Estimation of Demographic Parameters for New Zealand Sea Lions Breeding on the Auckland Islands - Updated Results

Objective 3: POP2007/1

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Introduction

Following the presentation of results at the CSP TWG meeting on 19 September 2008, additional analyses where requested with an increase in the number of age groups and the inclusion of model diagnostics. The basic estimation methods used here are unchanged from those outlined in my report date 28 August 2008. The only notable changes are that an additional age structure has been considered (4 age-classes: 0-3, 4-7, 8-14 and 15+); the quadratic relationship between demographic parameters and age has been removed; and that resighting probabilities have been made age-class specific (0-3, 4+), however results are largely unchanged. Model diagnostics do not indicate poor model fit.

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.

Whether an animal survives between breeding seasons *t* and *t*+1 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 or breeding status of the animal in year *t* (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 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).

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

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

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

Survival and breeding probabilities were allowed to vary in accordance with animal age. Three different age structures were considered: constant for all ages, 3 age classes (0-3, 4-14, 15+) and 4 age classes (0-3, 4-7, 8-14, 15+). These age classes were decided upon through discussion with Dr Louise Chilvers (DOC). There are no breeding individuals in the 0-3 age class hence these survival and breeding probabilities were set to 0. Tag loss probabilities were assumed constant with respect to animal age. Following this primary analysis, an exploratory model was also fit to the data where survival and breeding probabilities were completely age-specific. Only 5,500 iterations were used with the first 500 being discarded as the burn-in period.

Within a breeding season, attempts are made to resight previously tagged individuals. There are a limited number of days of field effort each year, 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 vary annually.

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

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

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

Markov chain Monte Carlo methods were used to obtain approximate posterior distributions for all parameters. Two chains of 25,000 iterations were run with the first 5,000 iterations of each chain being discarded as the burn-in period. Chains were checked for convergence and good mixing. Uniform prior distributions were assumed for all probabilities except tag loss when an animal had 2 tags in the previous year, in which case a Dirichlet(1,1,1) prior distribution was used. The natural log of the odds ratio δ was assigned a normal prior distribution with zero mean and SD = 10.

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.

The posterior distribution of the deviance value for the observed data could 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

Data was extracted from the Auckland Island sea lion database by Laura Boren (DOC contractor) with additional verification by Darryl MacKenzie (Proteus), for females tagged

between 1990 – 2008. As estimation is primarily focused on adult females, only data from the 1990-2003 tagging cohorts were used. Due to the inconsistent field effort prior to 1998, data from 1990-1997 was not considered and all analyses are conditional upon the first encounter of a female in the period 1998-2008. 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).

When an animal was retagged during the period 1998-2008, the new tag number was treated as an older animal that had been tagged for the first time, while the old identity was treated as a 'loss on recapture'. This is a standard technique for dealing with retagged animals in mark-recapture analyses.

Results

Examples of Convergence

Due to the large number of parameters, traces of the MCMC chains are not presented here, though examples are given in Figures 1-3. Generally, convergence was reached within the first 1000 iterations, well within the 5000 burn in period.

Strict Definition of 'Breeder'

Posterior distributions for the resight probabilities were consistent regardless of the age-structure used to model survival and breeding probabilities, hence only those from the model with 4 age-classes are presented here (Figures 4-7). In all cases, the daily probability of resighting a tagged breeder (red-shaded) is higher than a tagged non-breeder (grey-shaded. Daily resight probabilities for individuals in the 0-3 age group are very low, as are the probabilities of resighting tagged individuals by PIT tag.

Deviance values and deviance-based Bayesian p-values for models with the different age-structures are given in Table 1. There is no strong indication of model lack of fit, although the p-value of close to 1 for the model with just a single age-class is interesting as typically this indicates over-fitting of the model to the data, but here it has occurred for the simplest model considered *(the results from the single age class model are currently being verified as this, and other results, are unexpected)*. The posterior distribution of the deviance values would indicate that the 3- and 4-age class models could be ranked similarly.

Figure 8 presents the posterior distributions for survival for non-breeders from each model with the different age structures, with a numerical summary given in Table 2. The equivalent results for breeders are given in Figure 9 and Table 3. These results indicate differences in survival amongst age groups, although there is little difference between using a 3- or 4-age class model. In all cases breeders and estimated to have higher survival than non-breeders.

The posterior distribution for breeding in year t by age group for non-breeders in year $t-1$ is given in Figure 10, and for breeders in Figure 11. Numerical summaries are given in Tables 4 and 5. The posterior distribution for the probability of breeding from the single age class model appears suspicious and is currently being checked for accuracy. From the 3- and 4-age class models, the posterior distribution for females aged 0-3 that were non-breeders in the previous year is essentially 0, but there has been the rare individual that has bred for the first time at age 4. Breeding probabilities for animals that were either breeders or non-breeders in the previous year are similar across the other age groups, although individuals that bred in the previous year have a higher probability of breeding in the current year.

Figure 12 illustrates the posterior distribution for the probability of an individual having no tags in year t given either 1 or 2 tags in year $t-1$, with Table 6 presenting a summary of the probabilities for all tag numbers. 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. Furthermore, if tag loss was not accounted for survival would be underestimated by approximately 0.09, although the presence of branded and PIT tagged animals partially mitigates this.

Liberal Definition of 'Breeder'

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

Deviance values and deviance-based Bayesian p-values for models with the different age-structures are given in Table 7. There is no strong indication of model lack of fit. The posterior distribution of the deviance values would indicate that the 3- and 4-age class models could be ranked similarly, and are better than the single-age class model.

Using the more liberal definition of breeder does not appreciable change any of the main results observed than when using the stricter definition. The main difference is that the posterior distributions for breeding probabilities tend to be slightly higher (Figures 13-17, Table 8-12).

Exploratory analysis of full age-specific models

Posterior distributions for survival and breeding probabilities under a fully age-specific model are given in Figures 18-21 and Figure 22-25, using the strict and liberal definition of breeder respectively. The distributions are characterised by a great deal of uncertainty which is due to the relatively small number of sea lions of a particular age each year, hence pooling into age classes would seem appropriate as a means of reducing the estimation uncertainty. It should be noted that by spreading the data so thinly over so many parameters, other effects such as annual variation in the demographic parameters may be influencing results, contributing to some of the apparent patterns in the estimates. It should also be noted that when sample sizes are very small, the influence of the prior distribution on the results is greater, causing the mean of the posterior distribution to be pulled toward 0.5. This may contribute to the apparent senescence effect.

While not definitive, in combination with the Bayesian p-values, these figures would suggest that the 3- or 4-age class models capture the main features of the population demographics. The exception may be for non-breeder survival in the 0-3 age class, where it would appear that perhaps survival is only markedly lower for pups of the year, and that 1-3 year olds have a similar survival rate to older animals. However there is the possibility for some confounding of survival rate estimates because of the very low resighting rates for younger

animals. Using the current 0-3 age classes, it may be appropriate to interpret the estimated survival rates as an annualised value for surviving from a pup to a 4-year old.

Discussion

The age classes used here are biologically reasonable (L Chilvers, pers comm.) and there is no evidence of poor model fit. Hence, I firmly believe that the results presented here are reasonable. There may be some desire to further partition the 0-3 and 15+ age groups, however in both cases there are important sample size considerations that may limit the utility of doing so. The resighting rates of females in the 0-3 age group is very small, indicating there are very few observations of such animals. As such, estimands of age-specific survival in this group may be unreliable. For the oldest age group one may expect some form of senescence to occur in either breeding or survival probabilities. However, there are very few individuals in this age group so again, further partitioning of the age group may led to unreliable estimands as the prior distribution will have a greater effect on results.

Using the more liberal definition of a "breeder" primarily only has an impact upon the breeding probabilities; all other parameters are essentially unchanged. Generally, breeding probabilities for the adult age classes increase by between 0.02-0.06, with the exception of the oldest age classes with individuals that were breeders in the previous year. It is not possible to determine from the available data which definition might be more correct.

References

Gelman et al. 2003. Bayesian Data Analysis. 2nd Ed. Chapman and Hall, Boca Raton, Florida, USA

Figures

Figure 1: Example trace plot of breeder survival.

