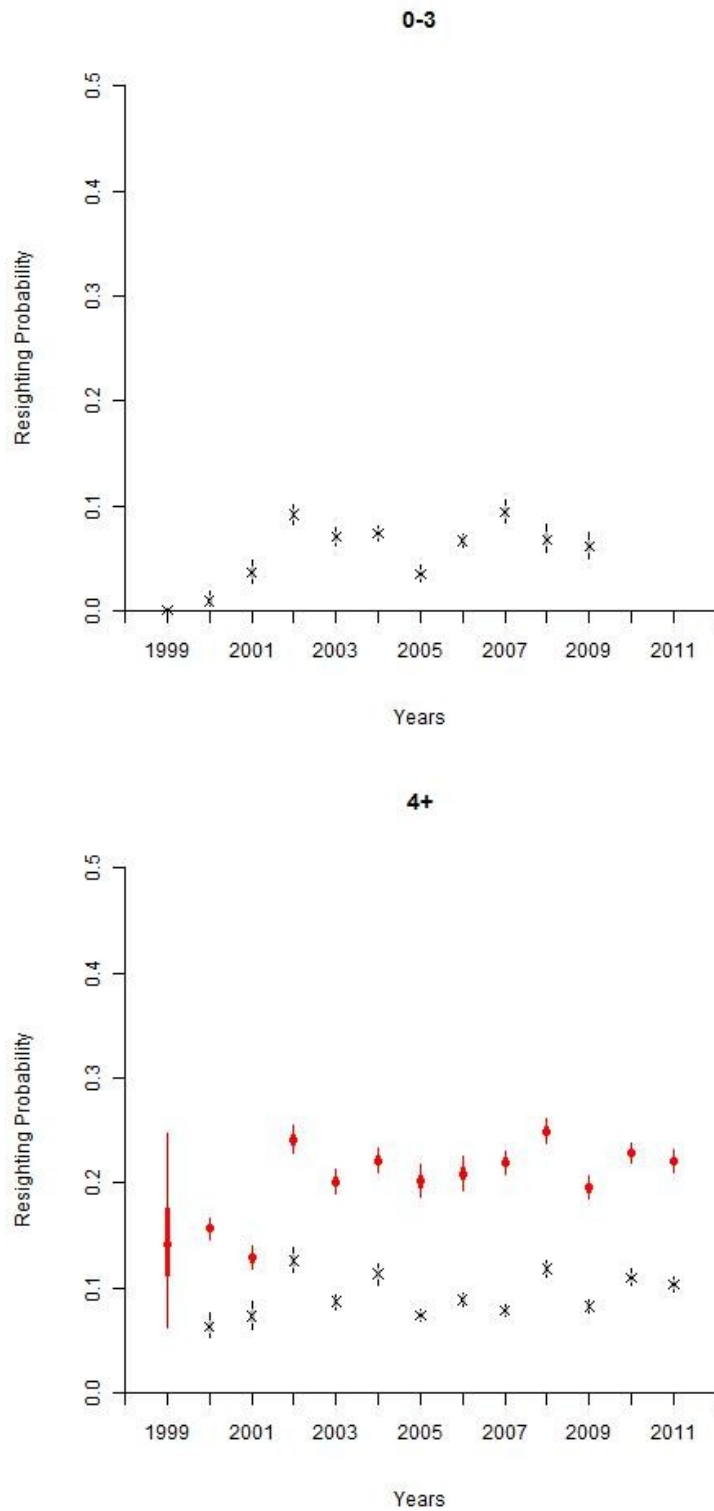
Figure 5: Posterior distribution for the daily probability of sighting a PIT tagged individual with no flipper tags in each year by age class. Resight probabilities for which there was no information in the data are not indicated. Grey-shaded distributions indicate non-breeders and red-shaded distributions breeders. Years are denoted in terms of the calendar year associated with the January portion of the field season.
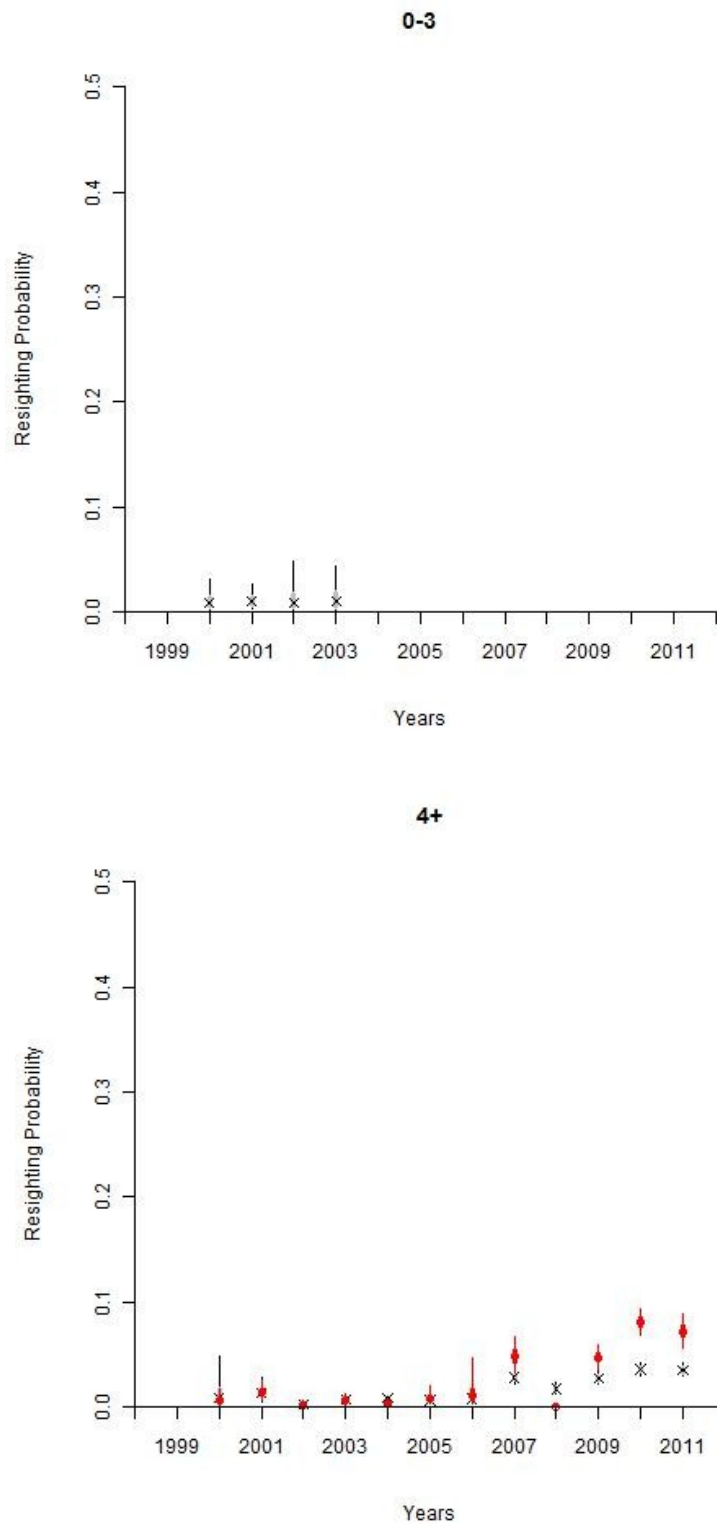
Figure 6: Posterior distribution for the daily probability of sighting an individual with 1 flipper tag in each year by age class. Resight probabilities for which there was no information in the data are not indicated. Grey-shaded distributions indicate non-breeders and red-shaded distributions breeders. Years are denoted in terms of the calendar year associated with the January portion of the field season.
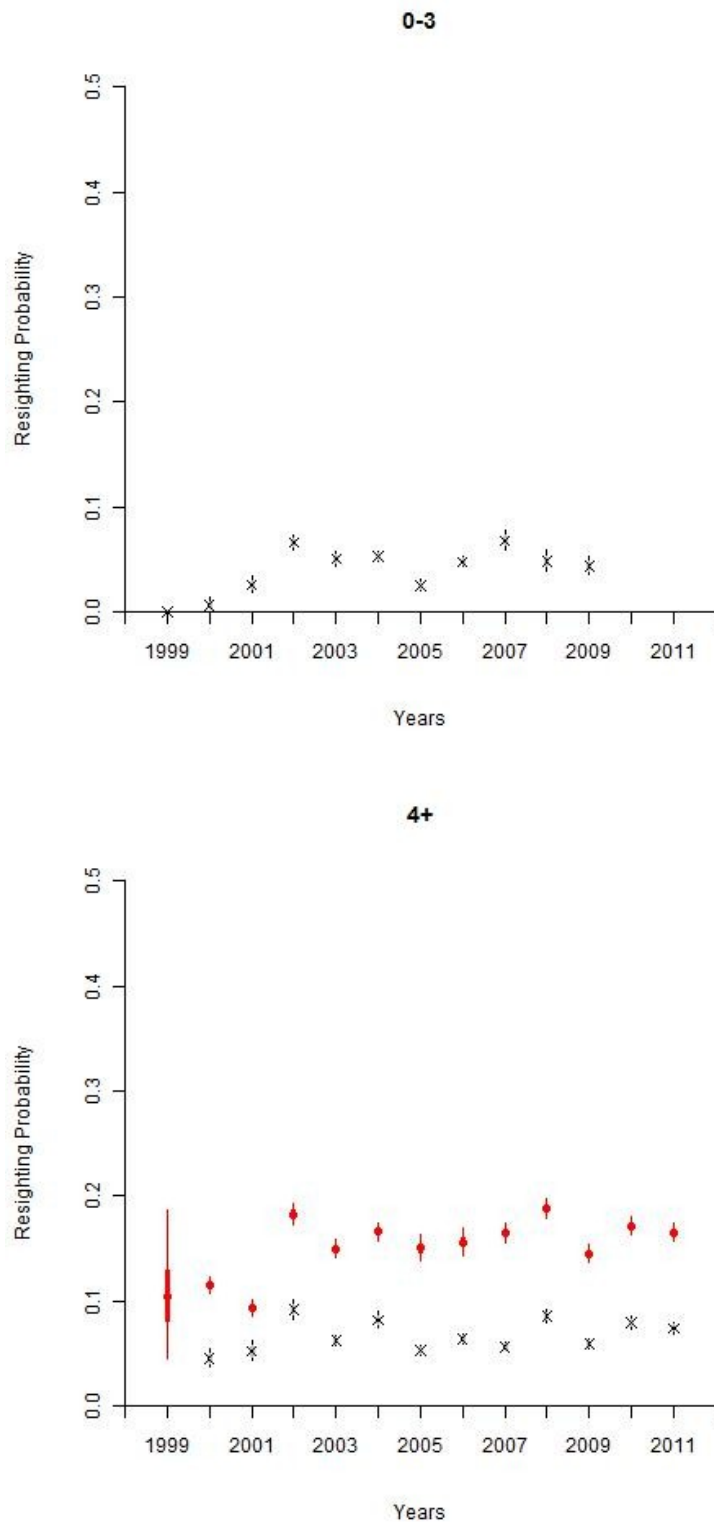
Figure 7: Posterior distribution for the daily probability of sighting an individual with 2 flipper tags in each year by age class. Resight probabilities for which there was no information in the data are not indicated. Grey-shaded distributions indicate non-breeders and red-shaded distributions breeders. Years are denoted in terms of the calendar year associated with the January portion of the field season.
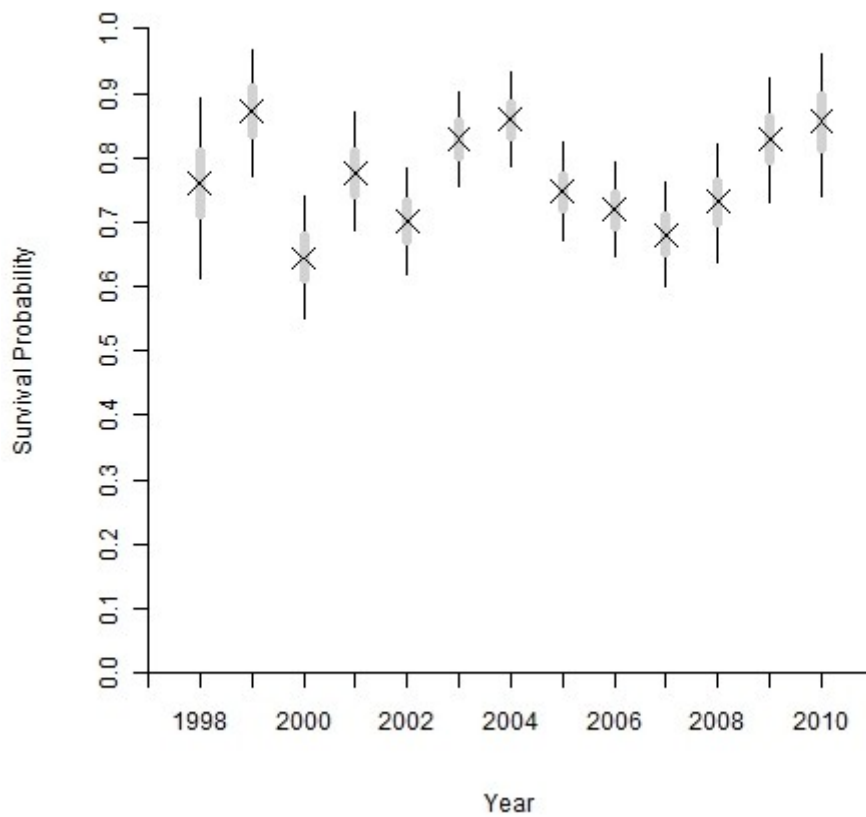
Figure 8: Using the strict definition of breeder, posterior distributions for the deviance value from models with 3 age-classes and; temporally-constant zero-inflation (black, mostly obscured on right); and no zero-inflation (charcoal, mostly obscured on left). Posterior distributions for the deviance value from models with linear age relationship and; temporally-constant zero-inflation (medium grey); and no zero-inflation (light grey). Smaller values indicate a better fit to the data.
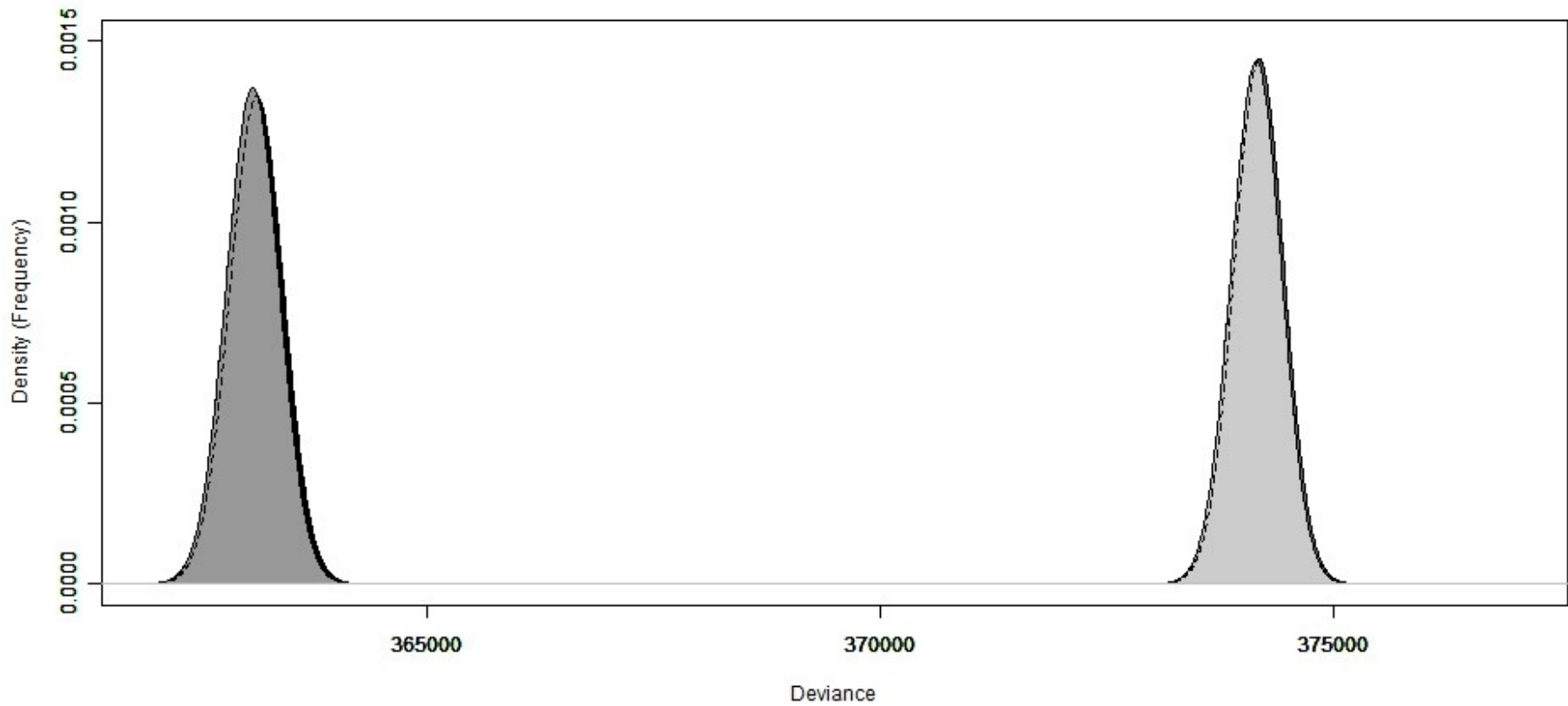
Figure 9: Plots of posterior (light grey) and predicted (dark grey) deviance values from each model with data using the strict definition of breeder. Bayesian p-values are indicated.