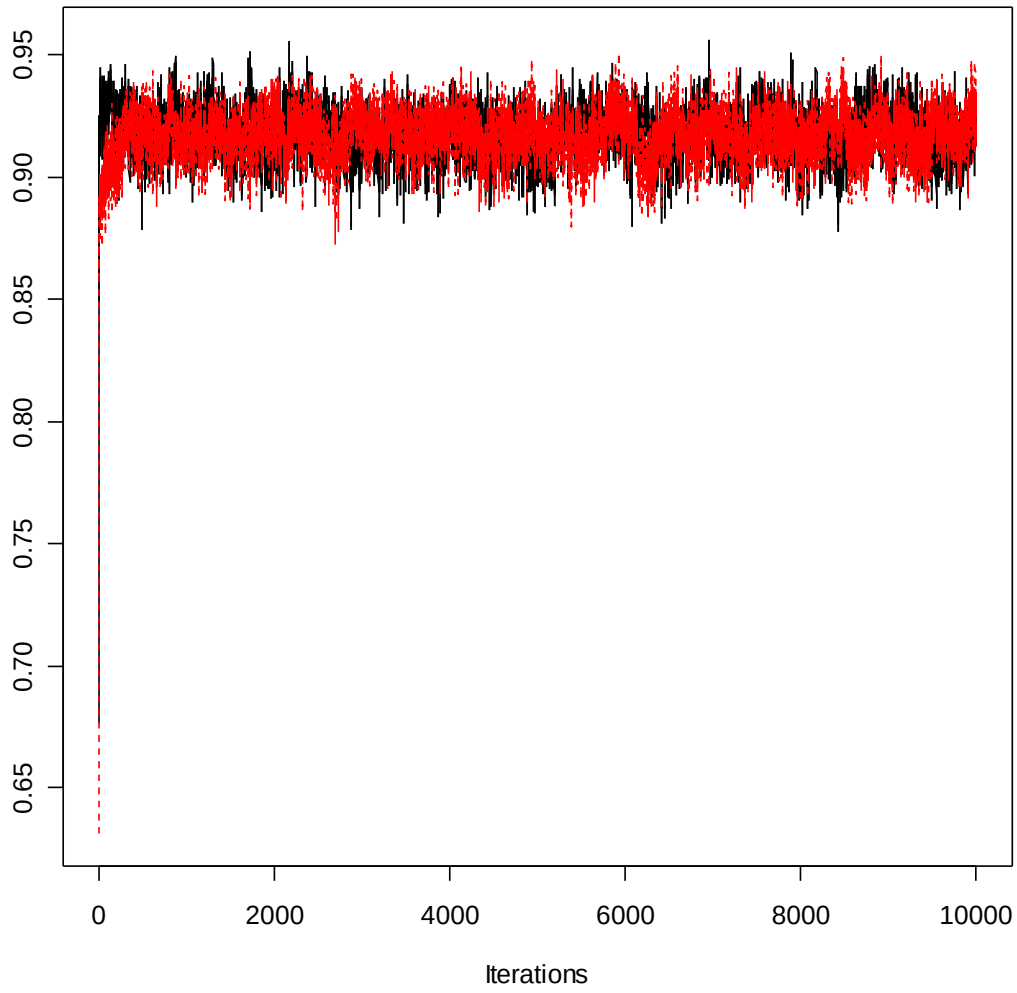

Figure 2: Example trace plot of non-breeder survival.

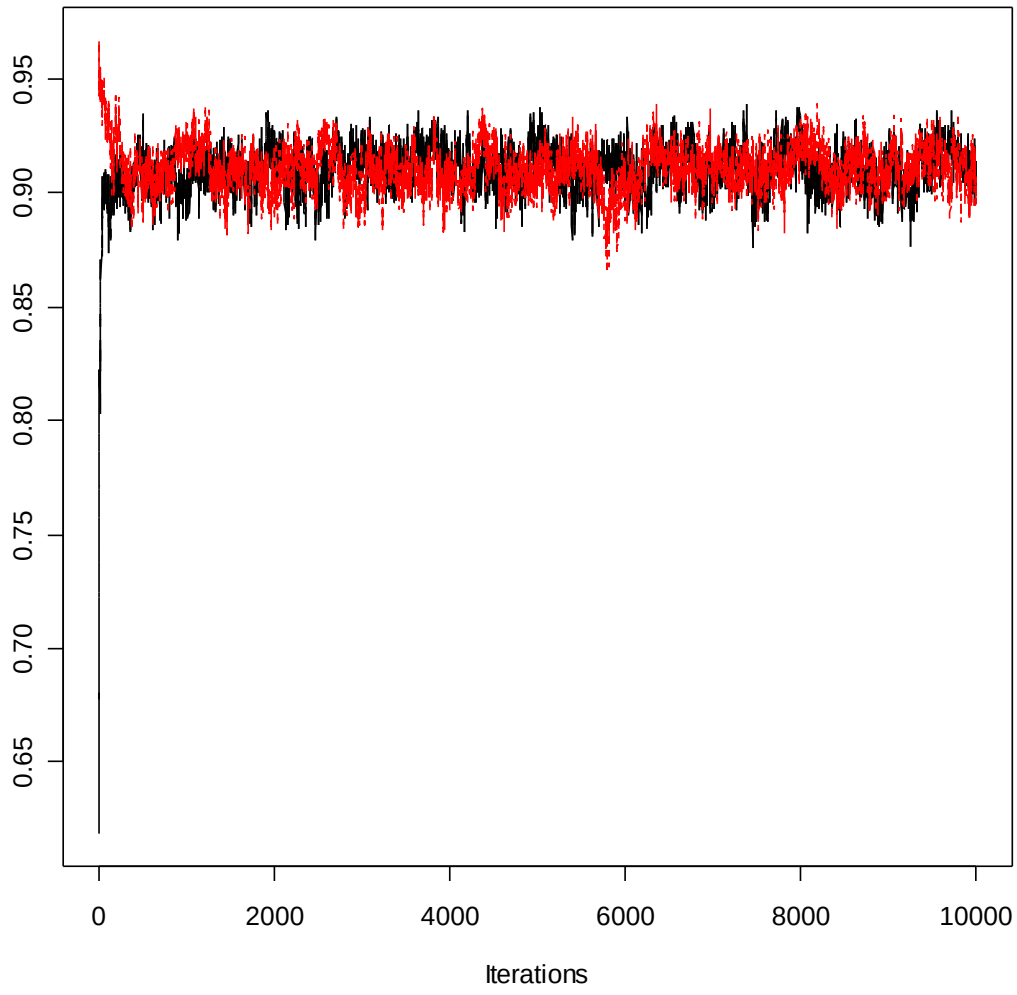

Figure 3: Example trace plot of probability of resighting a branded females.

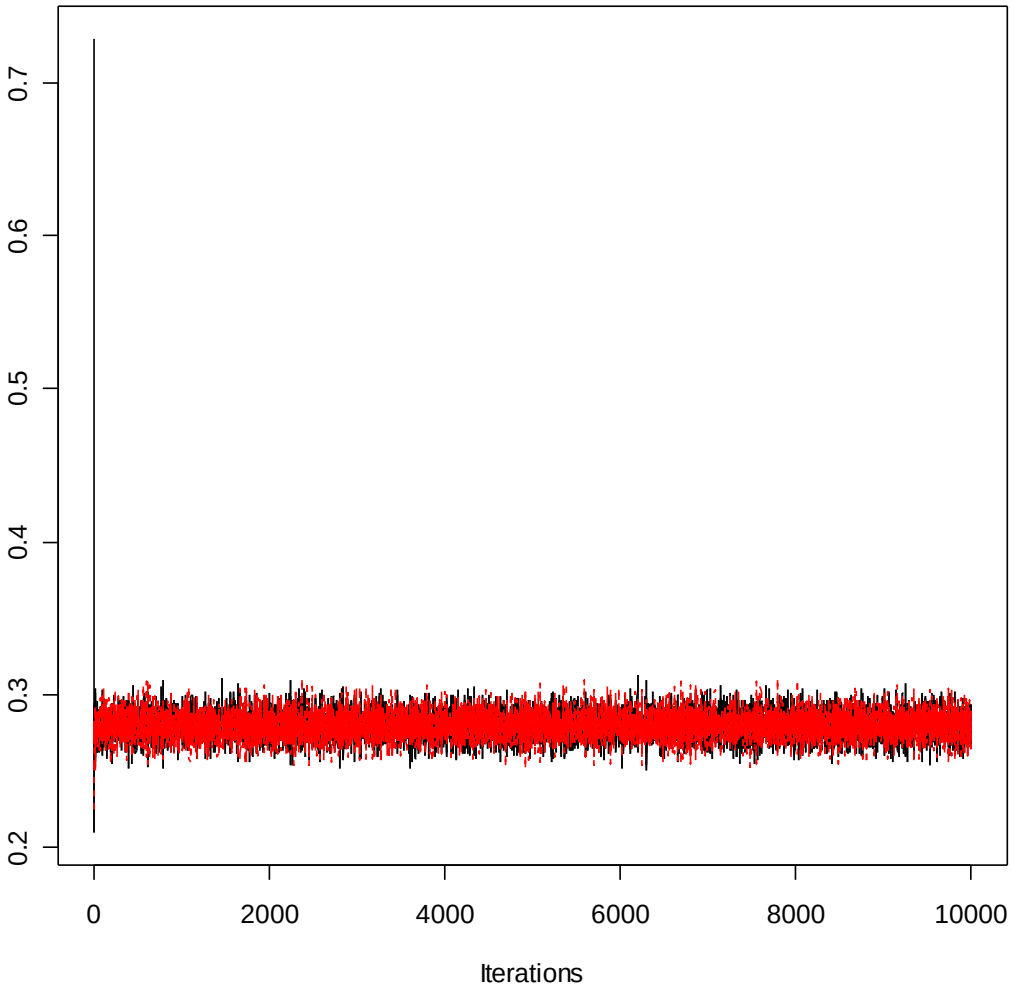

Figure 4: Posterior distribution for the daily probability of sighting a branded individual in each year by age class. Resight probabilities for which there was no information in the data are not indicated. Grey-shaded distributions indicate non-breeders and red-shaded distributions breeders.

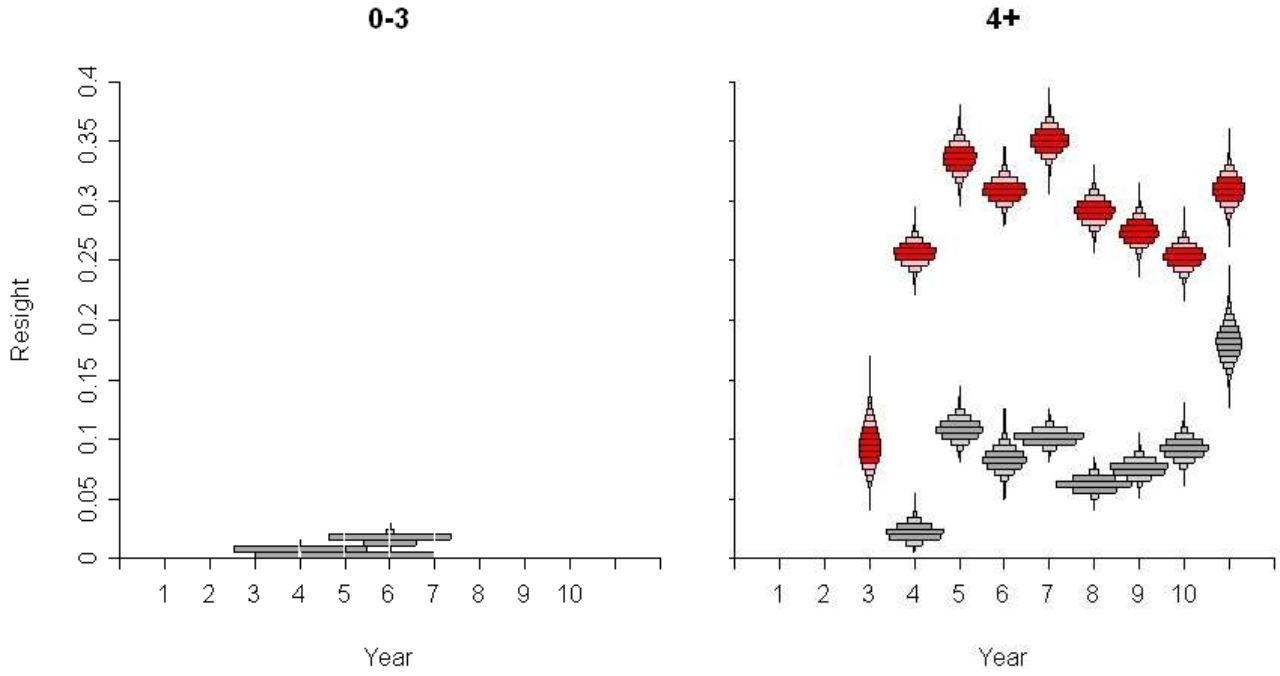

Figure 5: Posterior distribution for the daily probability of sighting a PIT tagged individual with no flipper tags in each year by age class. Resight probabilities for which there was no information in the data are not indicated. Grey-shaded distributions indicate non-breeders and red-shaded distributions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

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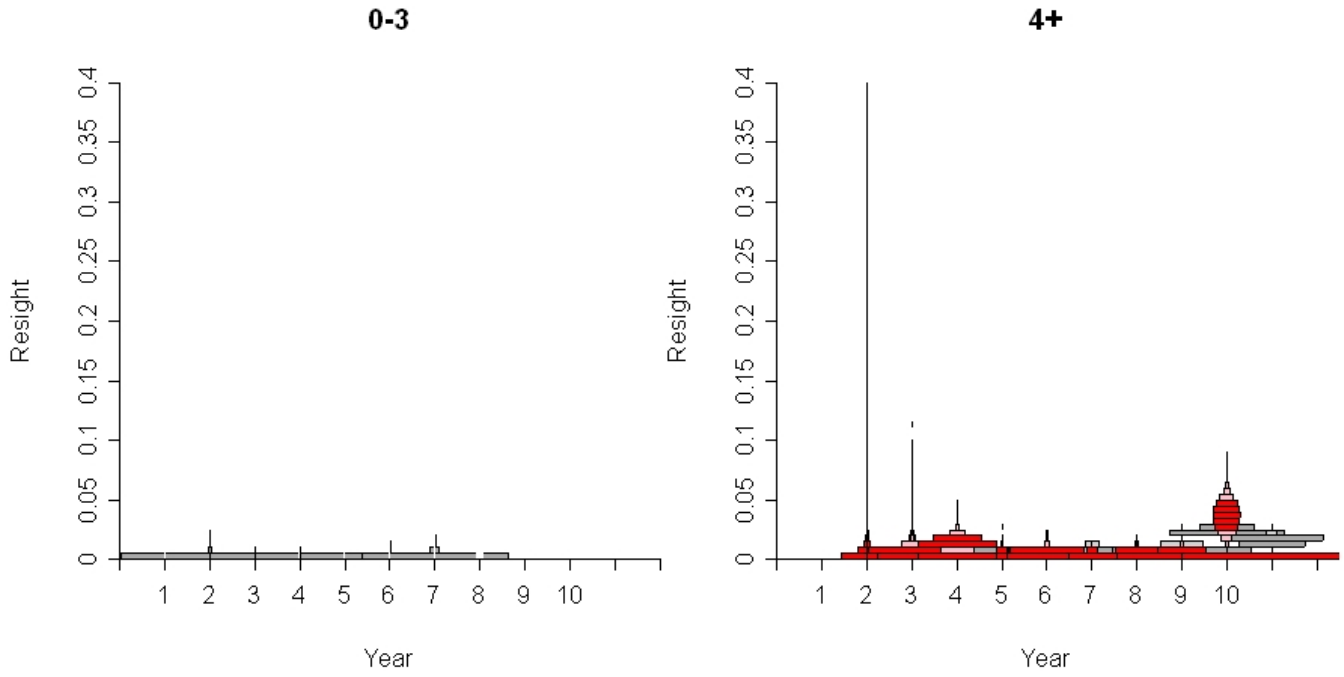


Figure 6: Posterior distribution for the daily probability of sighting an individual with 1 flipper tag in each year by age class. Resight probabilities for which there was no information in the data are not indicated. Grey-shaded distributions indicate non-breeders and red-shaded distributions breeders.

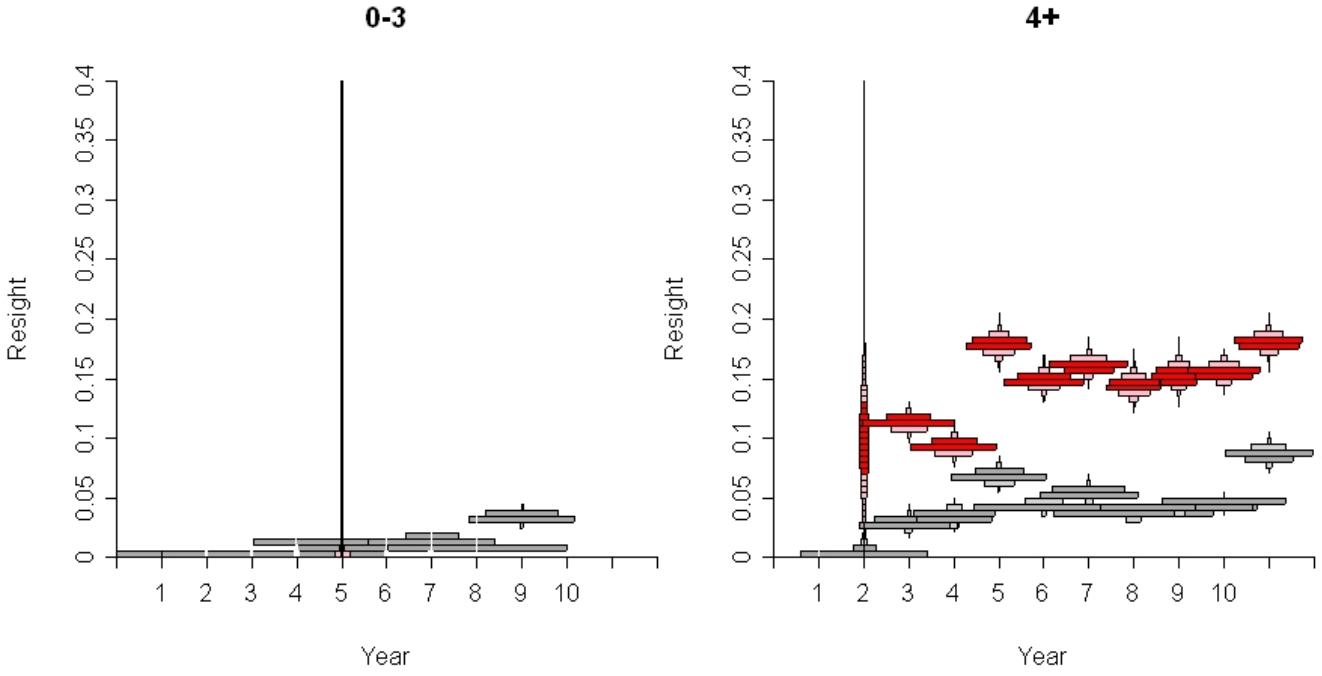


Figure 7: Posterior distribution for the daily probability of sighting an individual with 2 flipper tags in each year by age class. Resight probabilities for which there was no information in the data are not indicated. Grey-shaded distributions indicate non-breeders and red-shaded distributions breeders.