3 Age Groups, No Zero-inflation

p-value = 0.041

3 Age Groups, Zero-inflation

p-value = 0.157

Linear Age Effects, No Zero-inflation

p-value = 0.043

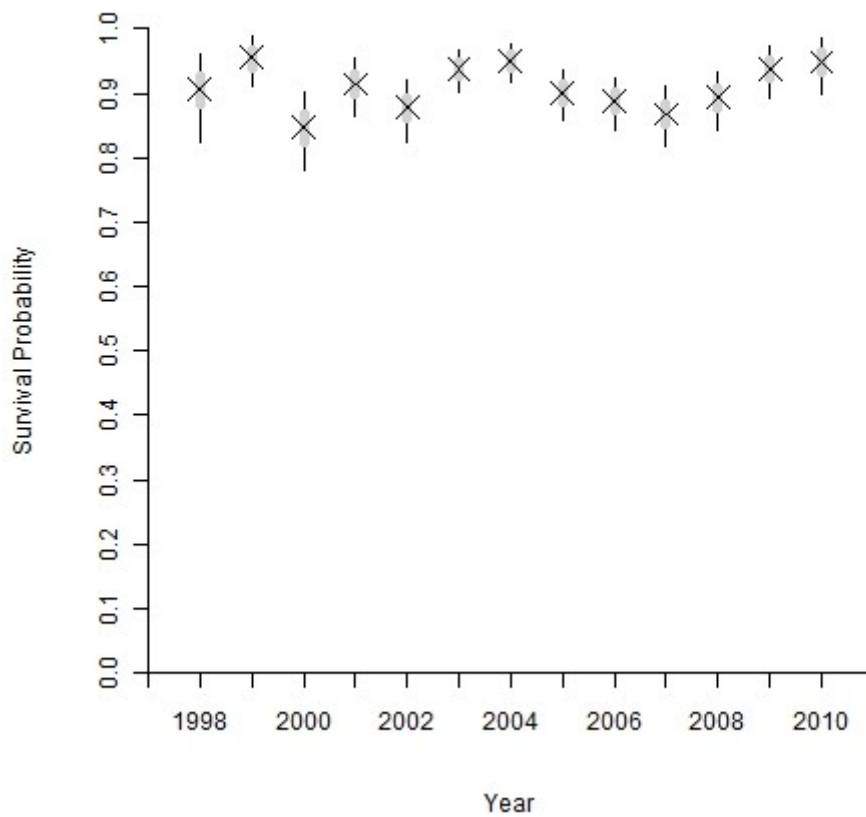Linear Age Effects, Zero-inflation

p-value = 0.168
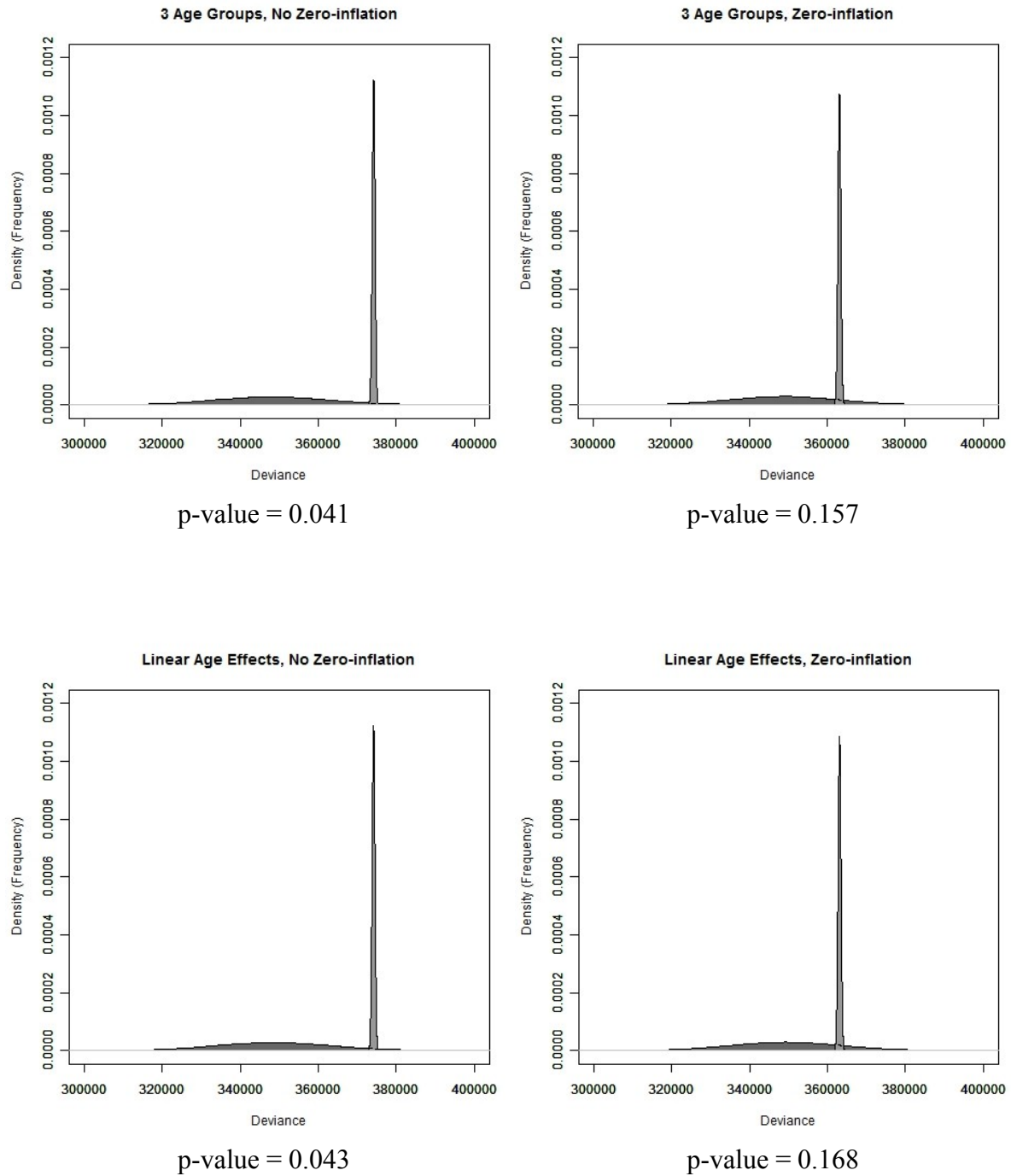
Figure 10: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were non-breeders aged 0-3 in year t, from model using age classes and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the median of the distribution, 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.
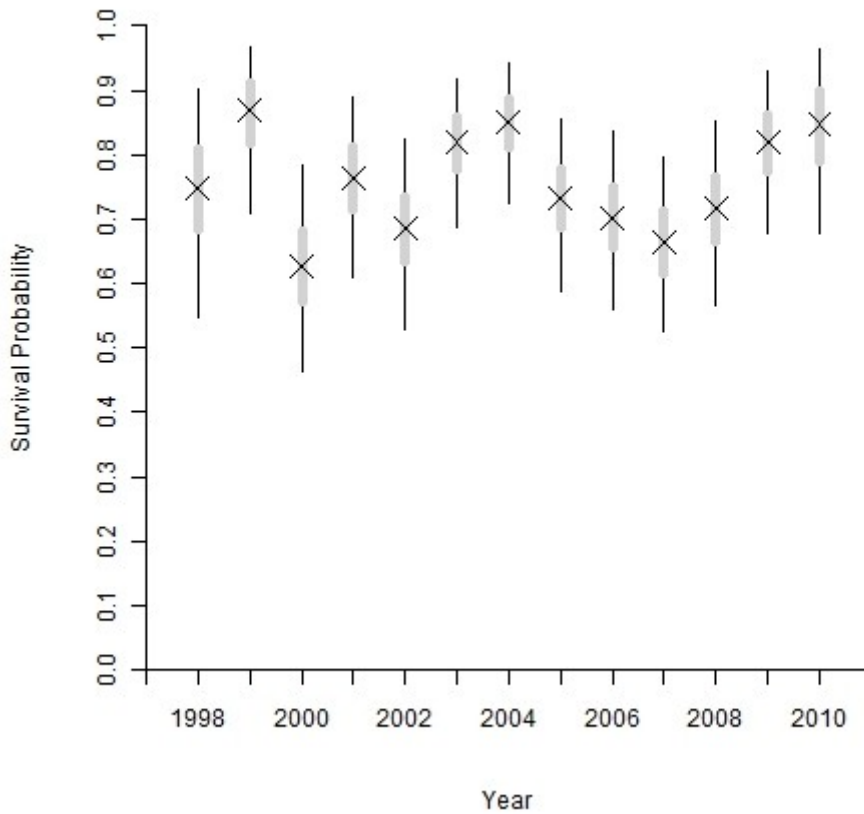
Figure 11: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were non-breeders aged 4-14 in year t, from model with age classes and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the median of the distribution, 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.
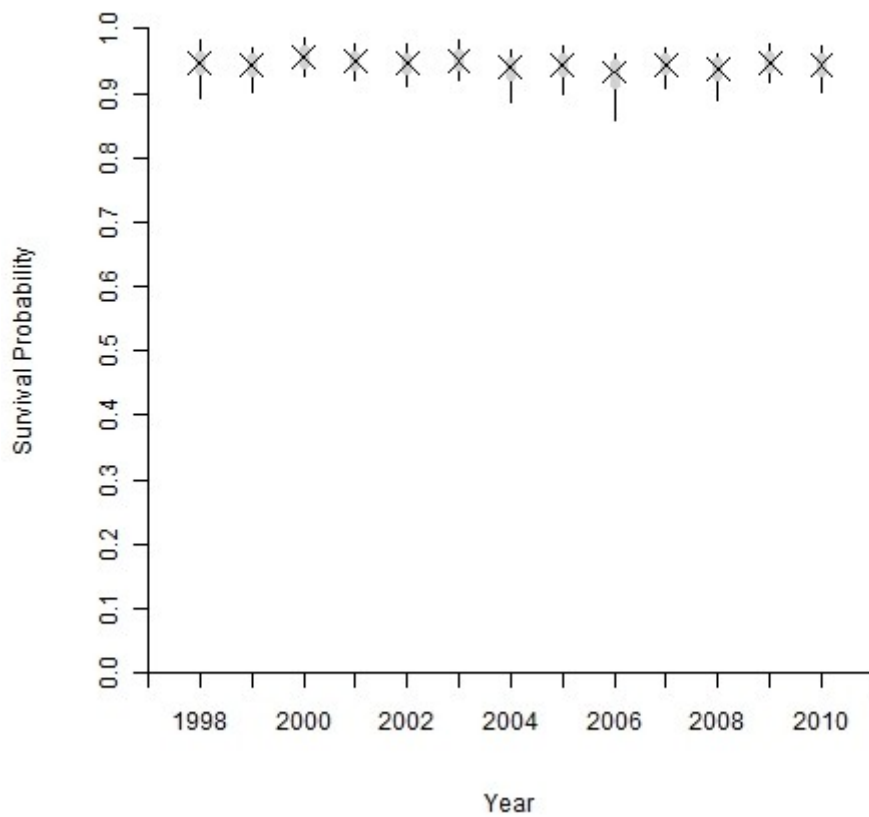
Figure 12: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were non-breeders aged 15+ in year t, from model with age classes and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the median of the distribution, thick 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.
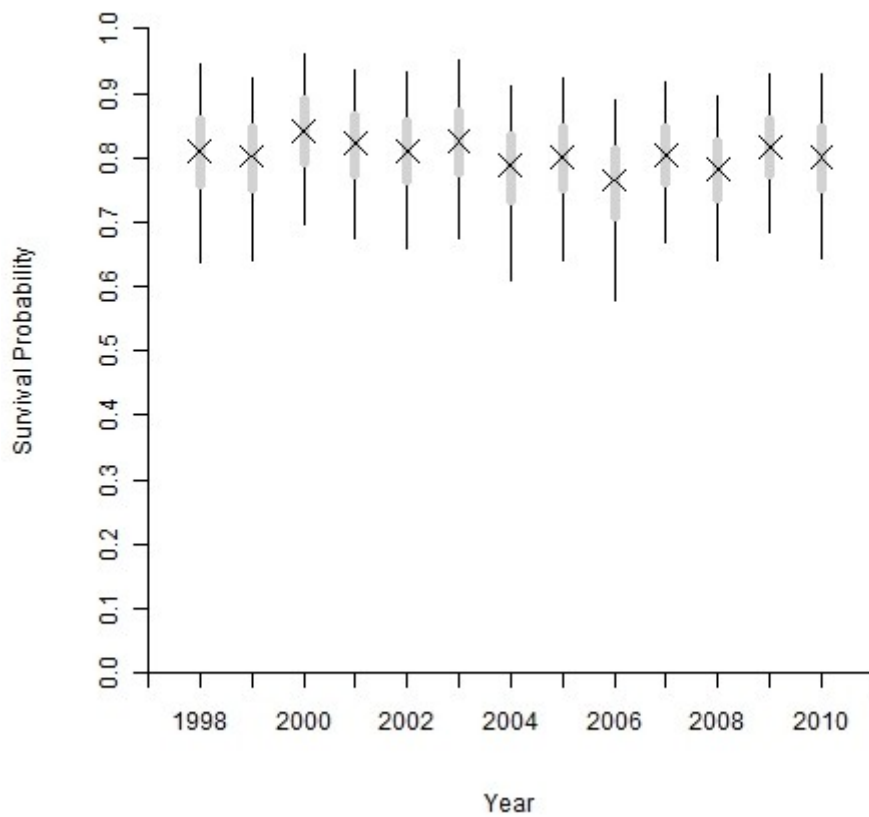
Figure 13: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were breeders aged 4-14 in year t, from model with age classes and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the median of the distribution, thick 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.
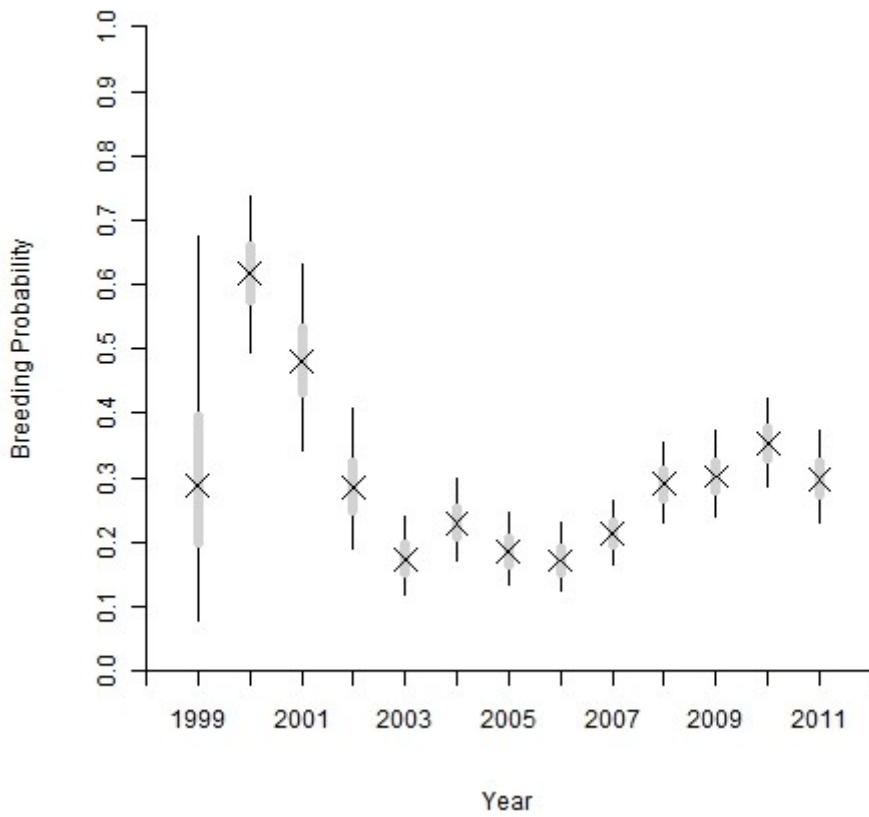
Figure 14: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were breeders aged 15+ in year t, from model with age classes and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the median of the distribution, thick 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.
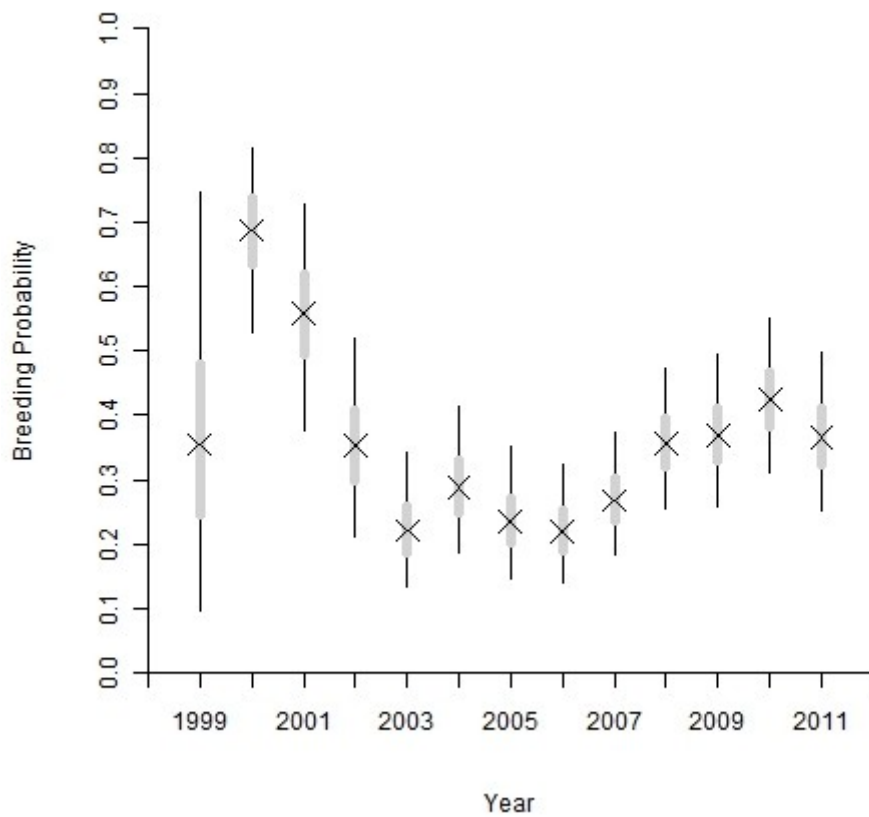
Figure 16: Posterior distribution for probability of breeding in year $t+1$ for individuals that were non-breeders aged 15+ in year t, from model with age classes and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey 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 $t+1$.
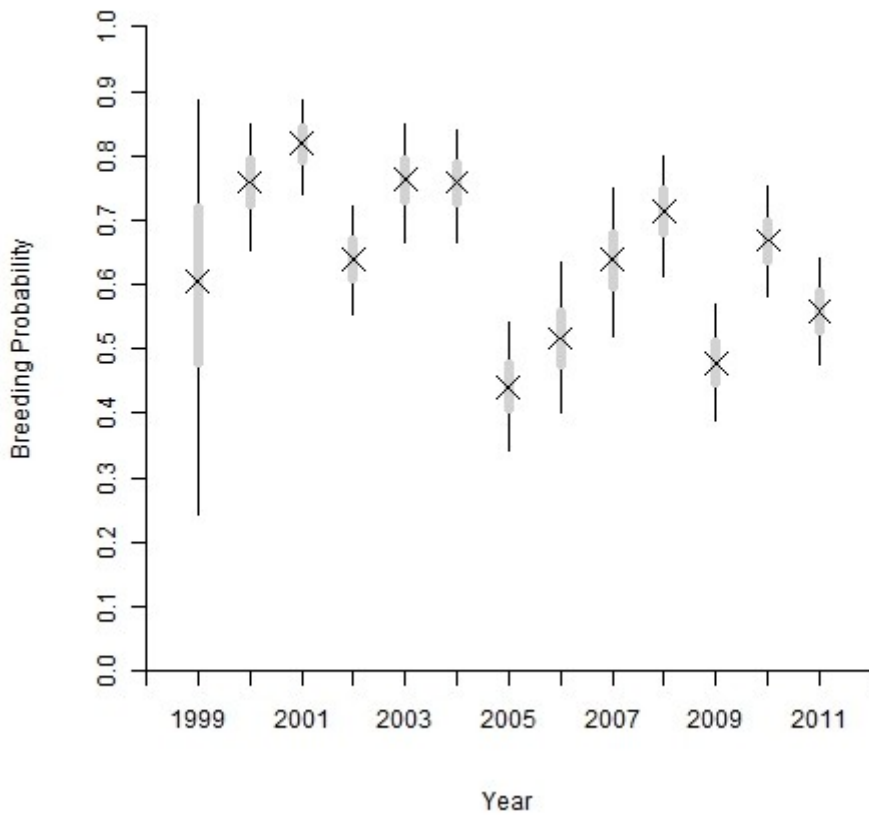
Figure 17: Posterior distribution for probability of breeding in year $t+1$ for individuals that were breeders aged 4-14 in year t, from model with age classes and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey 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 $t+1$.
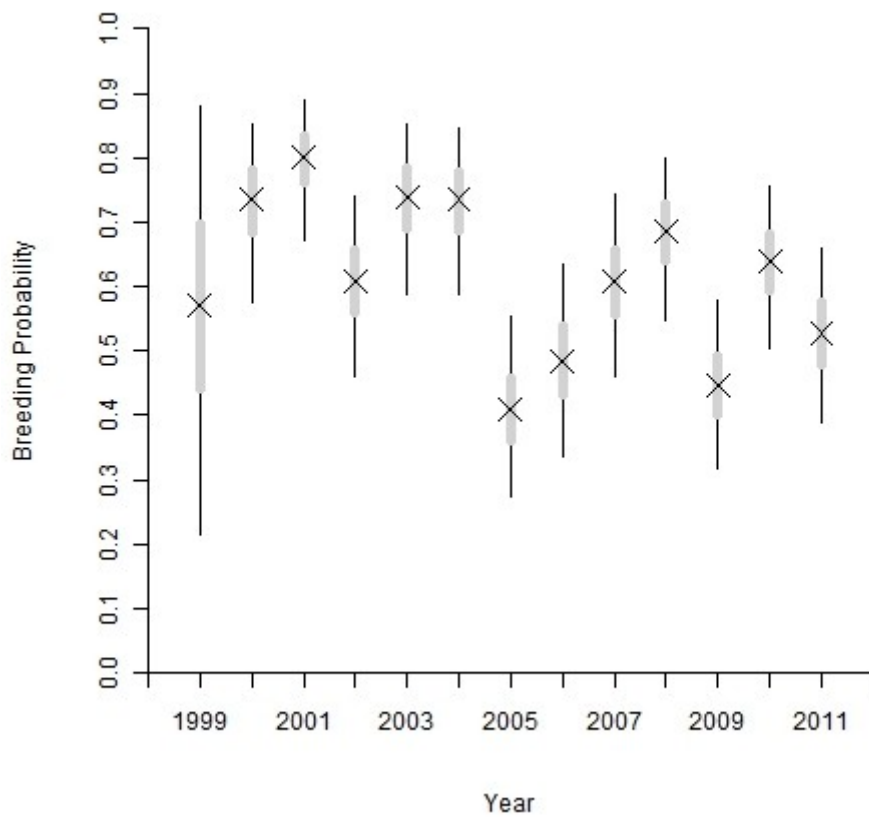
Figure 18: Posterior distribution for probability of breeding in year *t*+1 for individuals that were breeders aged 15+ in year *t*, from model with age classes and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the median of the distribution, thick grey 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.
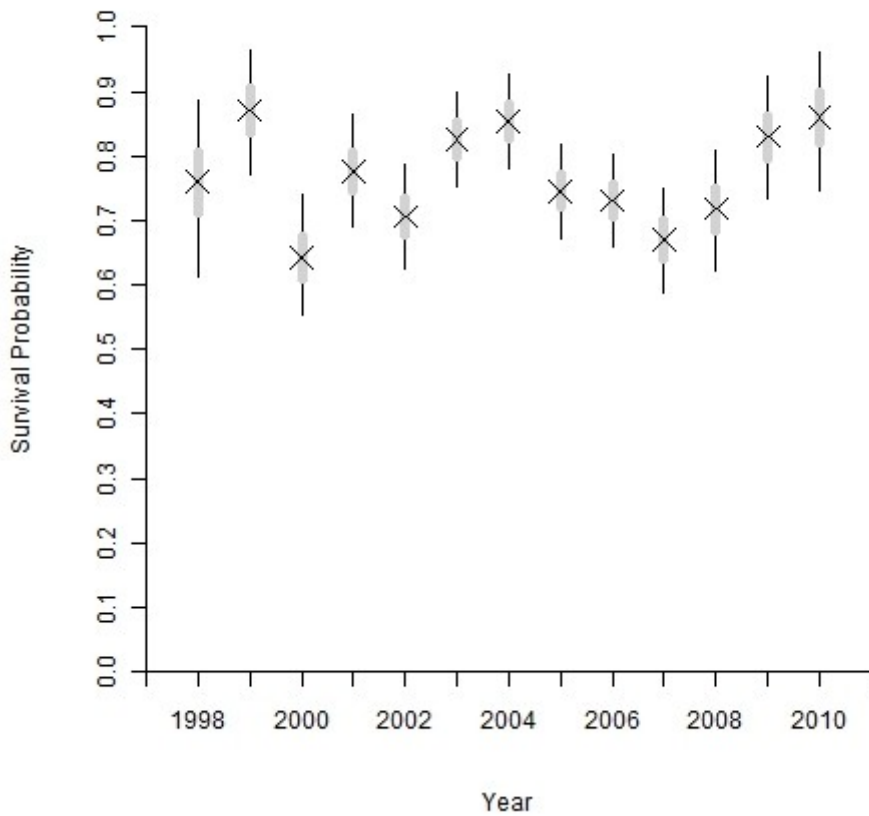