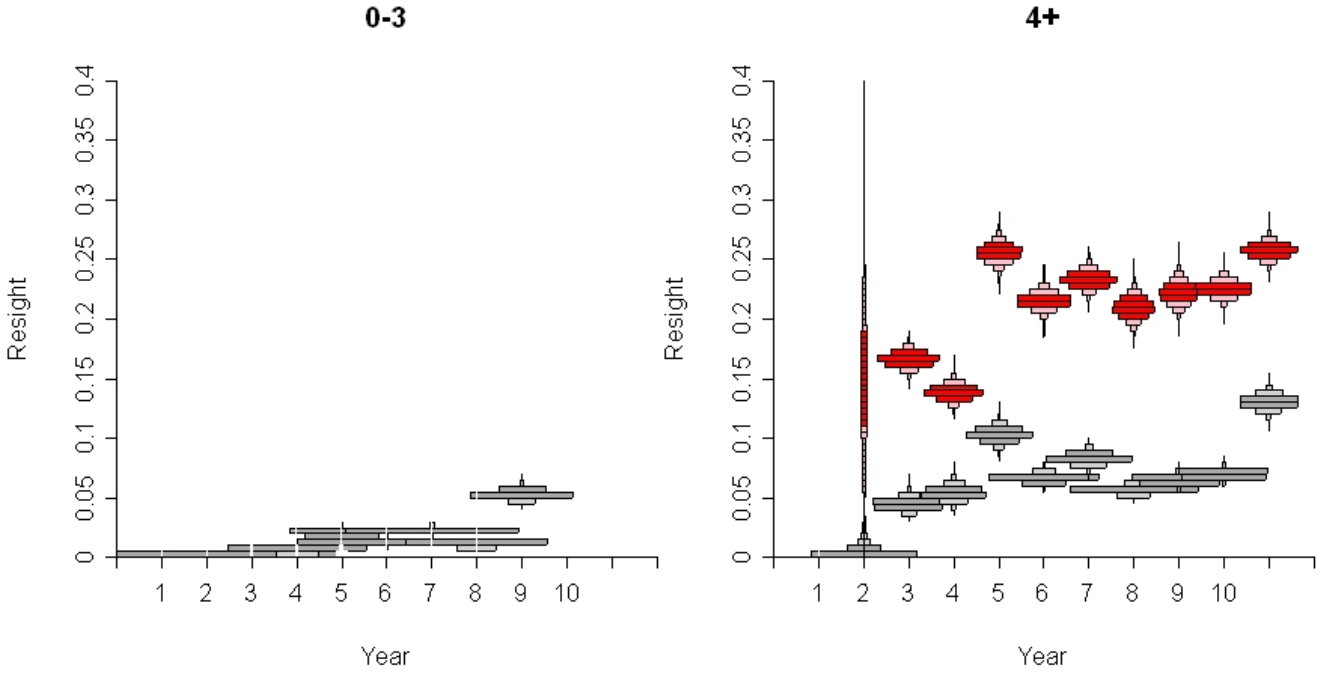
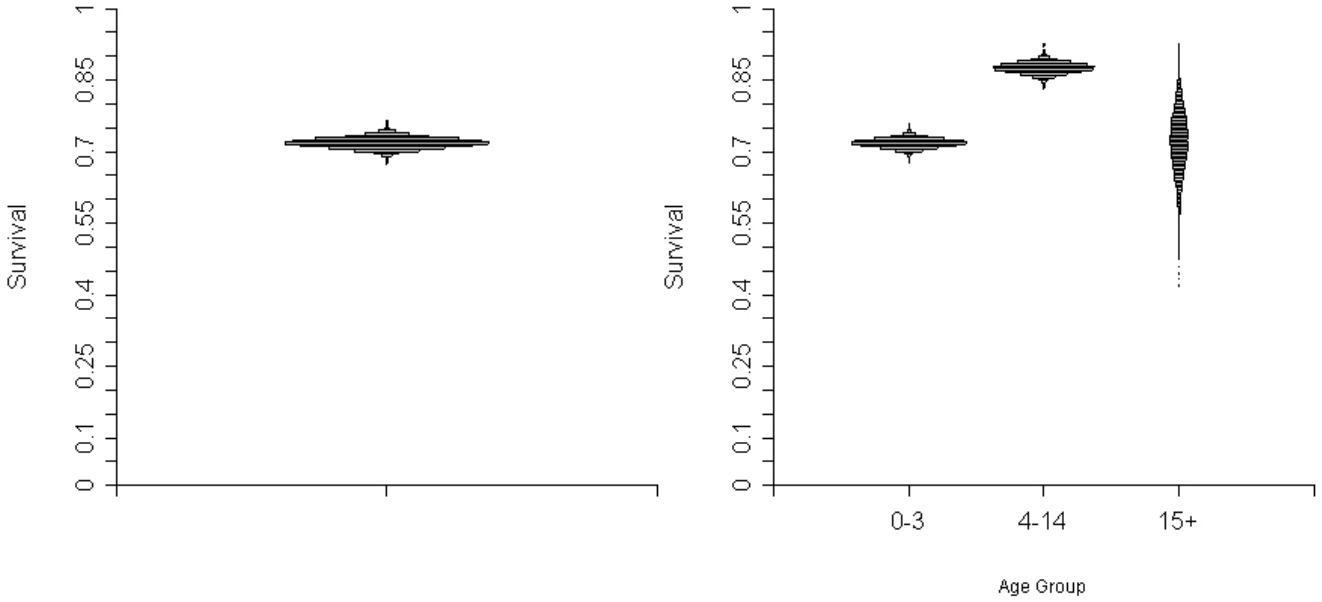


Figure 8: Illustration of posterior distribution for probability of survival from year *t* to *t*+1 by age group for individuals that were non-breeders in year *t*, from models with different age structures.



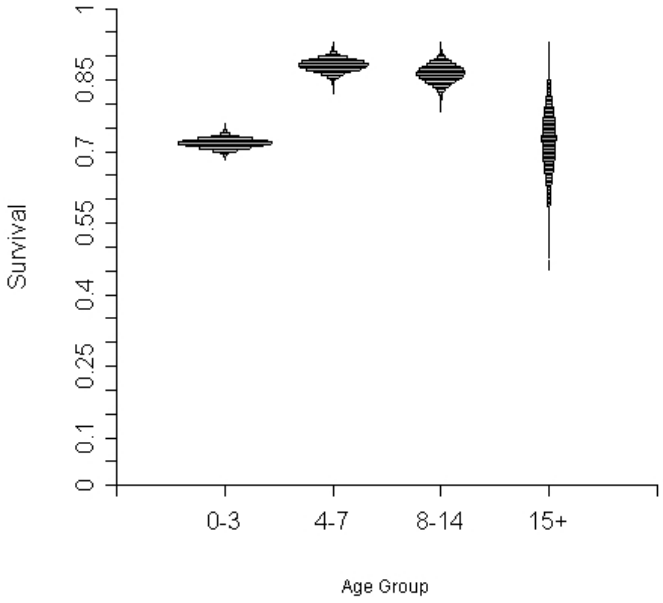
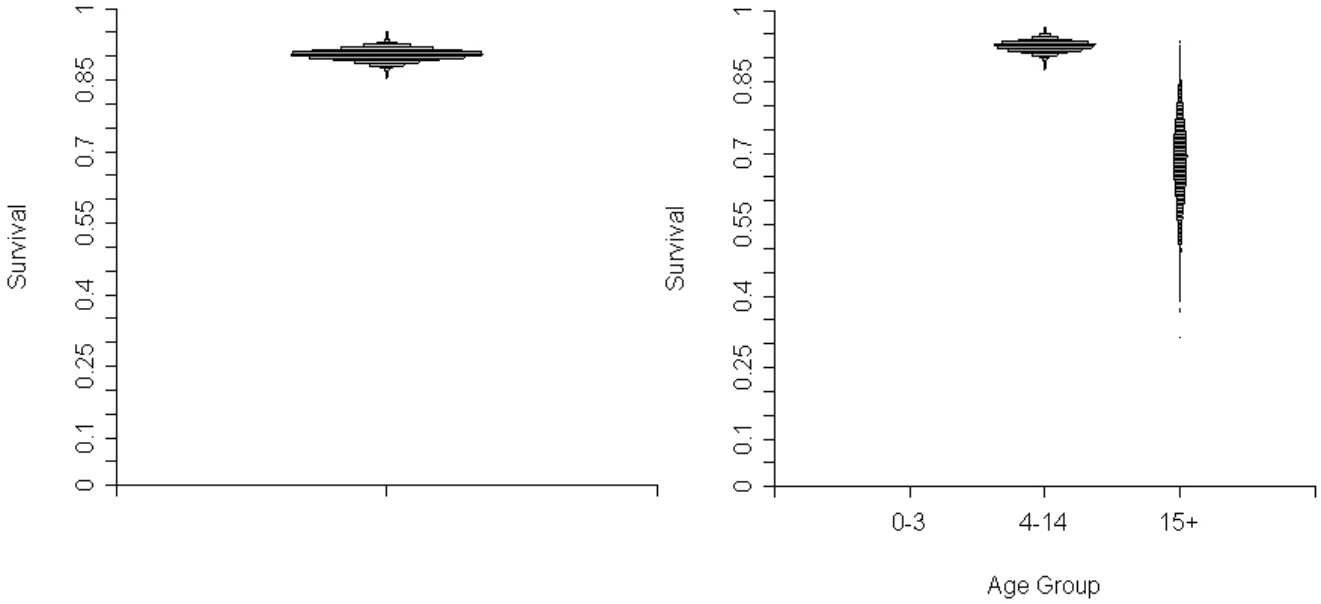