Figure 19: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were non-breeders aged 0-3 in year t, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses 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.
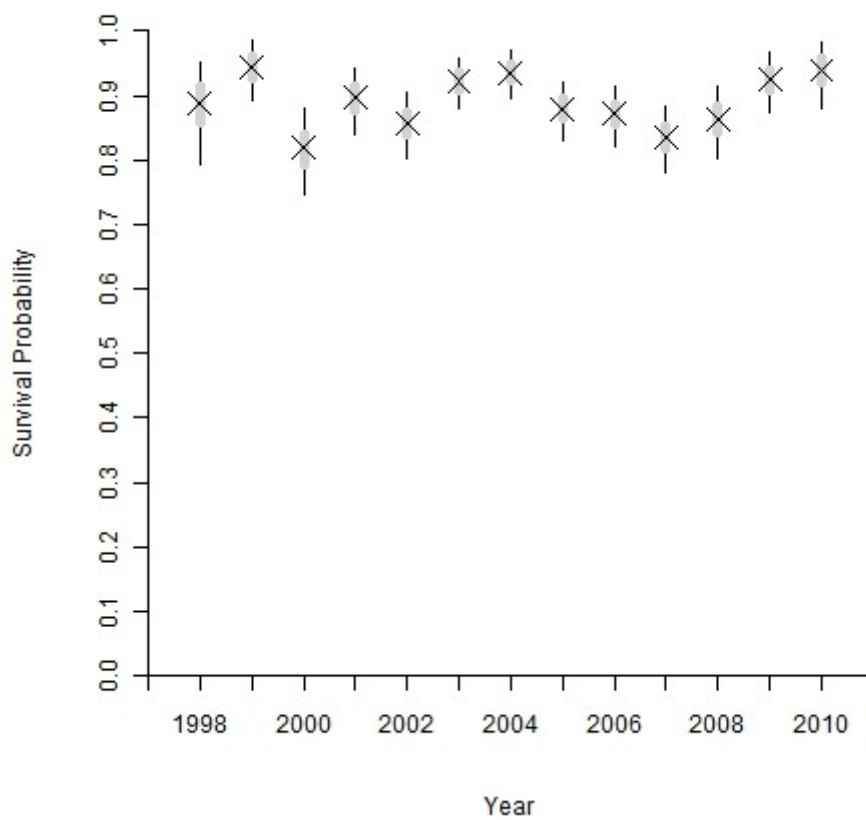
Figure 20: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were non-breeders aged 9 in year t, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses 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.
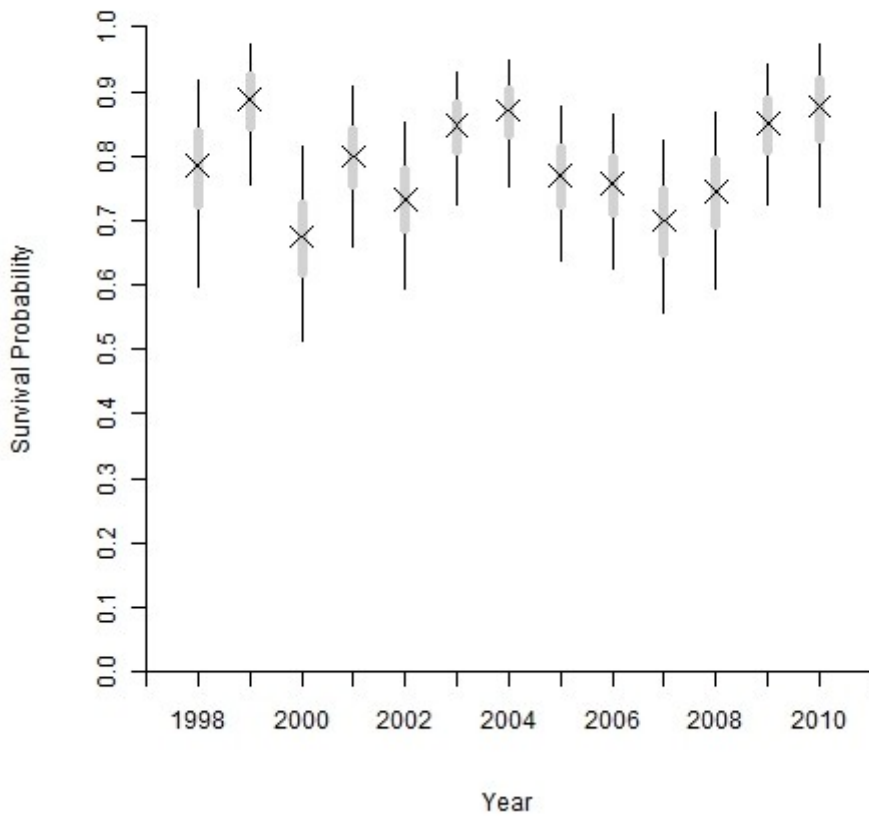
Figure 22: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were breeders aged 9 in year t, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate 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.
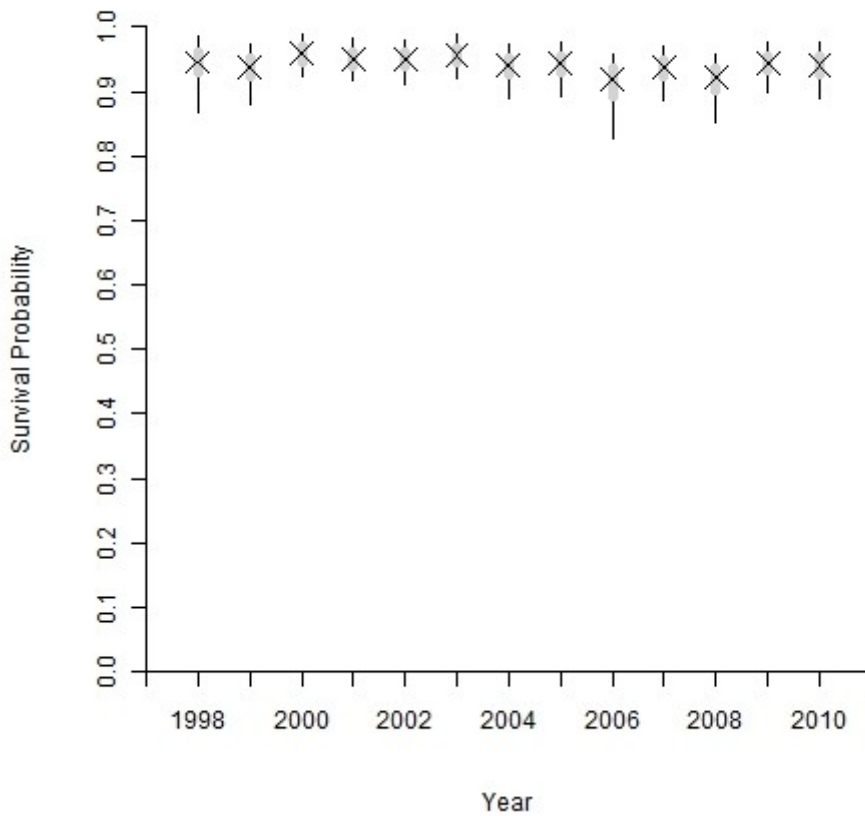
Figure 23: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were breeders aged 18 in year t, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate 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.
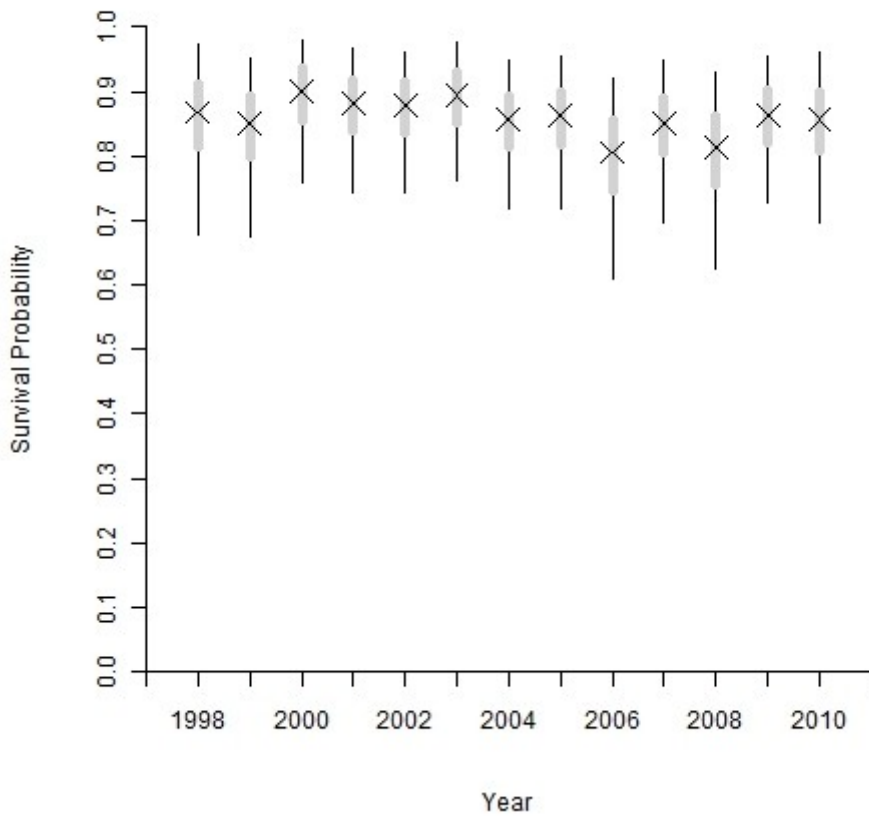
Figure 24: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were non-breeders of age in year t, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses 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.
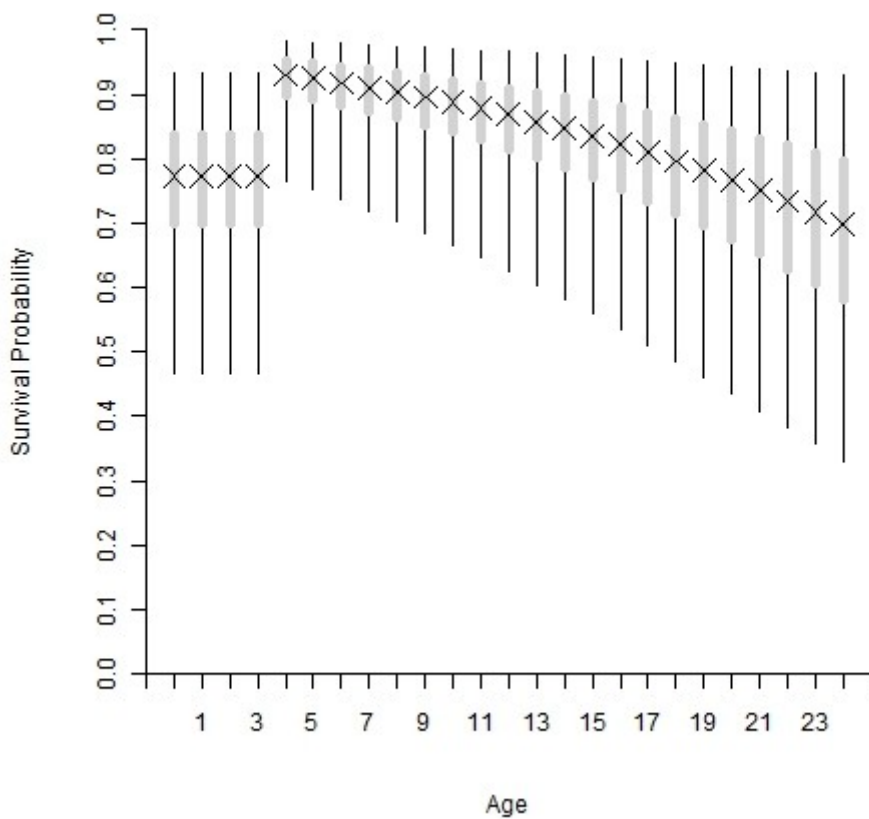
Figure 25: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were breeders of age in year t, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate 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.
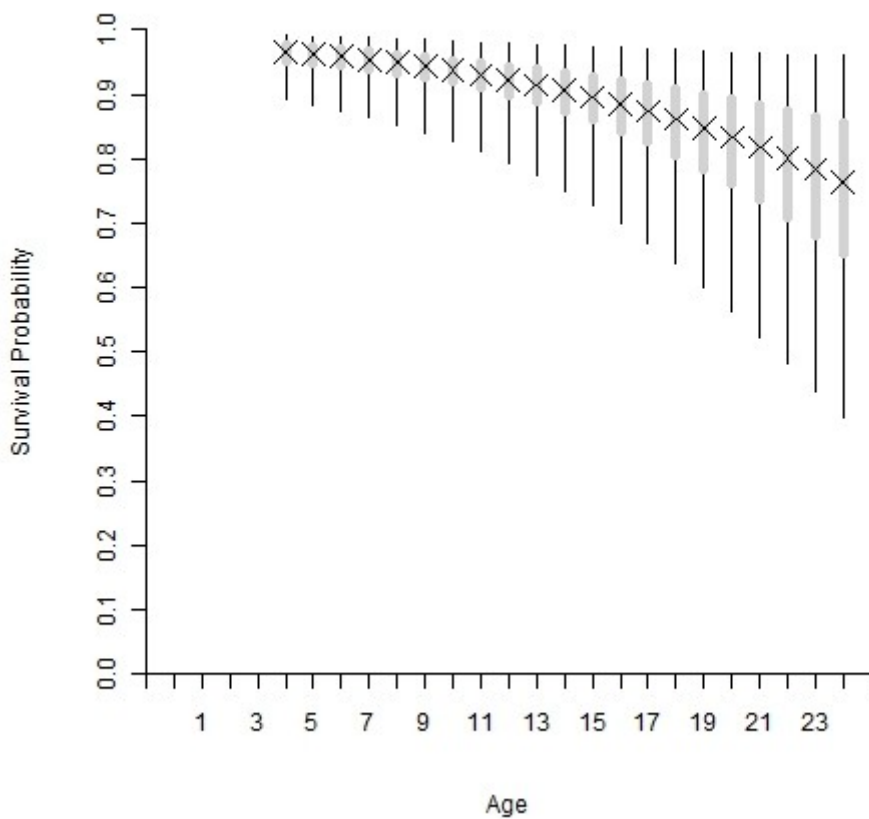
Figure 26: Posterior distribution for probability of breeding in year $t+1$ for individuals that were non-breeders aged 9 in year t, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate 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 $t+1$.
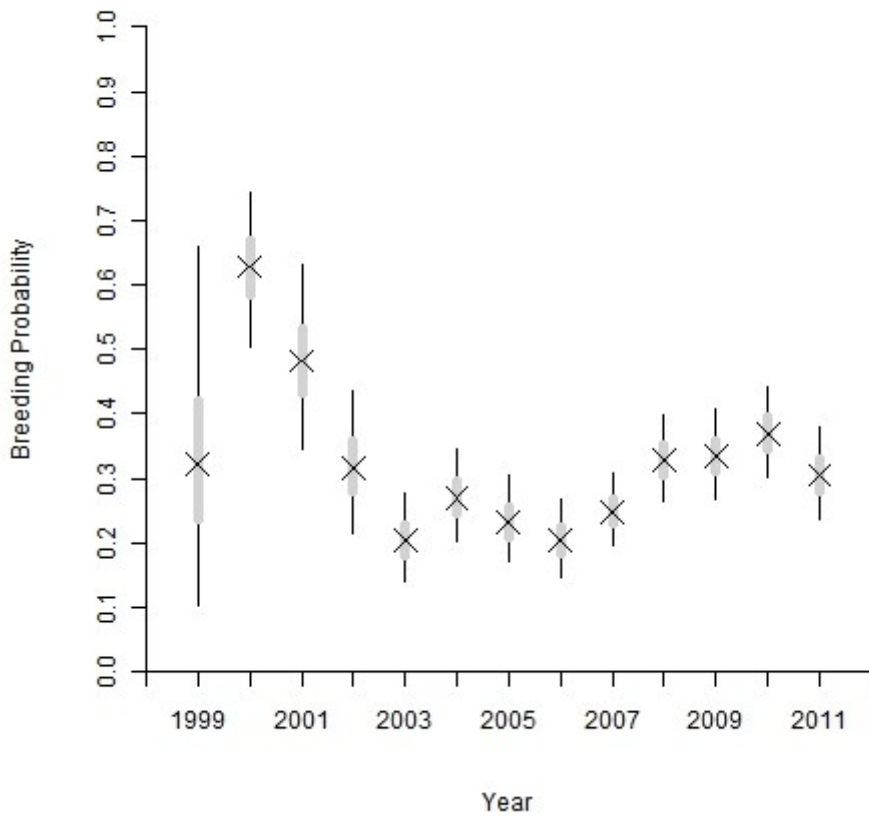
Figure 27: Posterior distribution for probability of breeding in year $t+1$ for individuals that were non-breeders aged 18 in year t, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate 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 $t+1$.
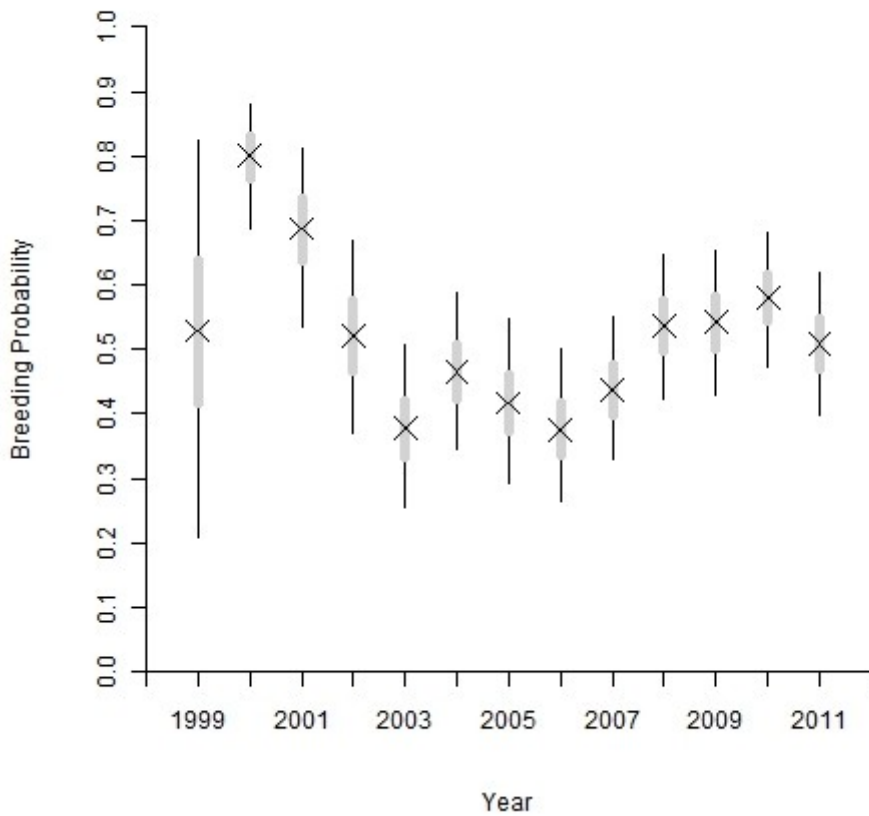
Figure 29: Posterior distribution for probability of breeding in year $t+1$ for individuals that were breeders aged 18 in year t, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate the 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 $t+1$.
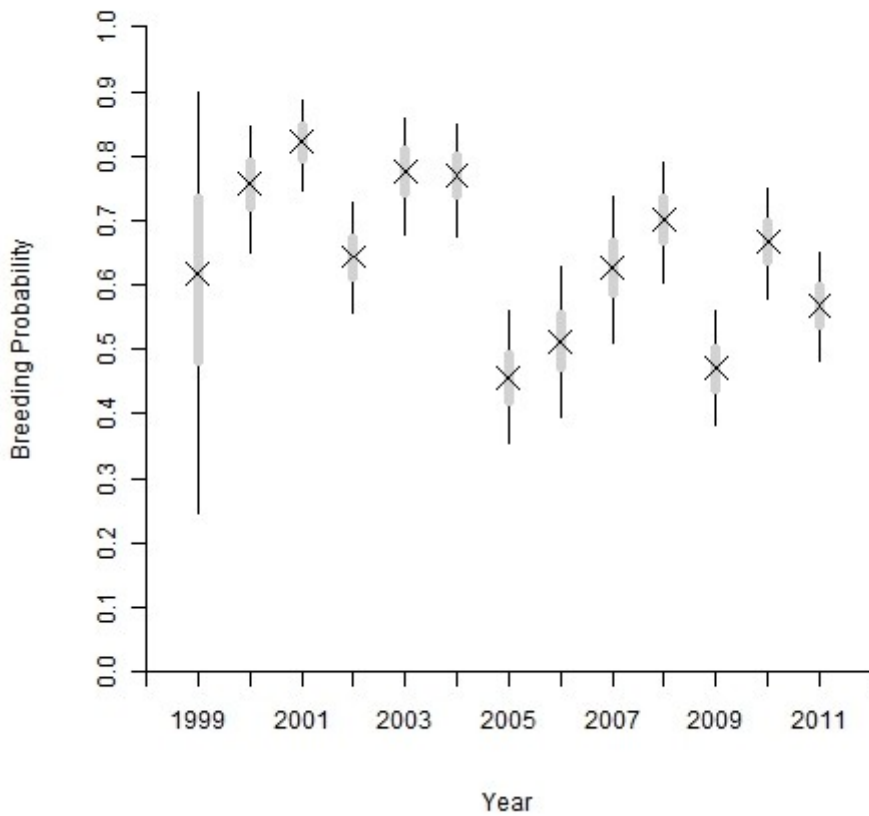
Figure 30: Posterior distribution for probability of breeding in year $t+1$ for individuals that were non-breeders of age in year t, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the strict definition of breeder. Crosses indicate 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 fie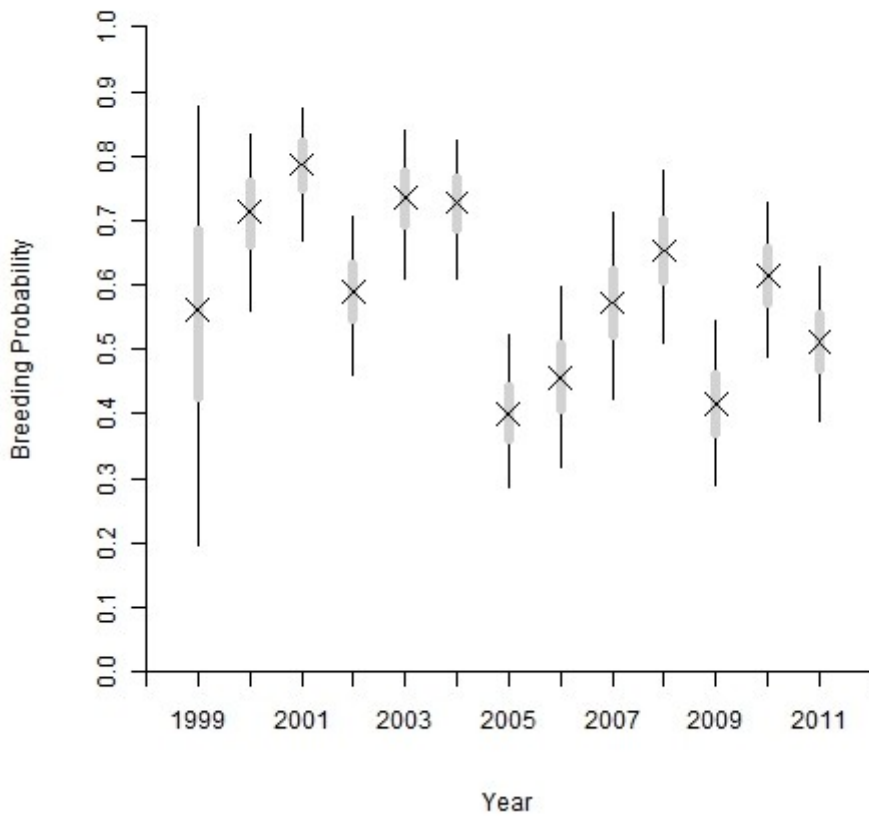ld season and indicate the year $t+1$. Note the width of the posterior distributions incorporate both annual variation and estimation uncertainty.