Figure 9: Illustration of posterior distribution for probability of survival from year *t* to *t*+1 by age group for individuals that were non-breeders in year *t*, from models with different age structures.



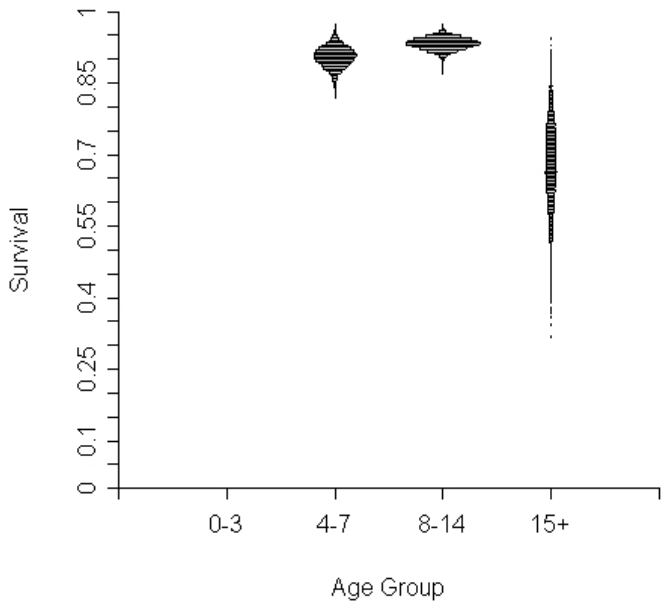
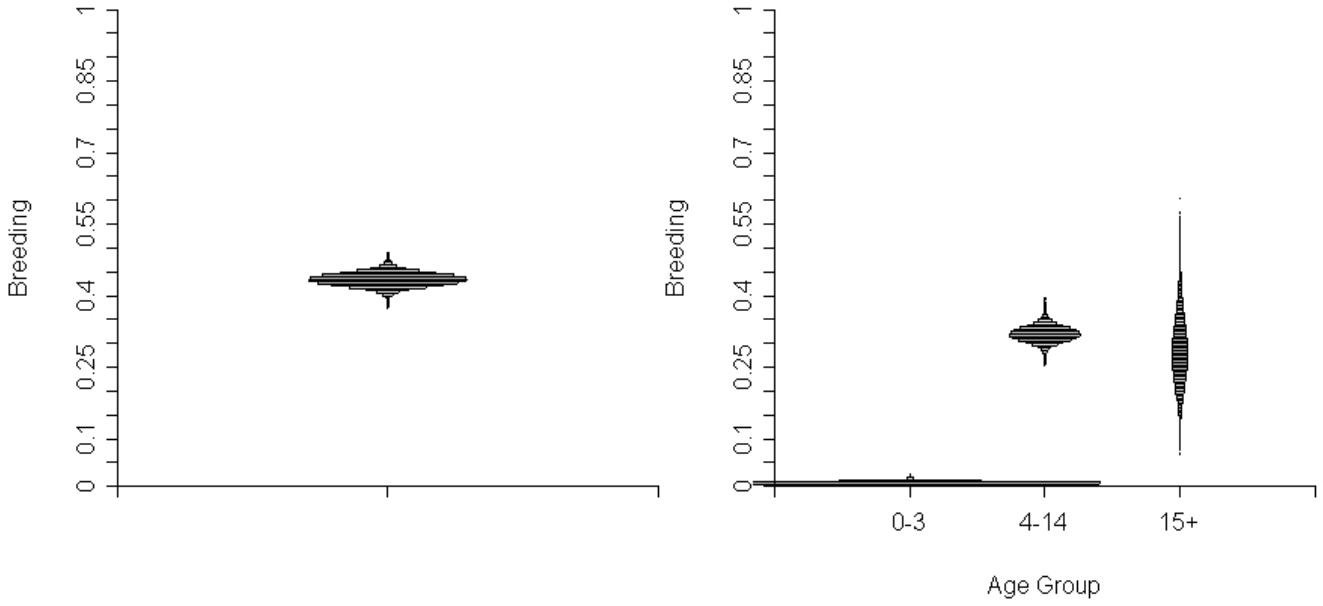


Figure 10: Illustration of posterior distribution for probability of breeding in year *t* by age group for individuals that were non-breeders in year *t*−1, from models with different age structures.



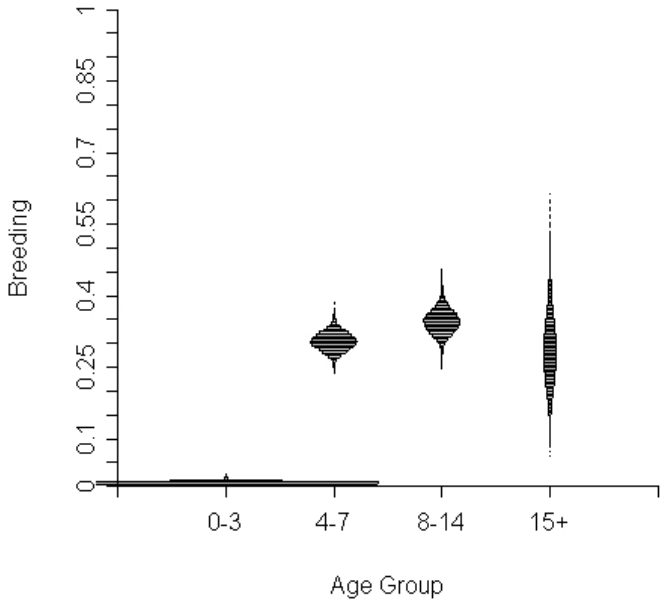
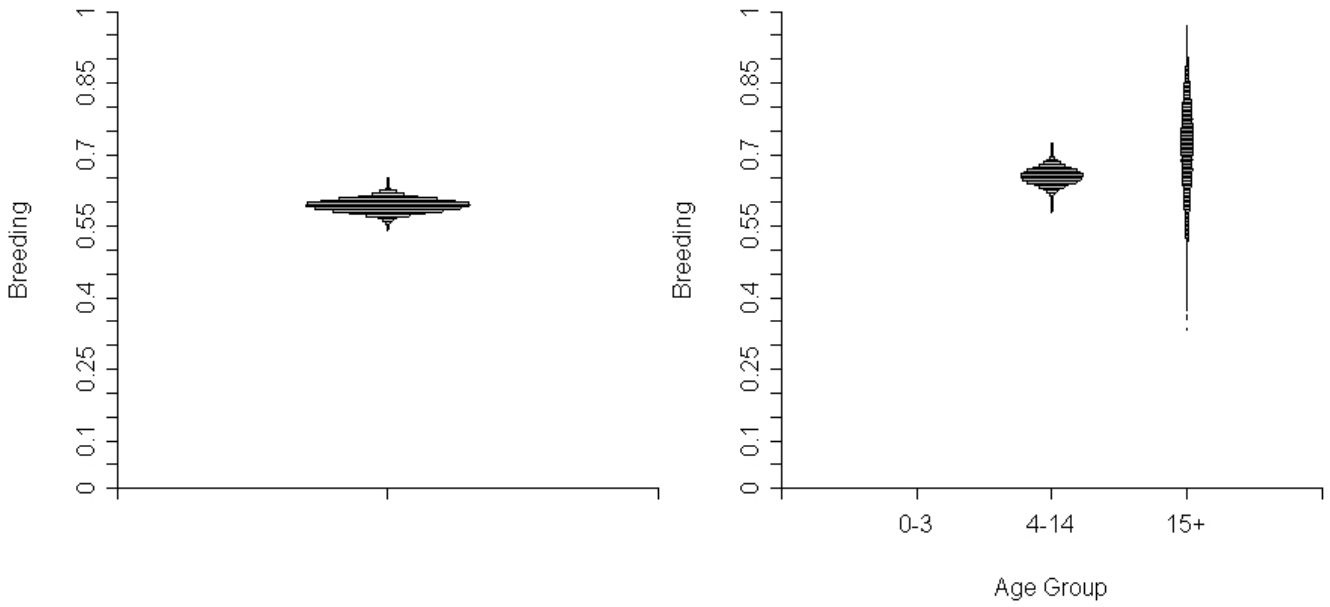


Figure 11: Illustration of posterior distribution for probability of breeding in year *t* by age group for individuals that were breeders in year *t*−1, from models with different age structures.