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.
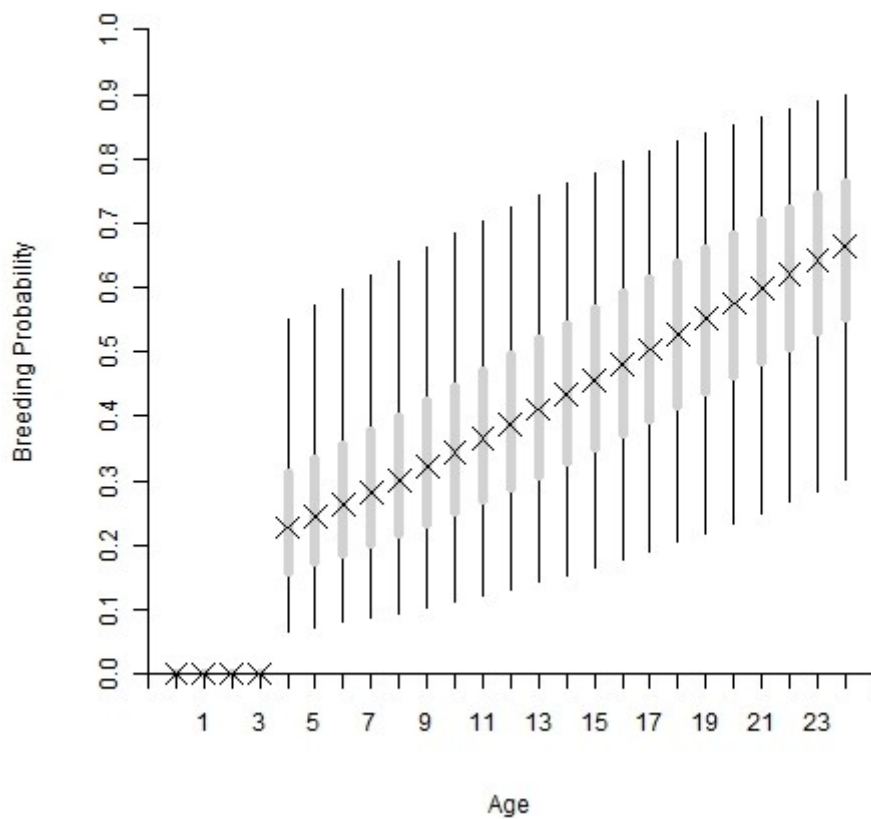
Figure 32: Using the liberal definition of breeder, posterior distributions for the deviance value from models with 3 age-classes and; temporally-constant zero-inflation (black, mostly obscured on right); and no zero-inflation (charcoal, mostly obscured on left). Posterior distributions for the deviance value from models with linear age relationship and; temporally-constant zero-inflation (medium grey); and no zero-inflation (light grey). Smaller values indicate a better fit to the data.
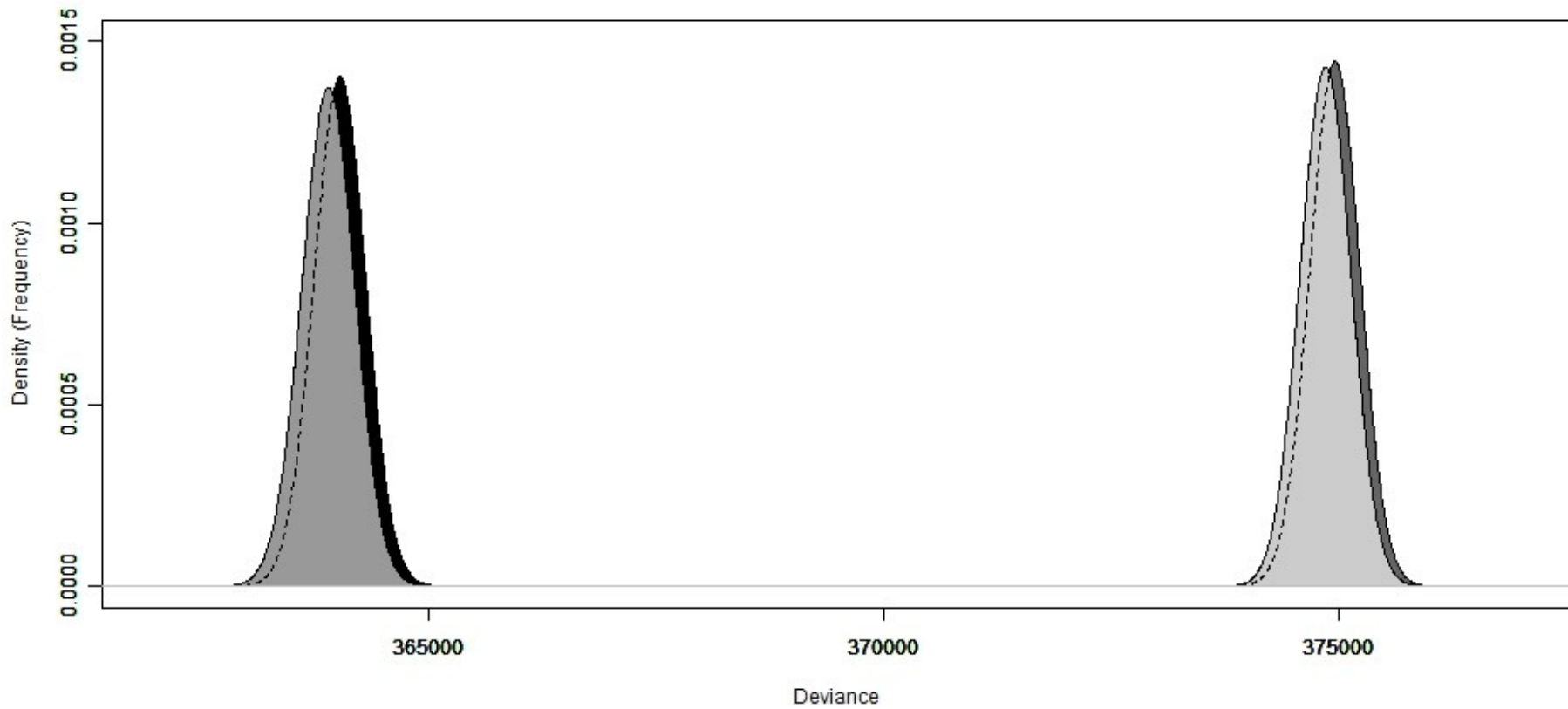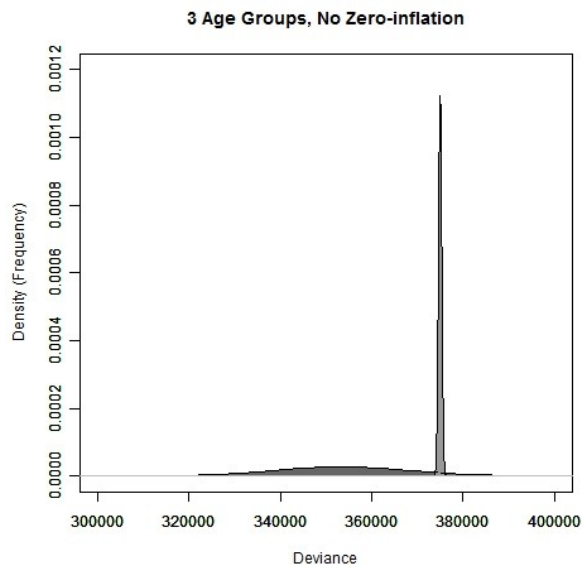
Figure 33: Plots of posterior (light grey) and predicted (dark grey) deviance values from each model with data using the liberal definition of breeder. Bayesian p-values are indicated.