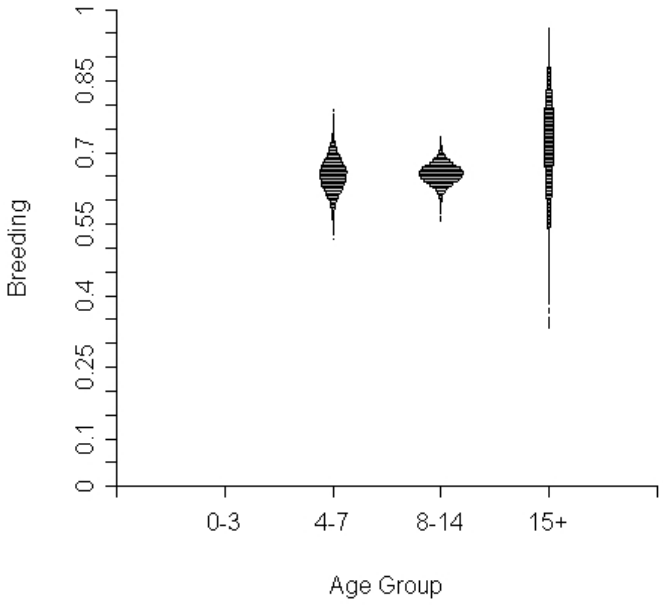


Figure 12: Posterior distribution for the probability of having no tags in year *t* given the number of tags in year *t*−1, from the model a) a single age class; b) 3 age classes; and c) 4 age classes, for survival and breeding probabilities.

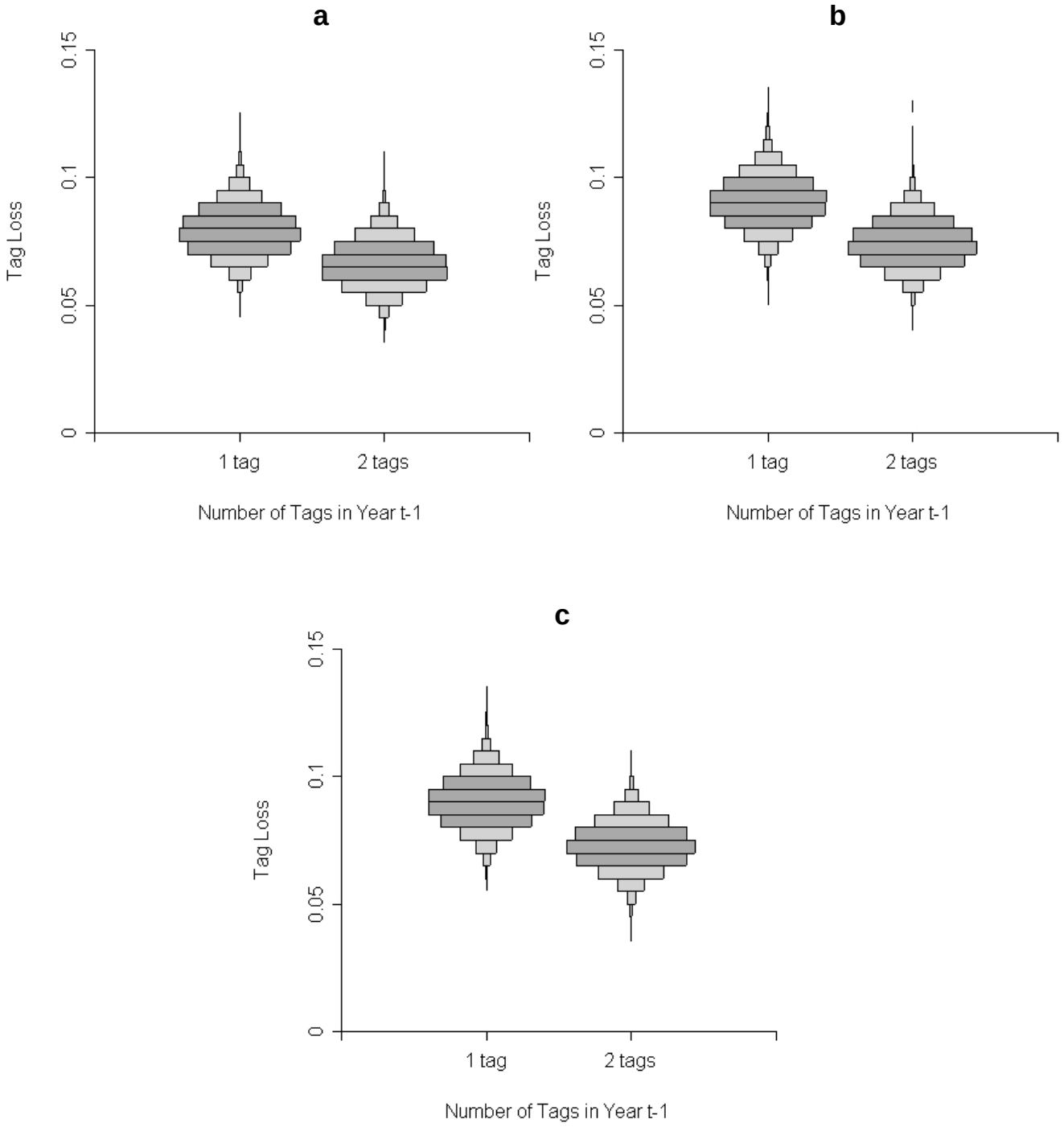
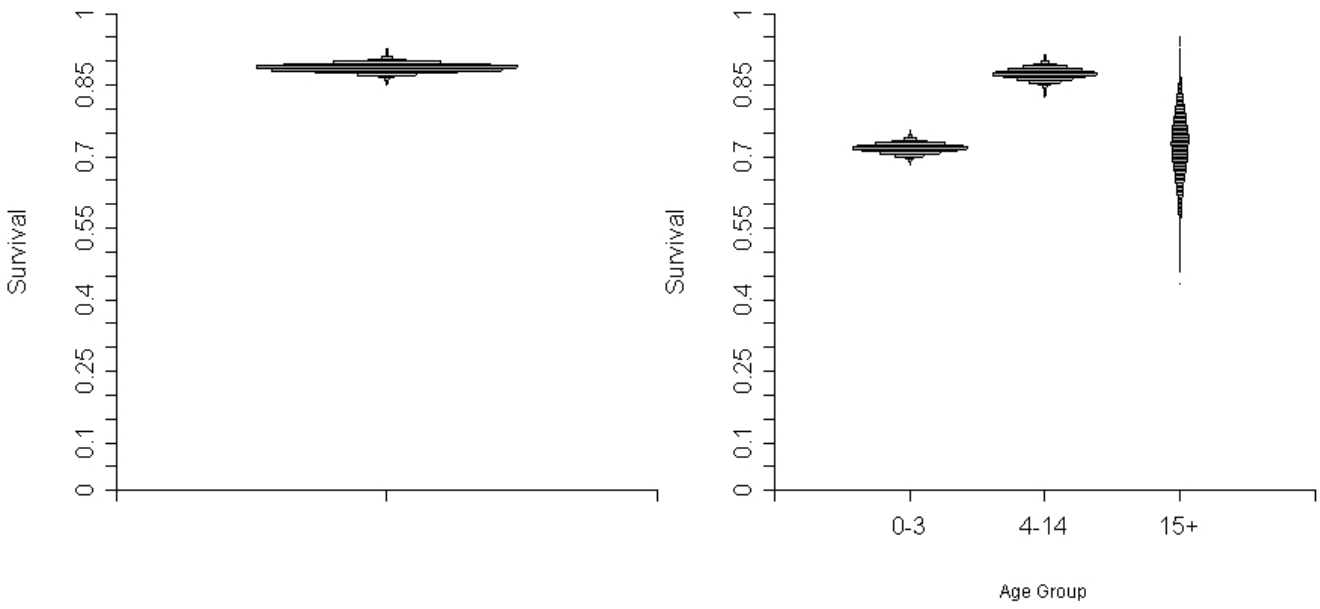


Figure 13: Illustration of posterior distribution for probability of survival from year *t* to *t*+1 by age group for individuals that were non-breeders in year *t*, from models with different age structures using the liberal definition of a breeder.



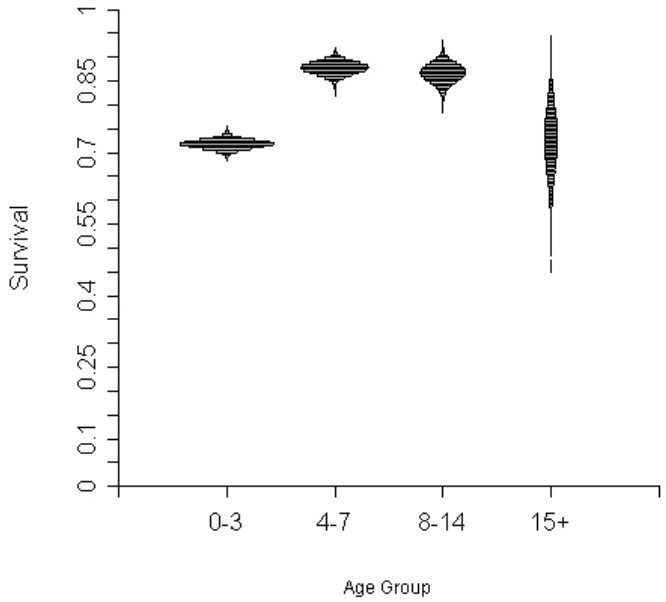


Figure 14: Illustration of posterior distribution for probability of survival from year *t* to *t*+1 by age group for individuals that were non-breeders in year *t*, from models with different age structures using the liberal definition of a breeder.

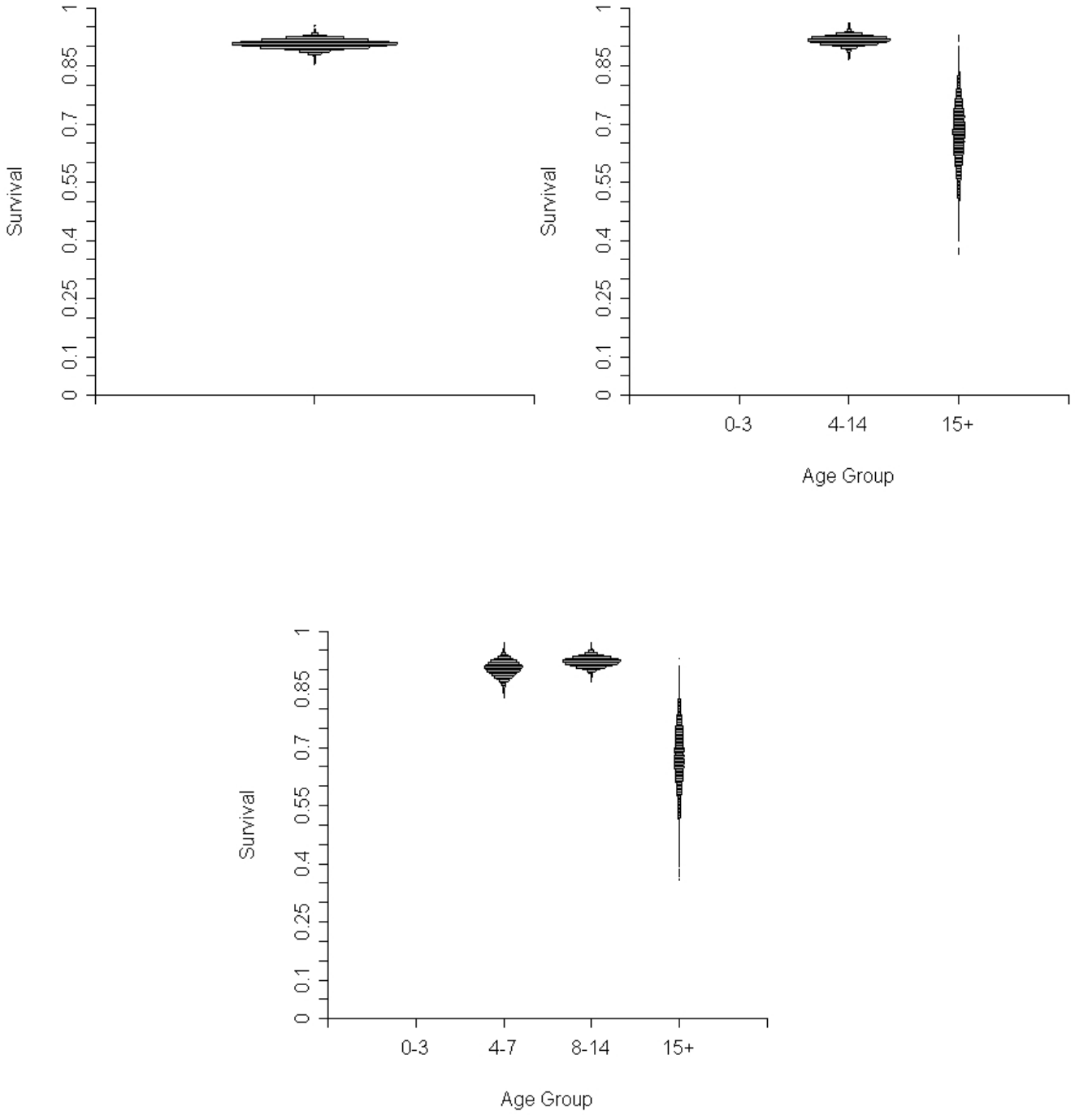
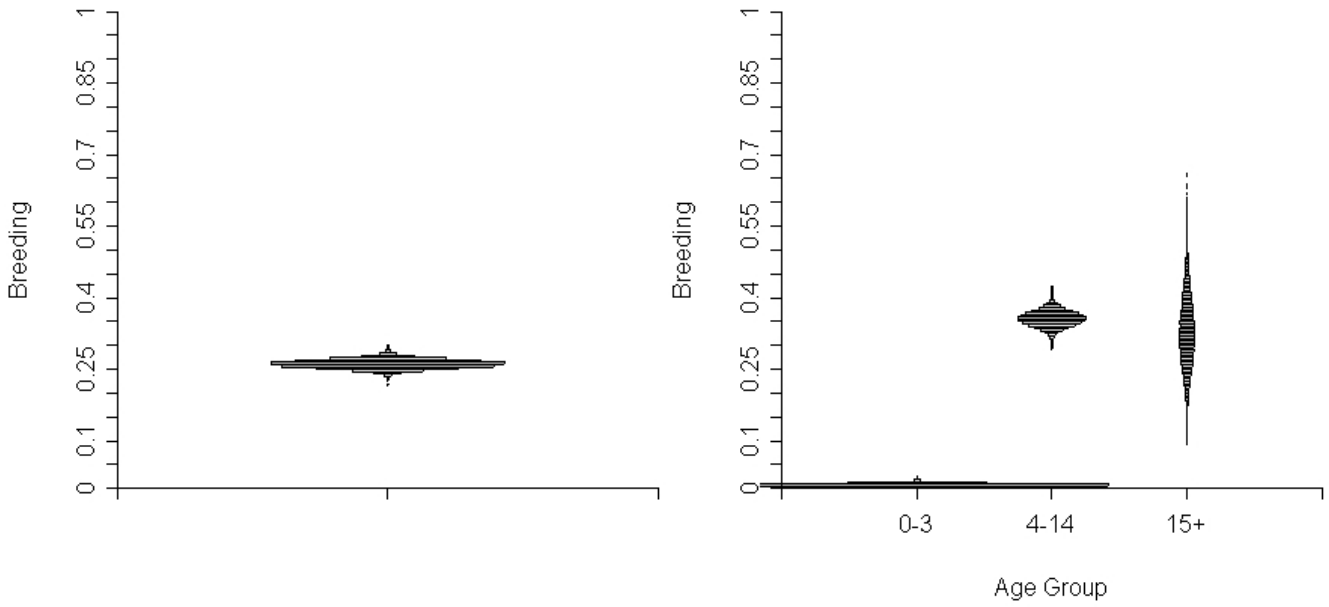


Figure 15: Illustration of posterior distribution for probability of breeding in year *t* by age group for individuals that were non-breeders in year *t*−1, from models with different age structures using the liberal definition of a breeder.