p-value = 0.075
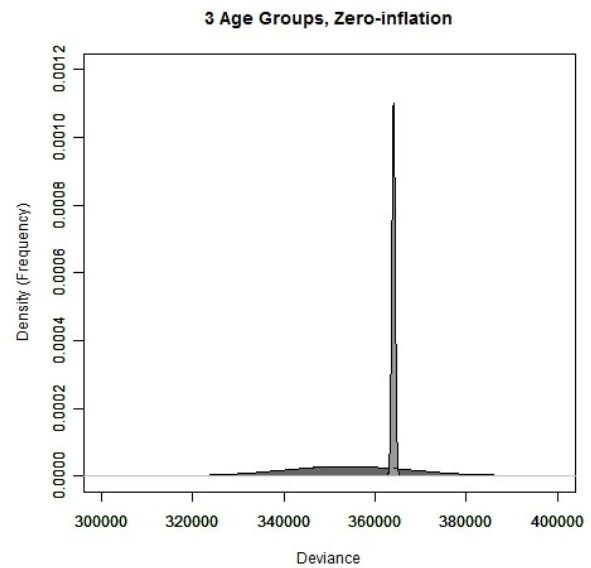
p-value = 0.240
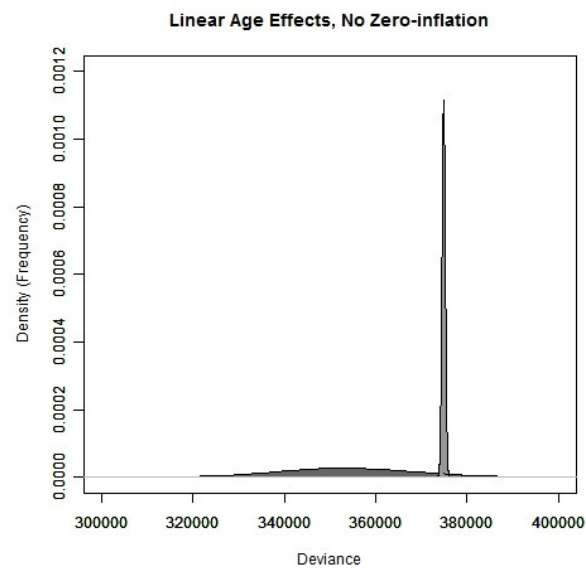
p-value = 0.079
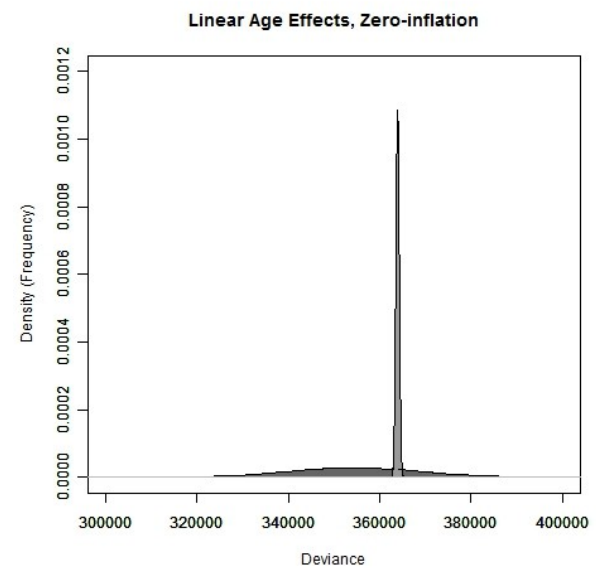
p-value = 0.259

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.
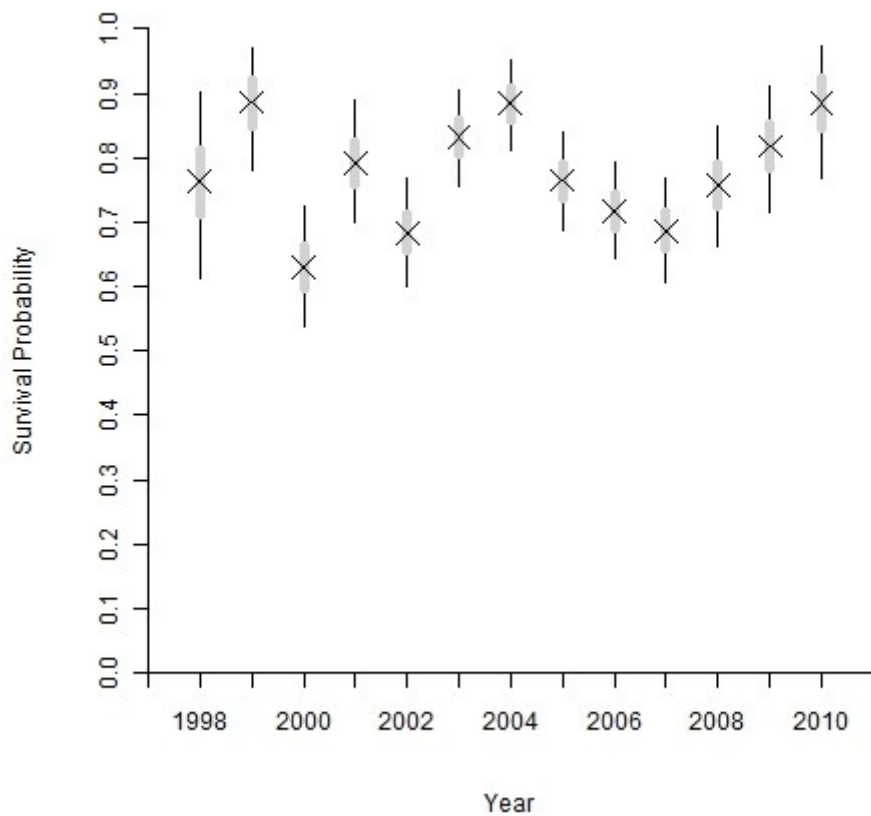
Figure 38: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were breeders aged 15+ in year t, from model with age classes and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick 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.
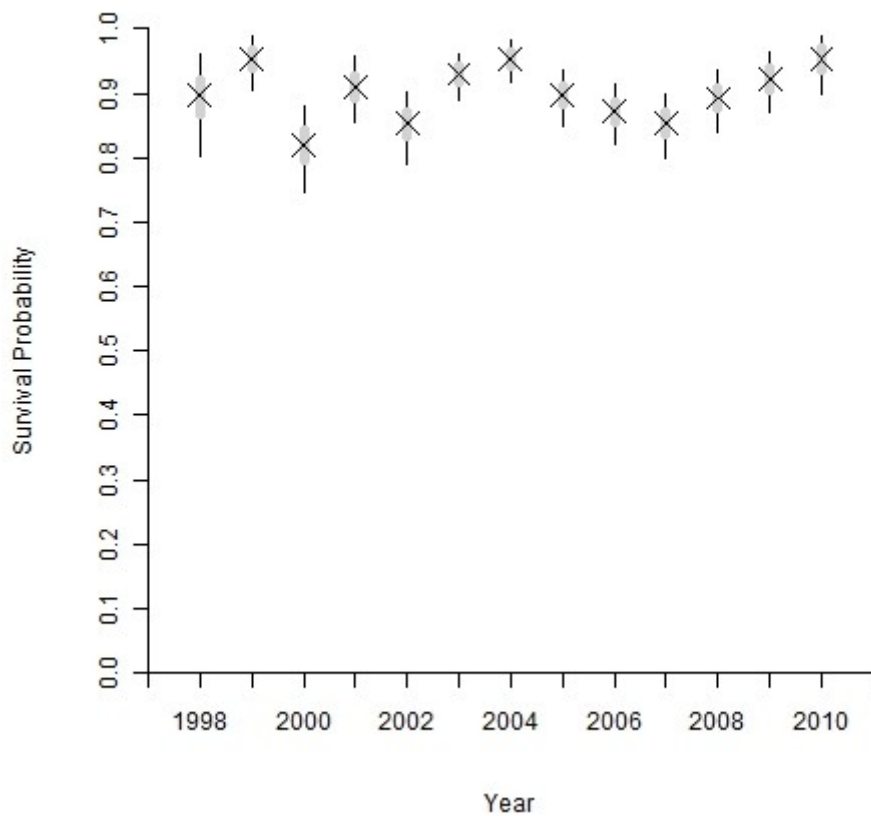
Figure 39: Posterior distribution for probability of breeding in year $t+1$ for individuals that were non-breeders aged 4-14 in year t, from model with age classes and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick 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 $t+1$.
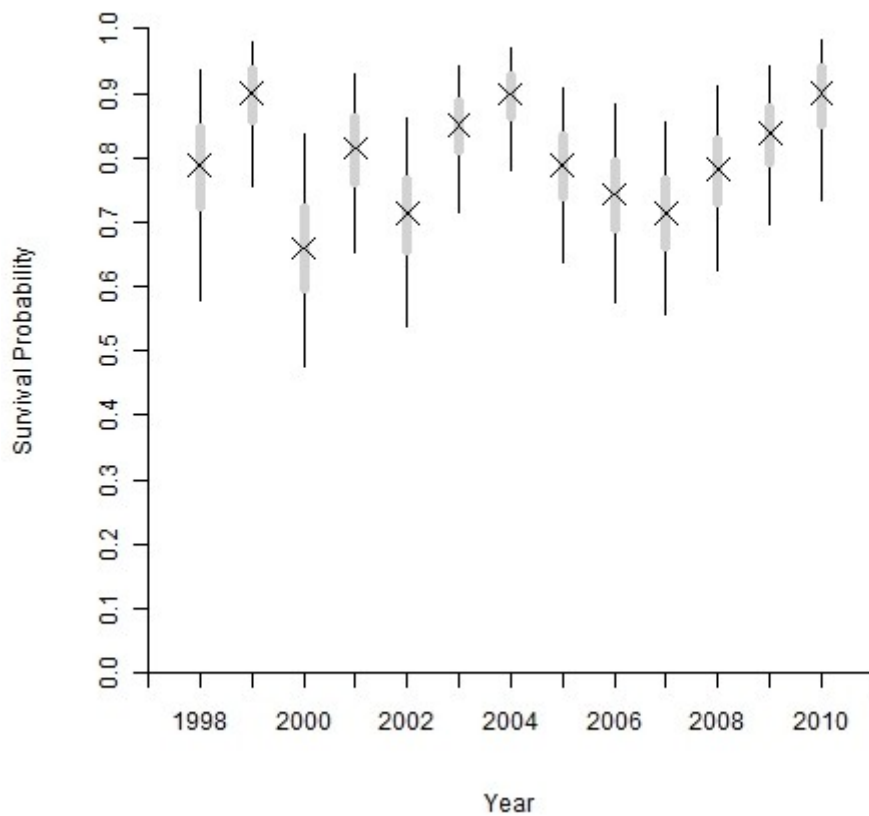
Figure 40: Posterior distribution for probability of breeding in year $t+1$ for individuals that were non-breeders aged 15+ in year t, from model with age classes and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick grey 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 $t+1$.
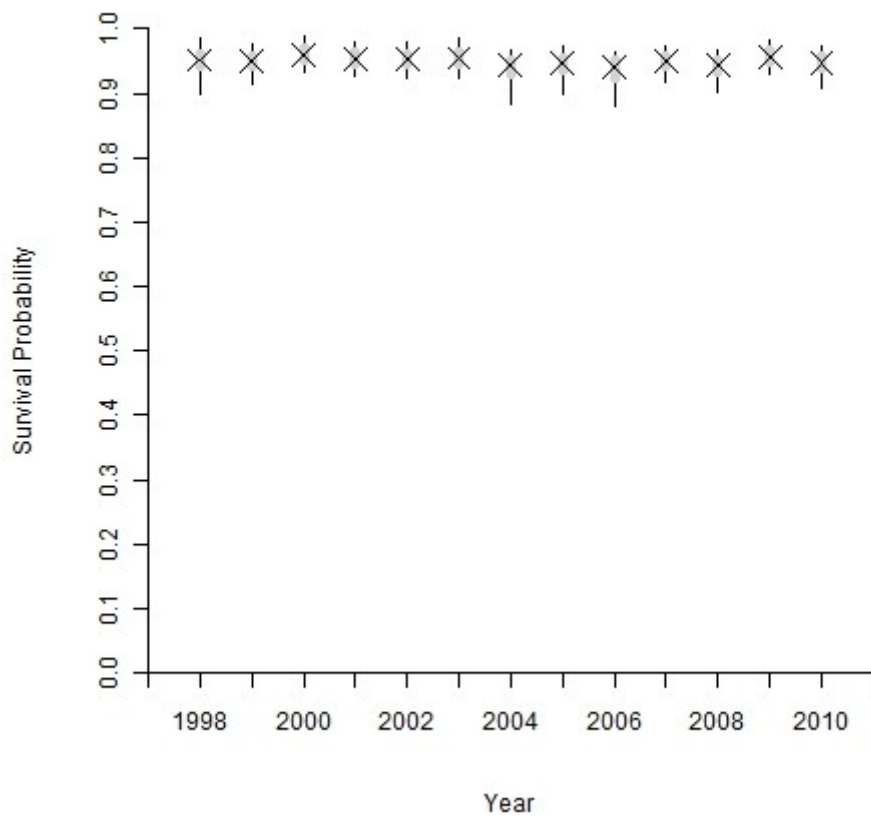
Figure 41: Posterior distribution for probability of breeding in year *t*+1 for individuals that were breeders aged 4-14 in year *t*, from model with age classes and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick grey 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.
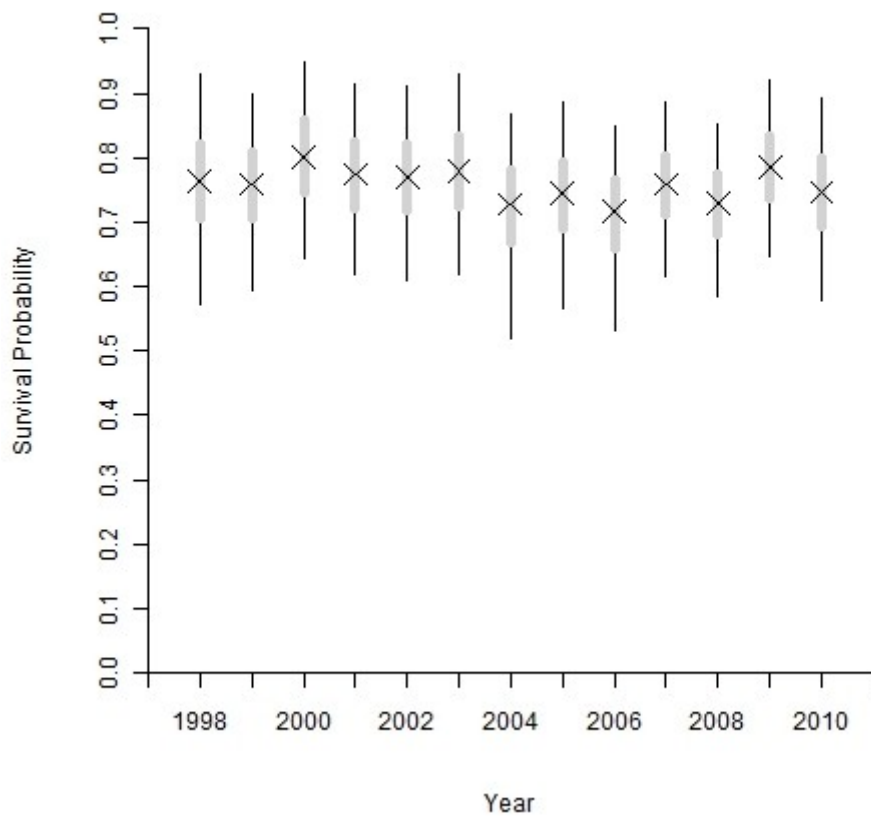
Figure 42: Posterior distribution for probability of breeding in year *t*+1 for individuals that were breeders aged 15+ in year *t*, from model with age classes and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate the median of the distribution, thick grey 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.
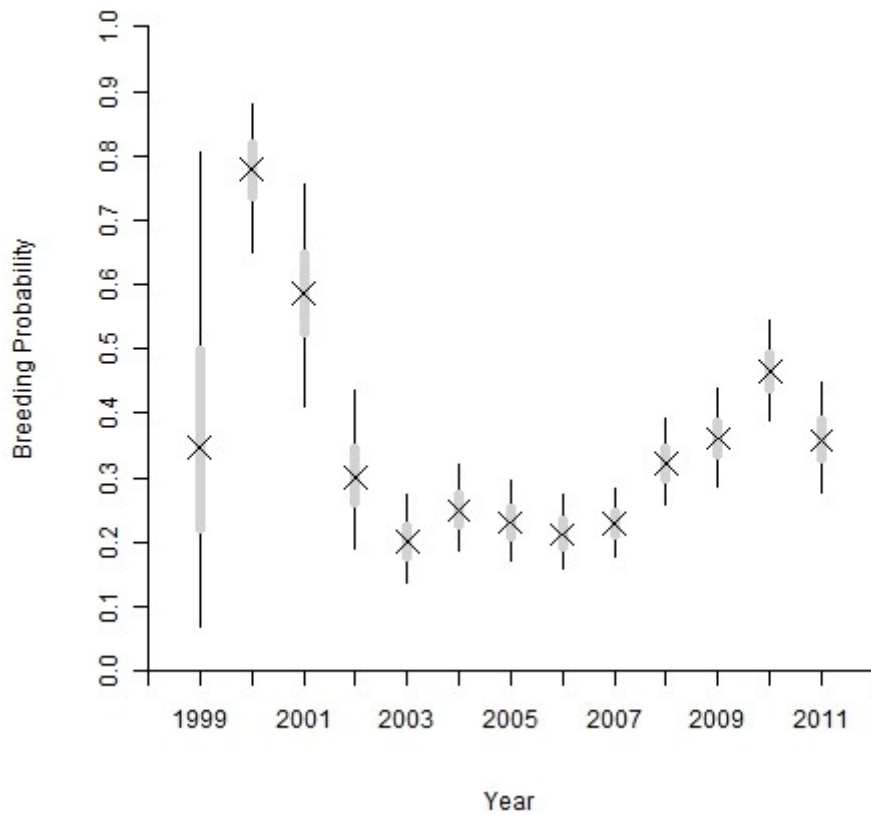
Figure 44: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were non-breeders aged 9 in year t, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses 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.
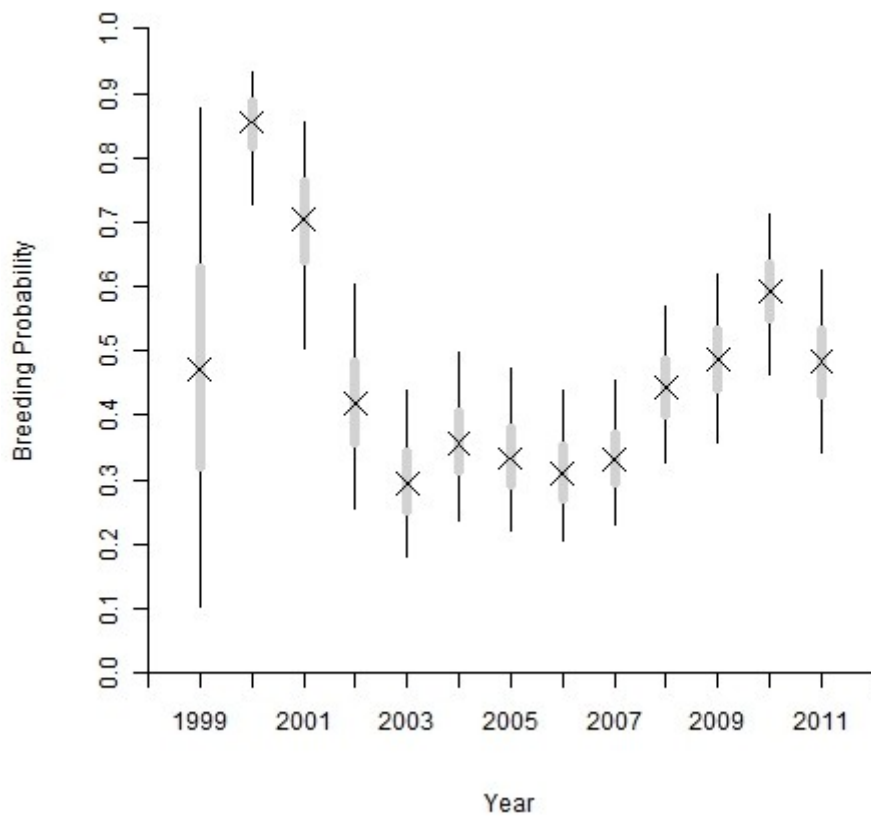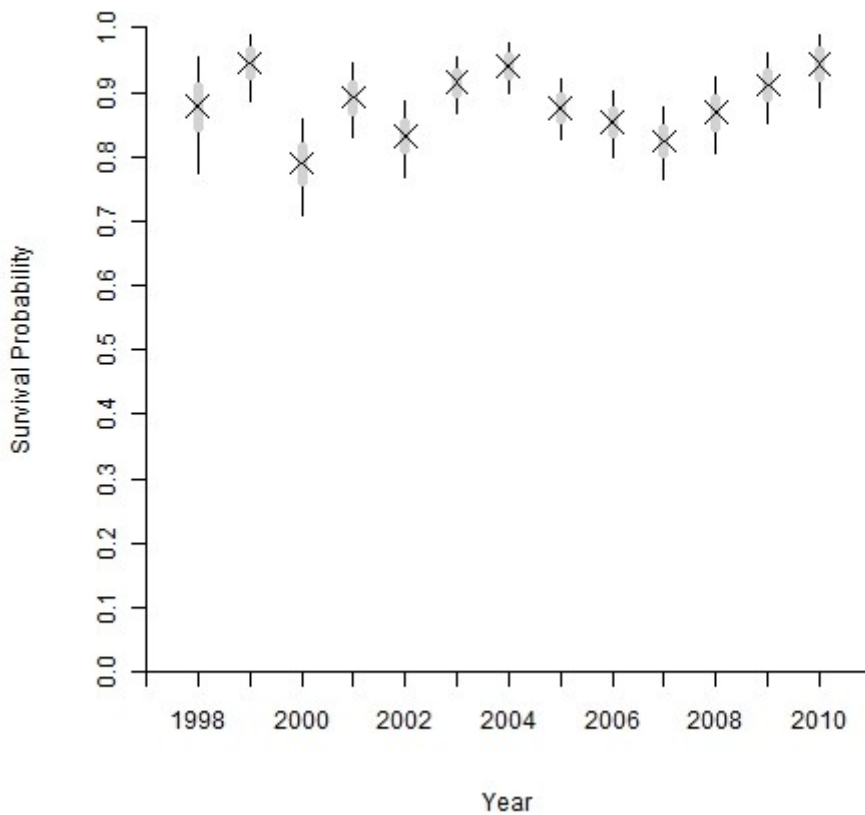
Figure 45: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were non-breeders aged 18 in year t, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses 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.
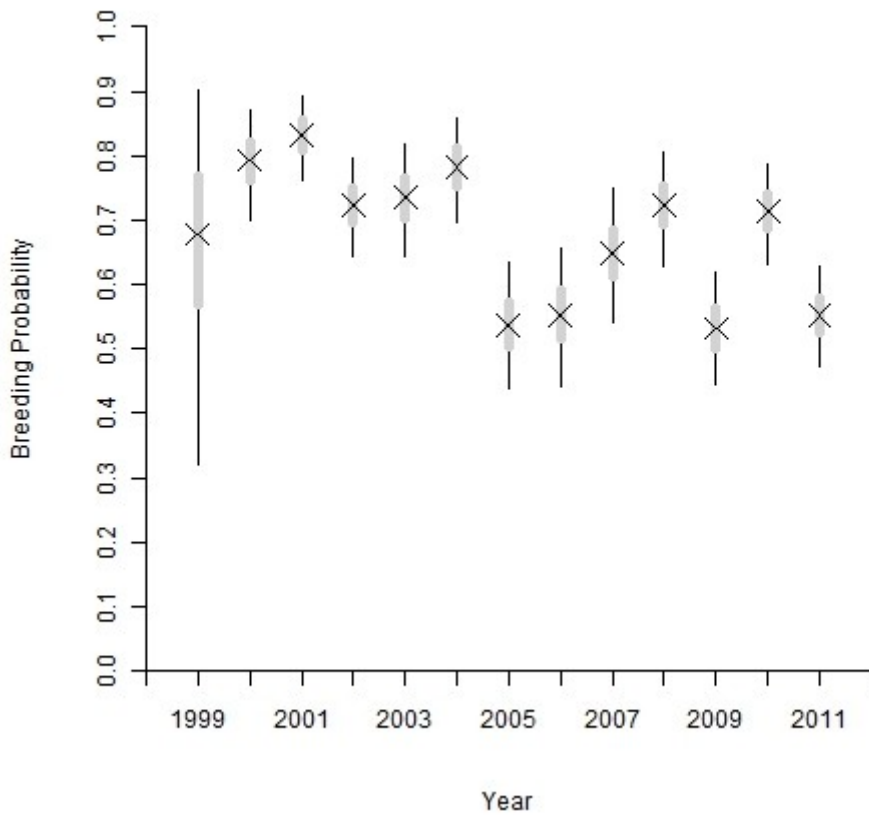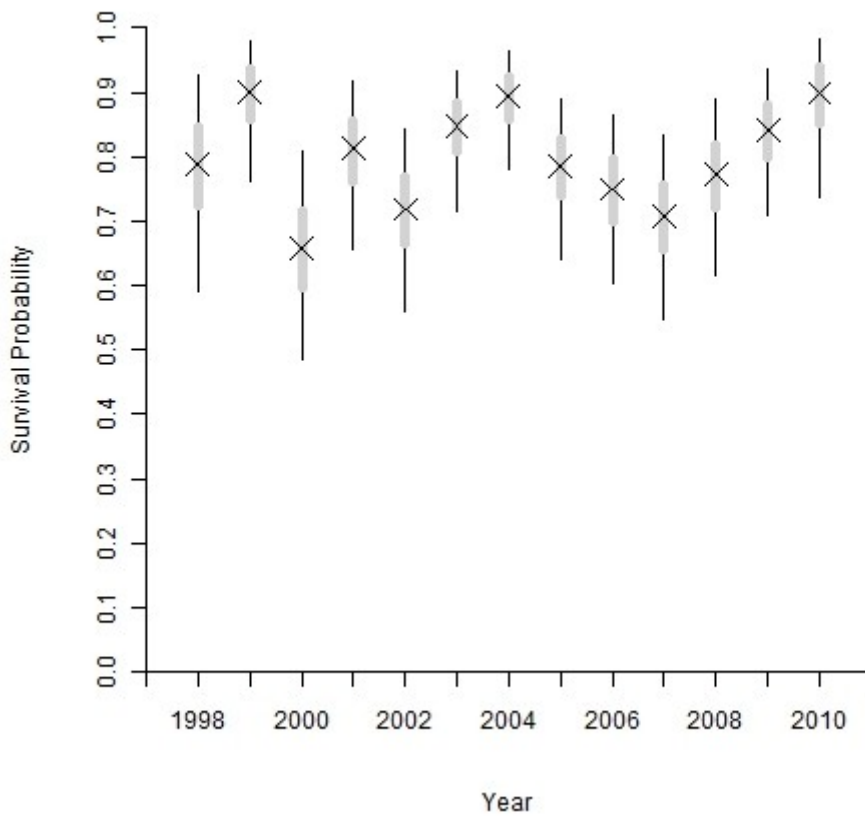
Figure 46: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were breeders aged 9 in year t, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate 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.
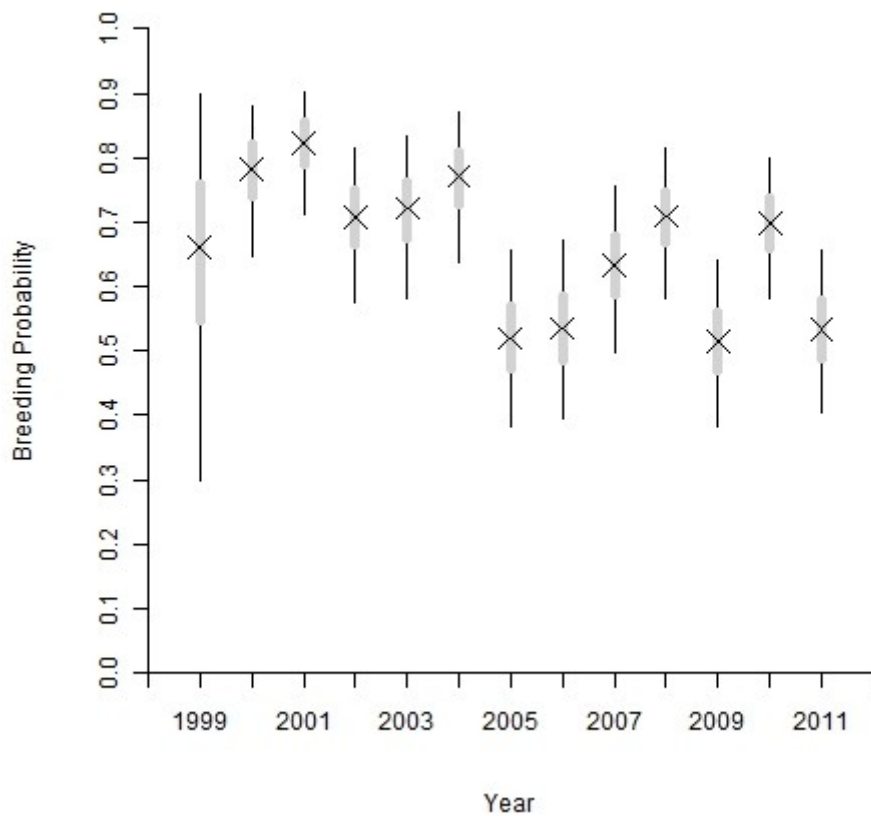
Figure 47: Posterior distribution for probability of survival from year t to $t+1$ for individuals that were breeders aged 18 in year t, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate 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.
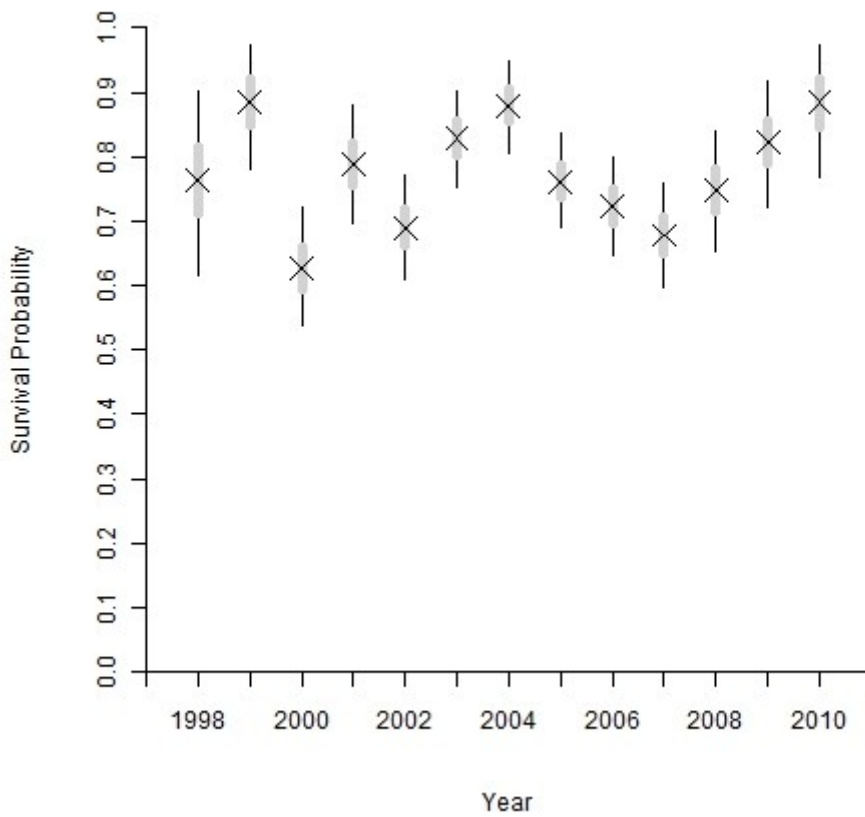
Figure 48: Posterior distribution for probability of survival from year *t* to *t*+1 for individuals that were non-breeders of age in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses 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 $t+1$.
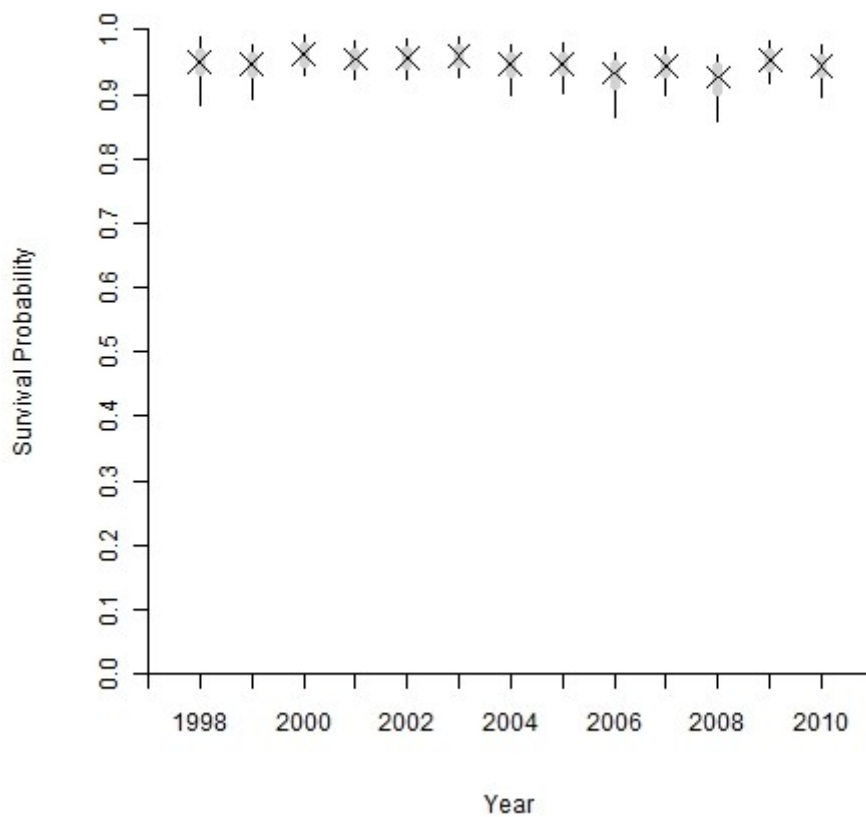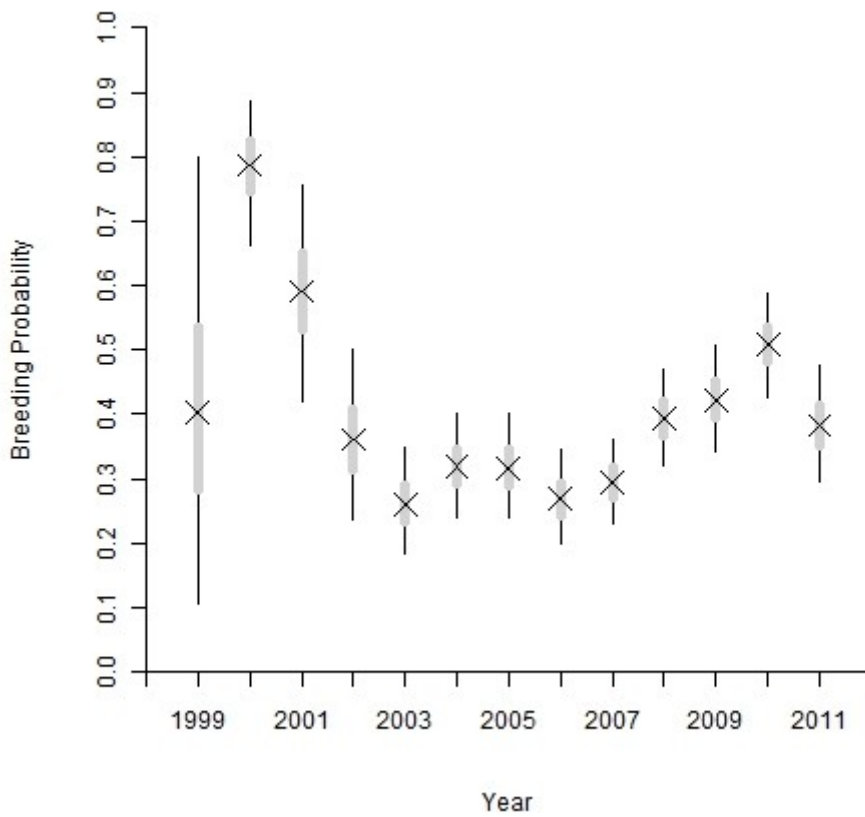
Figure 51: Posterior distribution for probability of breeding in year *t*+1 for individuals that were non-breeders aged 18 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate 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.
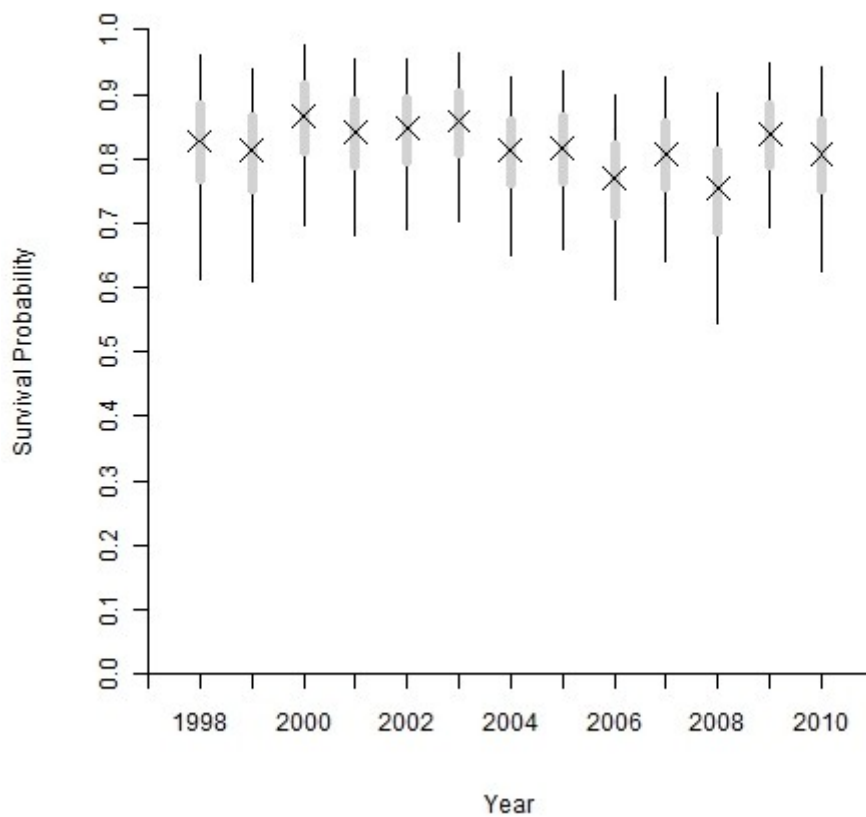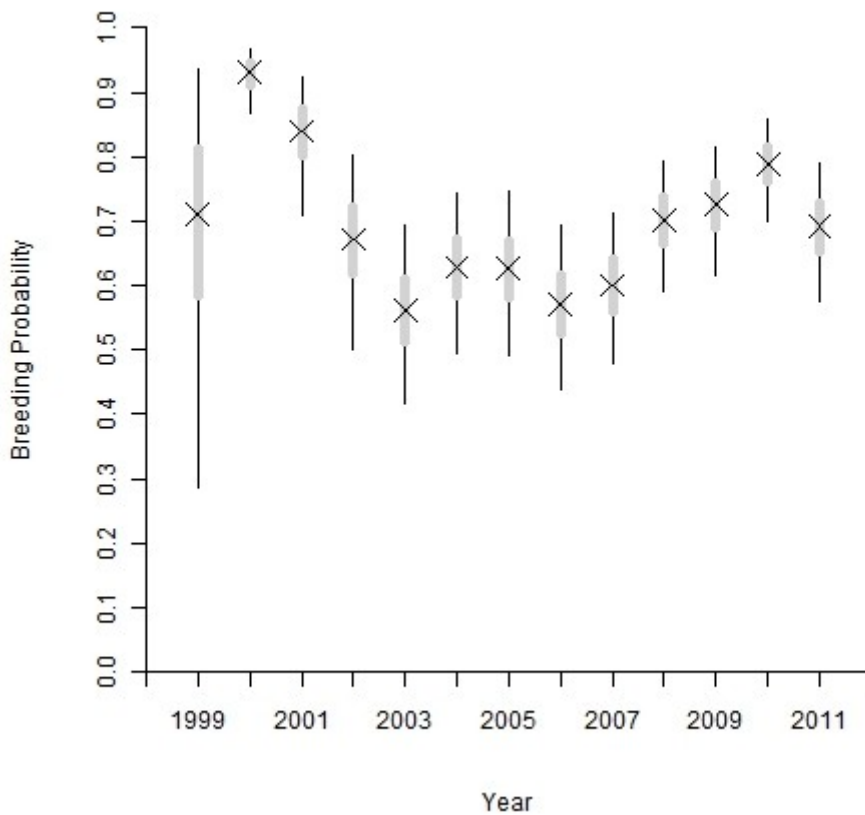
Figure 52: Posterior distribution for probability of breeding in year *t*+1 for individuals that were breeders aged 9 in year *t*, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate 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.
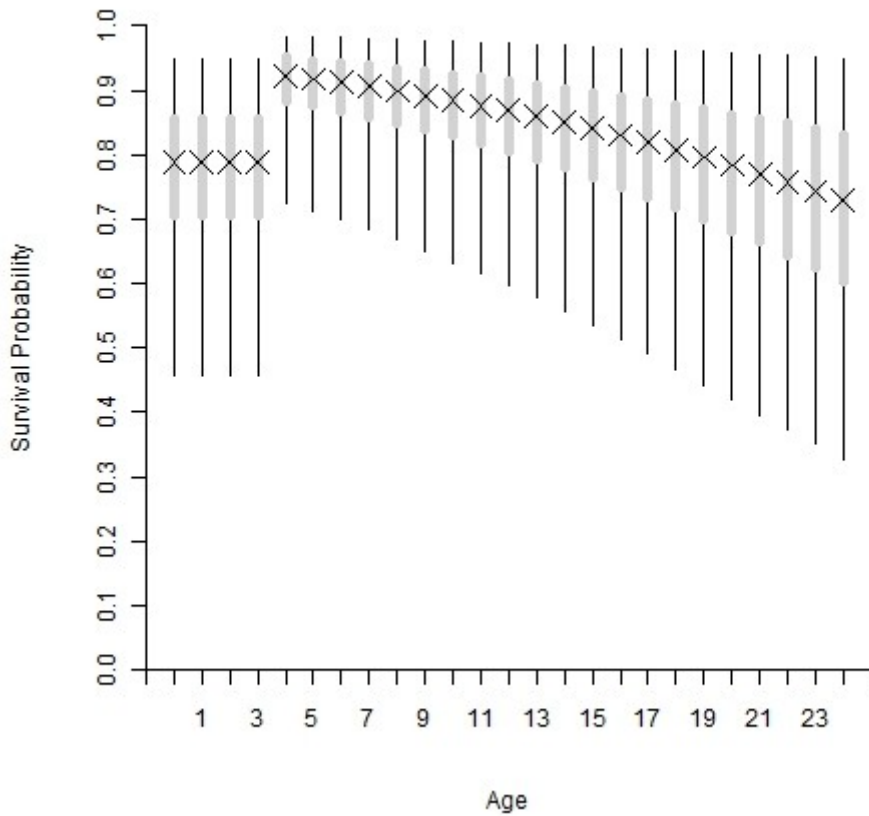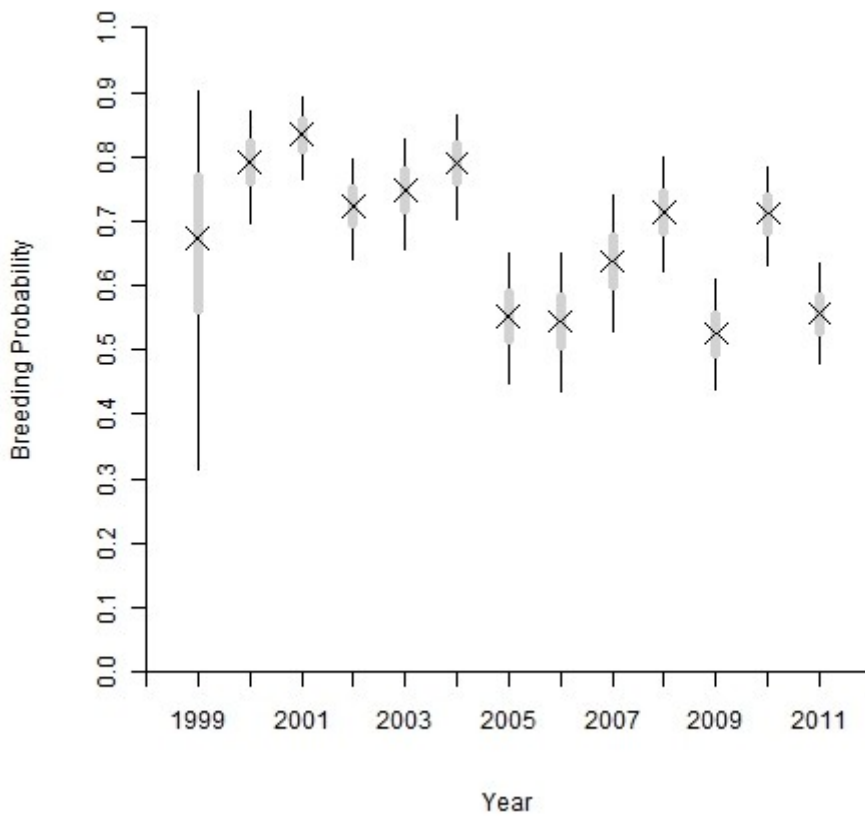
Figure 53: Posterior distribution for probability of breeding in year $t+1$ for individuals that were breeders aged 18 in year t, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate 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.
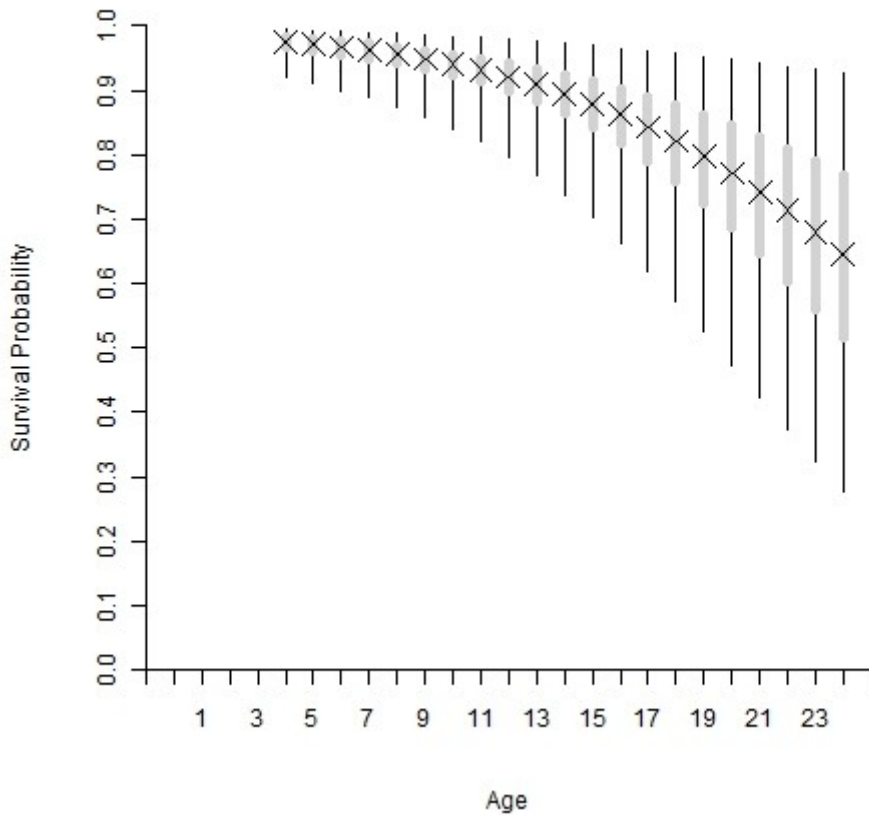
Figure 55: Posterior distribution for probability of breeding in year $t+1$ for individuals that were breeders of age in year t, from model using logit-linear relationship with age for females aged 4+ and time-constant zero-inflation factor, using the liberal definition of breeder. Crosses indicate the 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.

Figure 56: Using the stricter definition of breeder, posterior distributions for the deviance value from models with 3 age-classes (light grey) and logit-linear relationship with age (white); linear (black) and quadratic (darkest grey) splines for sea-lions aged 4+; and linear (dark-medium grey) and quadrtic (light-medium grey) splines for all ages. All models assumed a zero-inflated binomial distribution for the resighting rates. Smaller values indicate a better fit to the data.
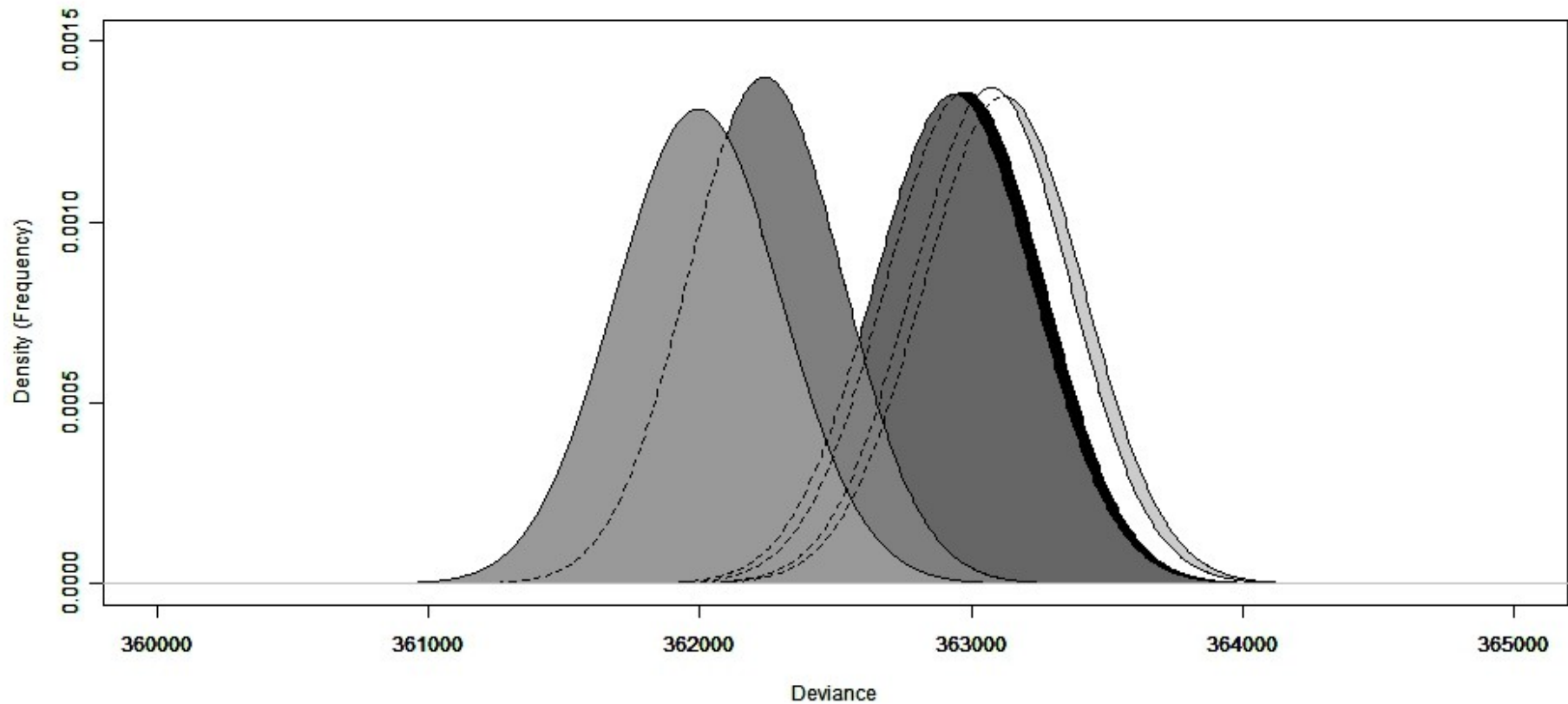
Figure 57: Posterior distributions for probability of survival from year t to $t+1$ for individuals that were non-breeders in year t as a function of age in year t, from the exploratory analysis using the stricter definition of breeder. Results are presented for models that had a linear (top-left) or quadratic (top-right) spline relationship with age for females aged 4+; and linear (bottom-left) or quadric (bottom-right) spline relations with age for all females. 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.
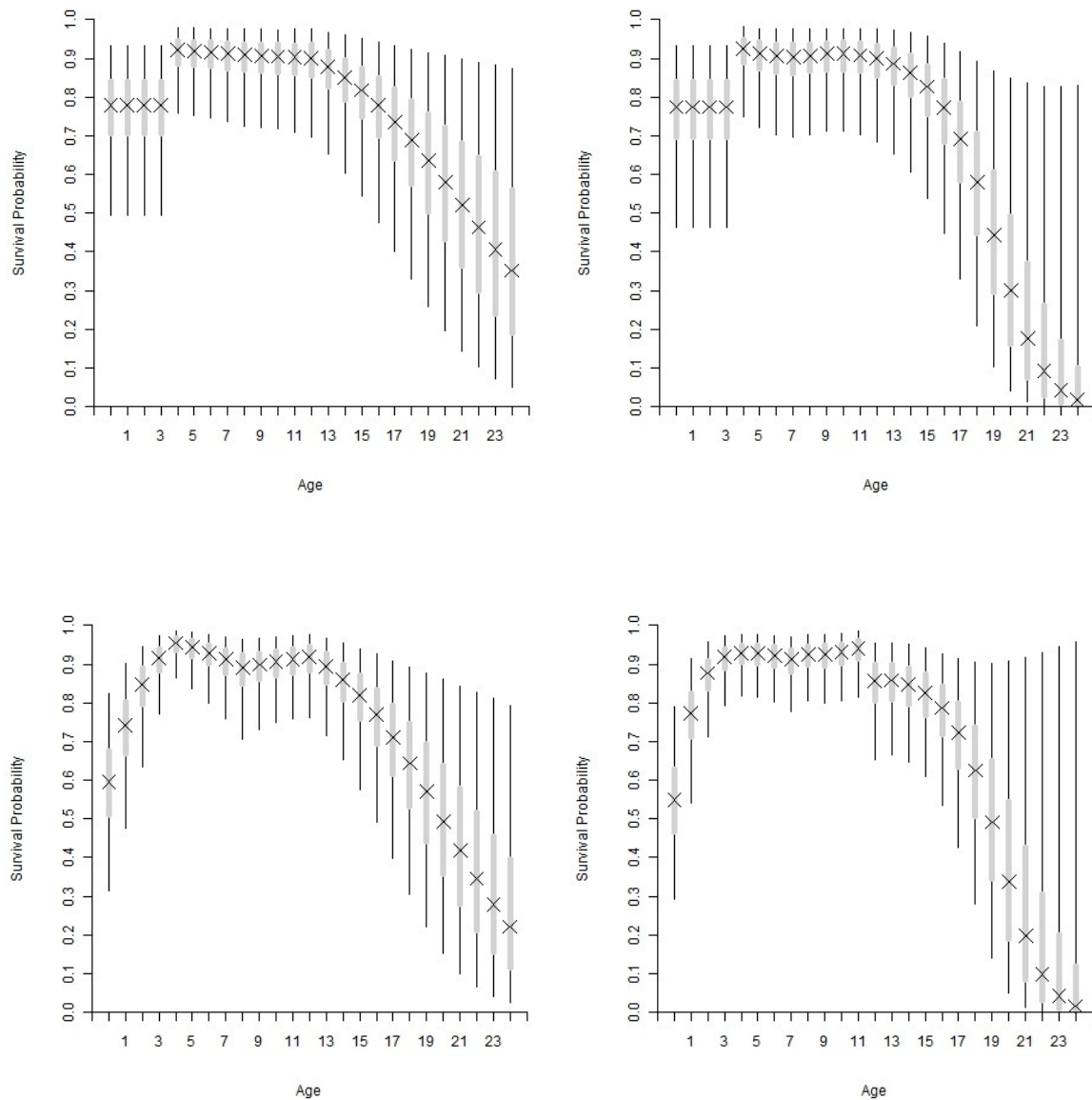
Figure 58: Posterior distributions for probability of survival from year *t* to *t*+1 for individuals that were breeders in year *t* as a function of age in year *t*, from the exploratory analysis using the stricter definition of breeder. Results are presented for models that had a linear (top-left) or quadratic (top-right) spline relationship with age for females aged 4+; and linear (bottom-left) or quadric (bottom-right) spline relations with age for all females. 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.
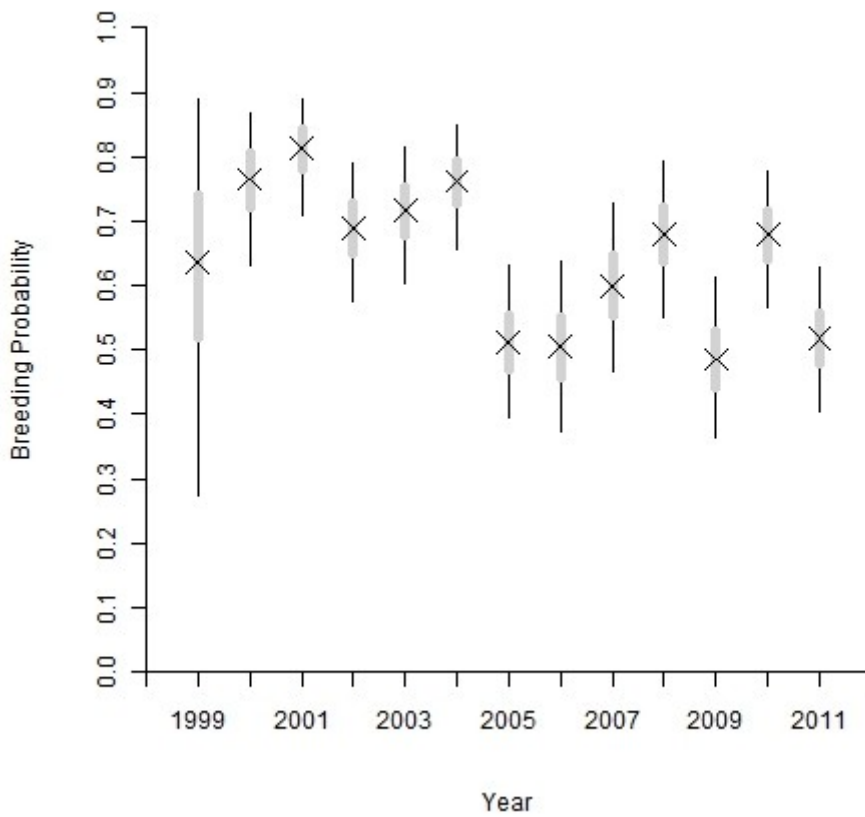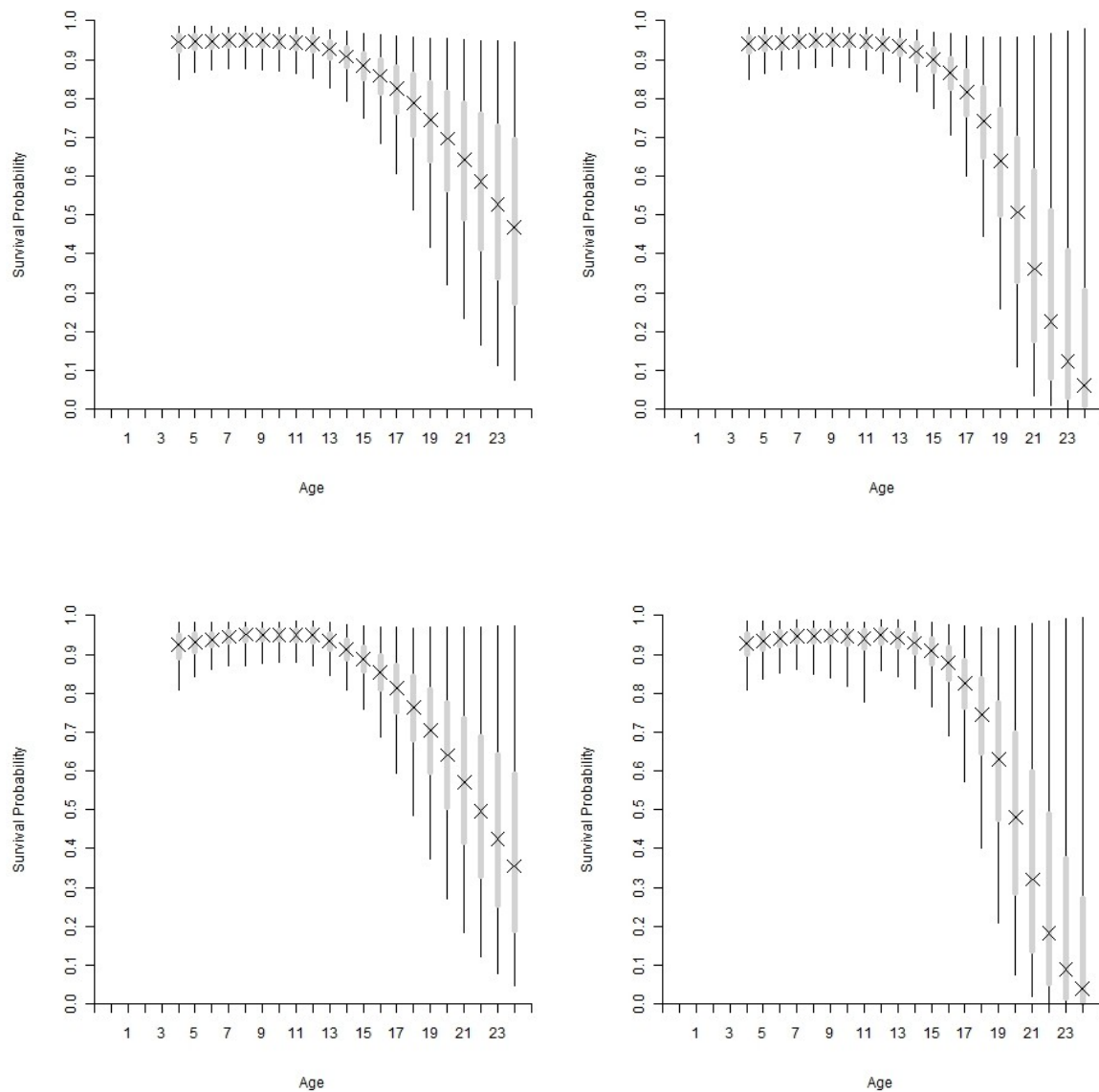
Figure 59: Posterior distributions for probability of breeding in year $t+1$ for individuals that were non-breeders in year t as a function of age in year t, from the exploratory analysis using the stricter definition of breeder. Results are presented for models that had a linear (top-left) or quadratic (top-right) spline relationship with age for females aged 4+; and linear (bottom-left) or quadric (bottom-right) spline relations with age for all females. 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.
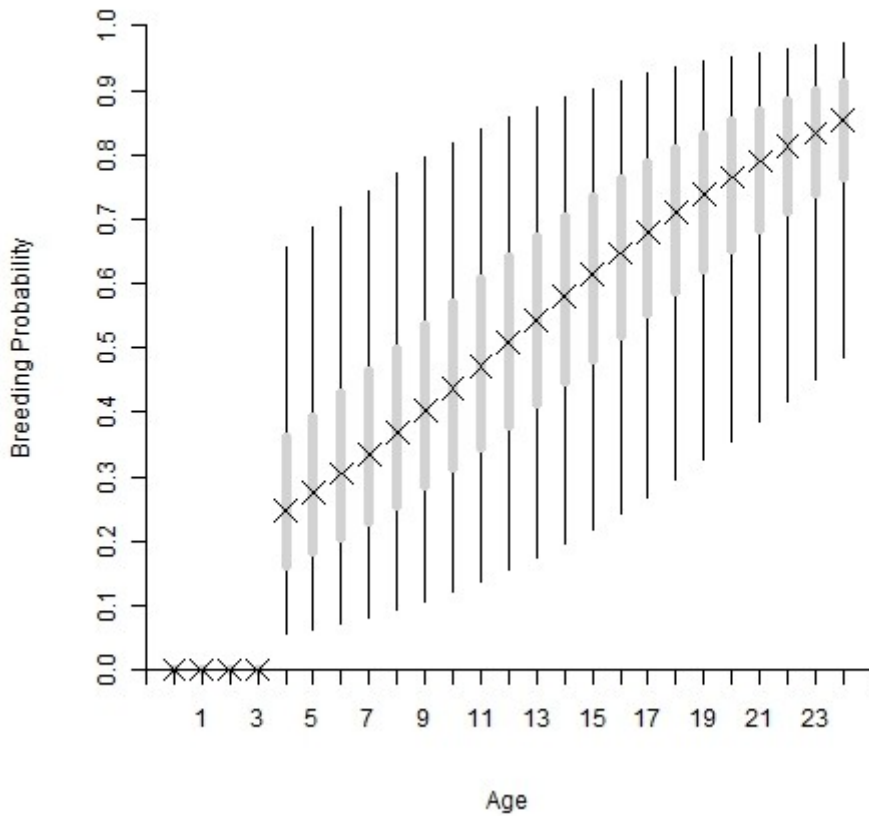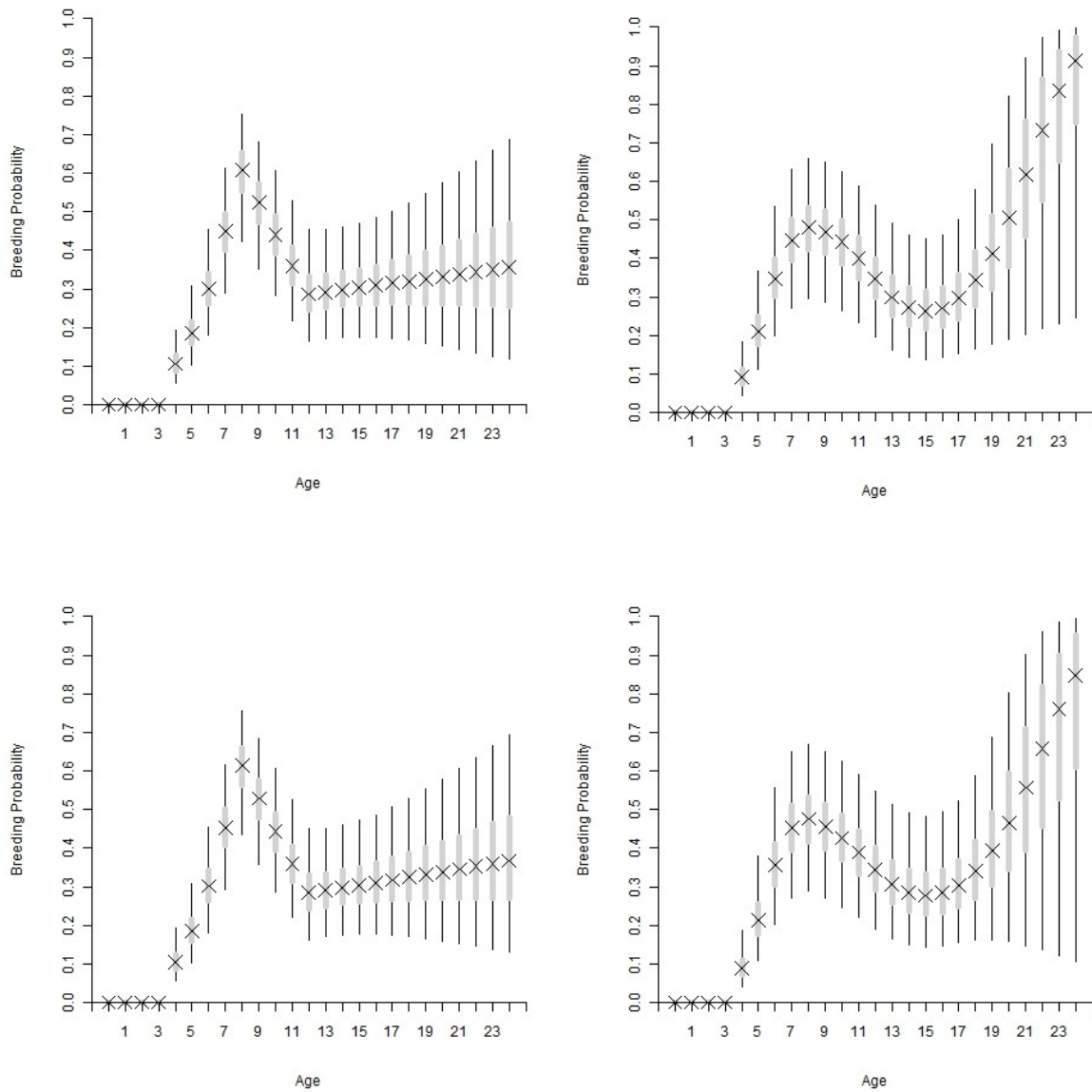
Figure 60: Posterior distributions for probability of breeding in year $t+1$ for individuals that were breeders in year t as a function of age in year t, from the exploratory analysis using the stricter definition of breeder. Results are presented for models that had a linear (top-left) or quadratic (top-right) spline relationship with age for females aged 4+; and linear (bottom-left) or quadric (bottom-right) spline relations with age for all females. 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.
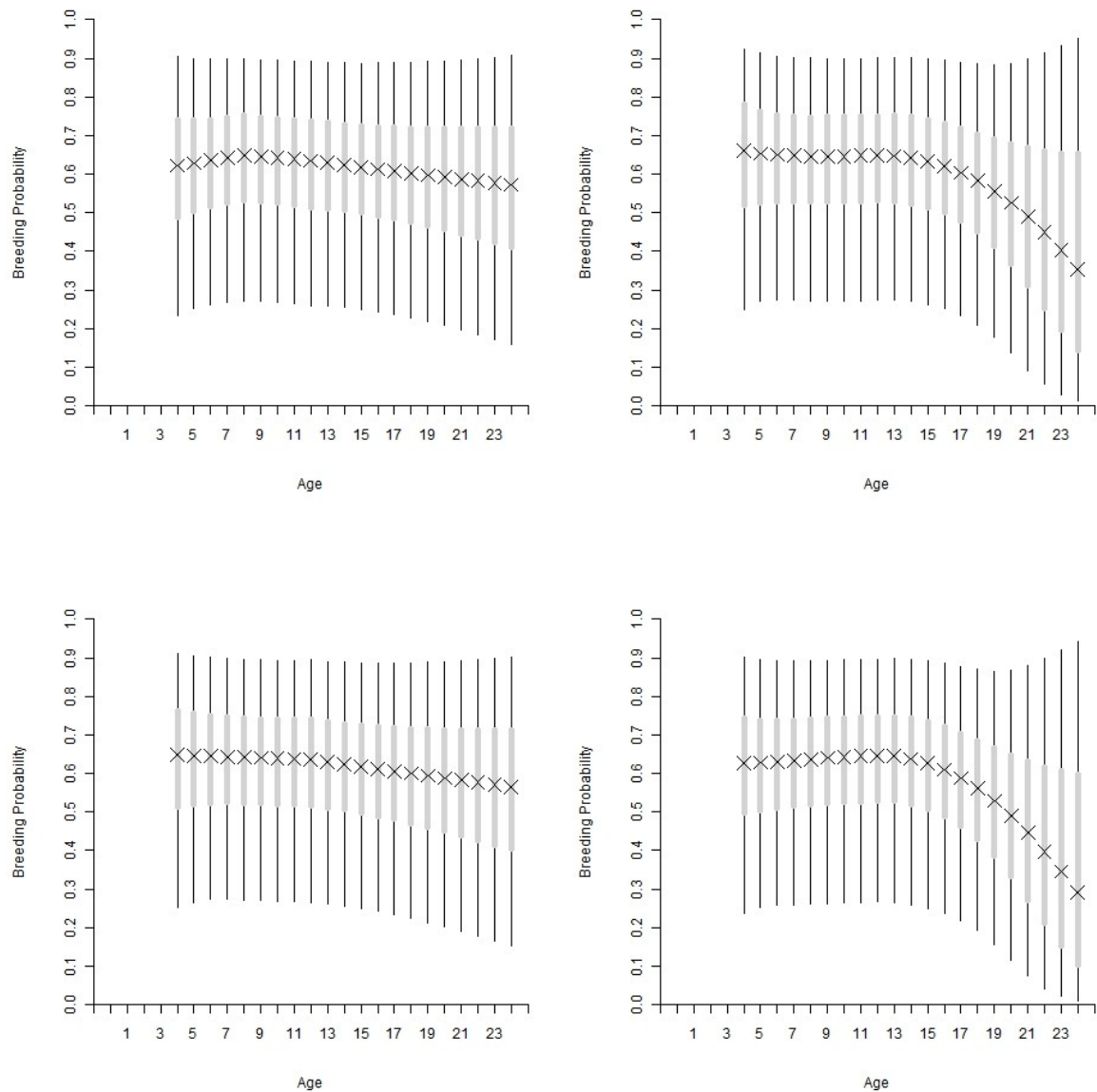
Tables

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, 0.05)
	1	0.14 (0.13, 0.16)
	2	0.82 (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 1:14) {                 ## 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 1:14){
                C_Alive[ii,jj,kk] <- 0
            }
            Cap.Pred[ii,jj] <- 0
        }

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

        for (kk in 1:14){
            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):14) {
                    logLike[ii,jj] <- logLike[ii,jj-1]
                    logLike.Pred[ii,jj] <- logLike.Pred[ii,jj-1]
            }

      } ## end individual loop

      Dev <- -2*sum(logLike[, 14])
      Dev.Pred <- -2*sum(logLike.Pred[, 14])
      p.value <- step(Dev.Pred-Dev)

} ### end model
```

Appendix 2

Proportion of tagged individuals known to be alive in each year by age. "-" indicates no indviduals of that age were known to be alive in that year, while "*" indactes there were individuals of that age, but they were not used in this analysis. The total number of individuals known to be alive each year is also indicated.

							Year							
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	2009/10	2010/11
0	98%	45%	37%	39%	24%	29%	28%	26%	25%	*	*	*	*	*
1	-	13%	13%	9%	16%	6%	12%	9%	5%	9%	*	*	*	*
2	-	-	9%	11%	10%	13%	6%	12%	9%	6%	10%	*	*	*
3	-	-	-	8%	12%	9%	12%	5%	12%	11%	7%	11%	*	*
4	-	-	-	-	9%	10%	8%	11%	5%	15%	12%	7%	12%	*
5	-	-	-	-	-	8%	9%	7%	11%	6%	16%	12%	7%	13%
6	0%	13%	-	-	-	-	7%	8%	6%	12%	6%	16%	12%	8%
7	2%	15%	12%	-	-	-	-	6%	7%	8%	11%	6%	14%	13%
8	-	10%	14%	10%	-	-	-	-	6%	9%	8%	11%	6%	16%
9	-	5%	10%	12%	9%	-	-	-	-	7%	9%	8%	12%	6%
10	-	-	5%	7%	11%	8%	-	-	-	-	7%	9%	8%	12%
11	-	-	-	4%	6%	9%	7%	-	-	-	-	8%	10%	9%
12	-	-	-	-	3%	5%	7%	6%	-	-	-	-	9%	11%
13	-	-	-	-	-	3%	4%	6%	5%	-	-	-	-	8%
14	-	-	-	-	-	-	2%	3%	5%	5%	-	-	-	-
15	-	-	-	-	-	-	-	2%	3%	6%	6%	-	-	-
16	-	-	-	-	-	-	-	-	1%	4%	5%	4%	-	-
17	-	-	-	-	-	-	-	-	-	1%	3%	4%	4%	-
18	-	-	-	-	-	-	-	-	-	-	1%	3%	4%	1%
19	-	-	-	-	-	-	-	-	-	-	-	0%	2%	3%
20	-	-	-	-	-	-	-	-	-	-	-	-	1%	1%
Total	262	471	639	692	655	709	792	807	772	562	490	427	374	307