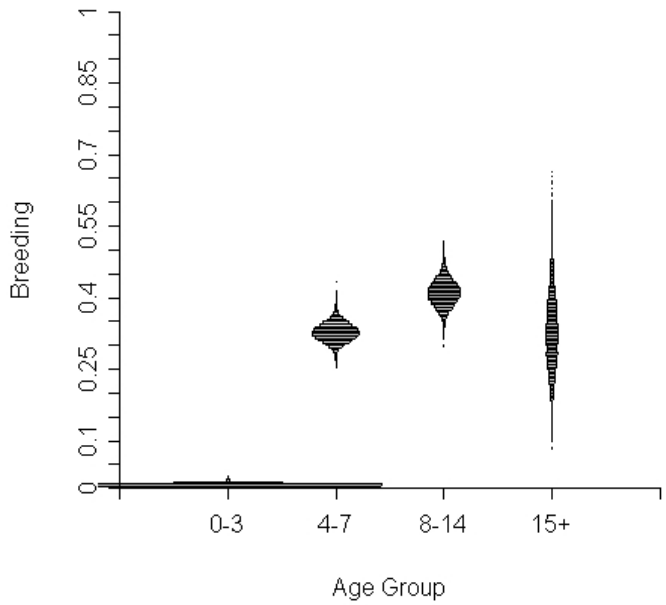
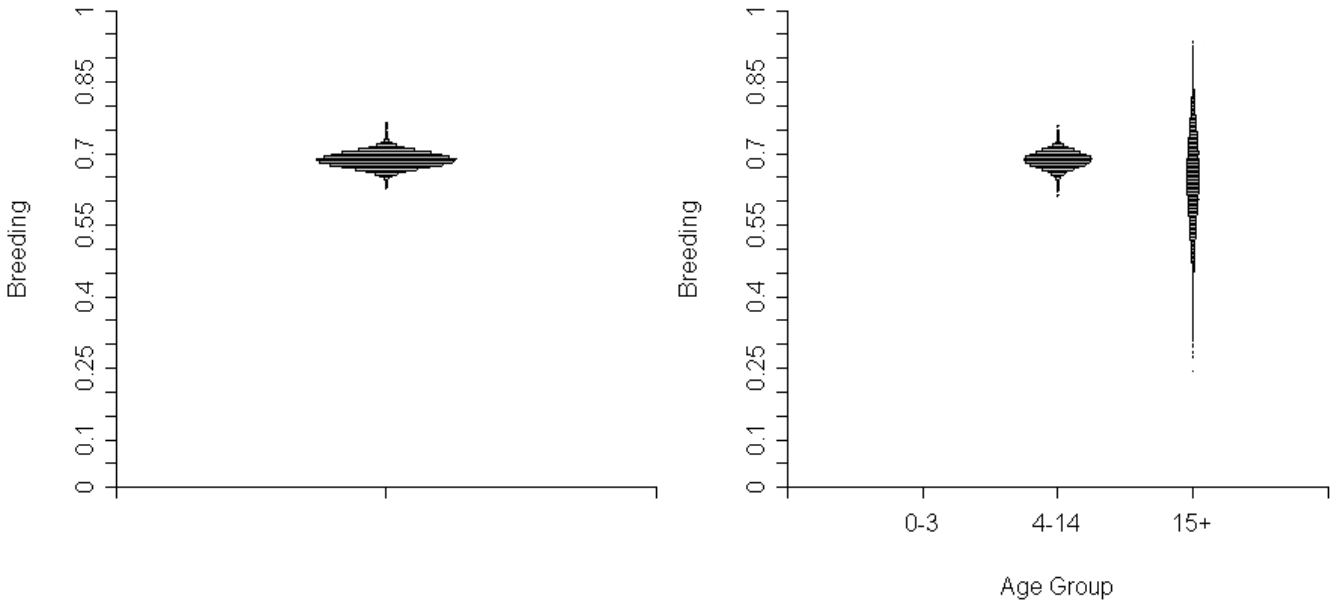


Figure 16: Illustration of posterior distribution for probability of breeding in year *t* by age group for individuals that were breeders in year *t*−1, from models with different age structures using the liberal definition of a breeder.



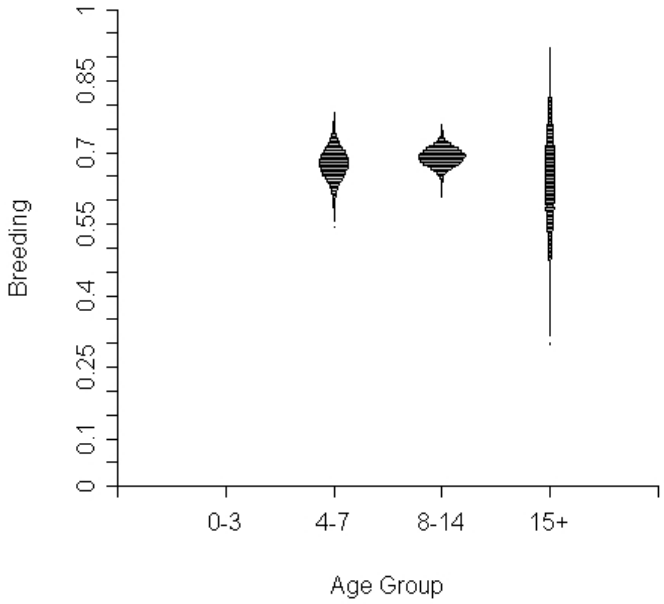


Figure 17: Posterior distribution for the probability of having no tags in year *t* given the number of tags in year *t*−1, from the model a) a single age class; b) 3 age classes; and c) 4 age classes, for survival and breeding probabilities using the liberal definition of a breeder.

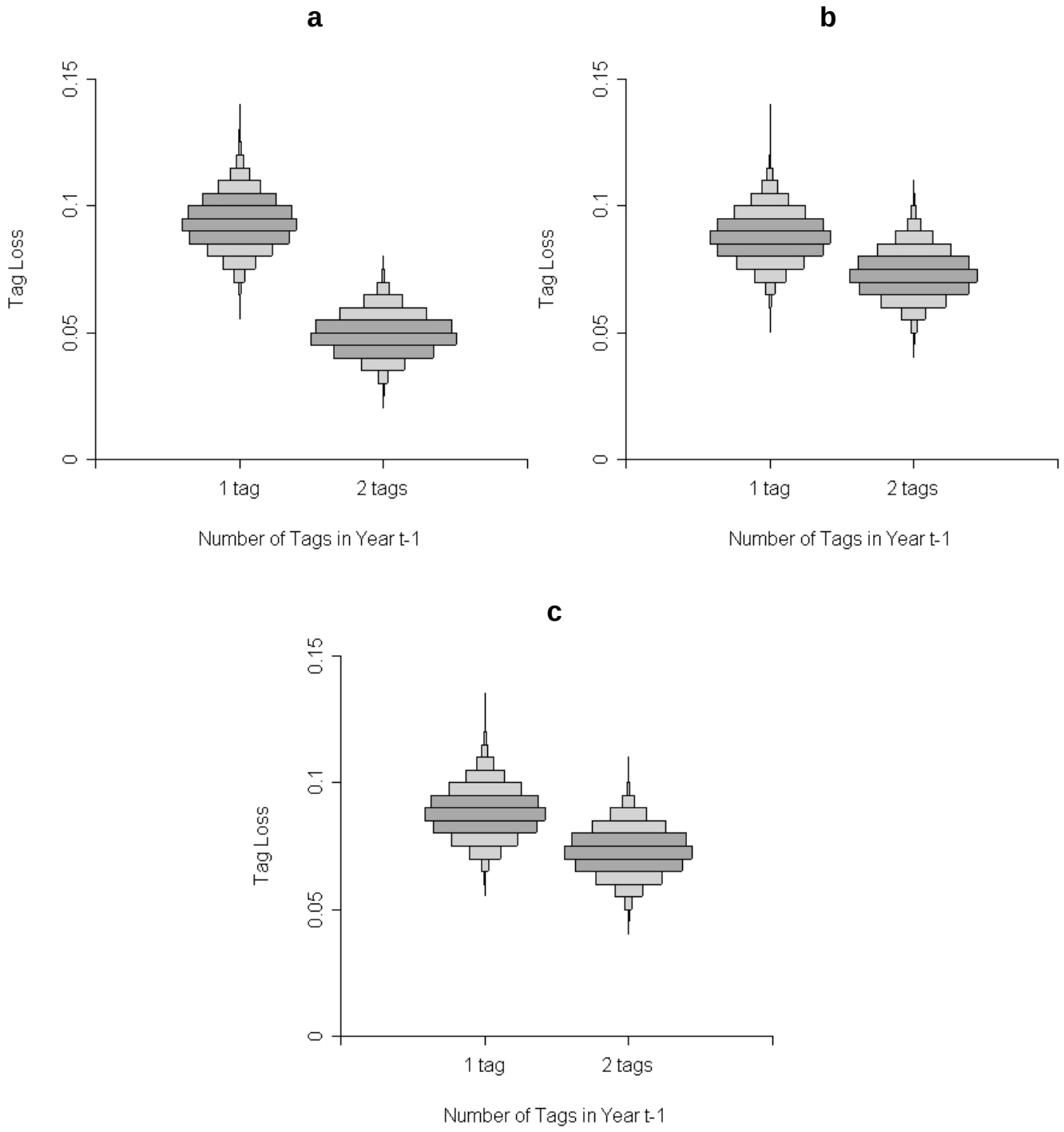


Figure 18: Posterior distributions for probability of survival from year *t* to *t*+1 by age for individuals that were non-breeders in year *t*, from full age-specific model, using the strict definition of breeder.

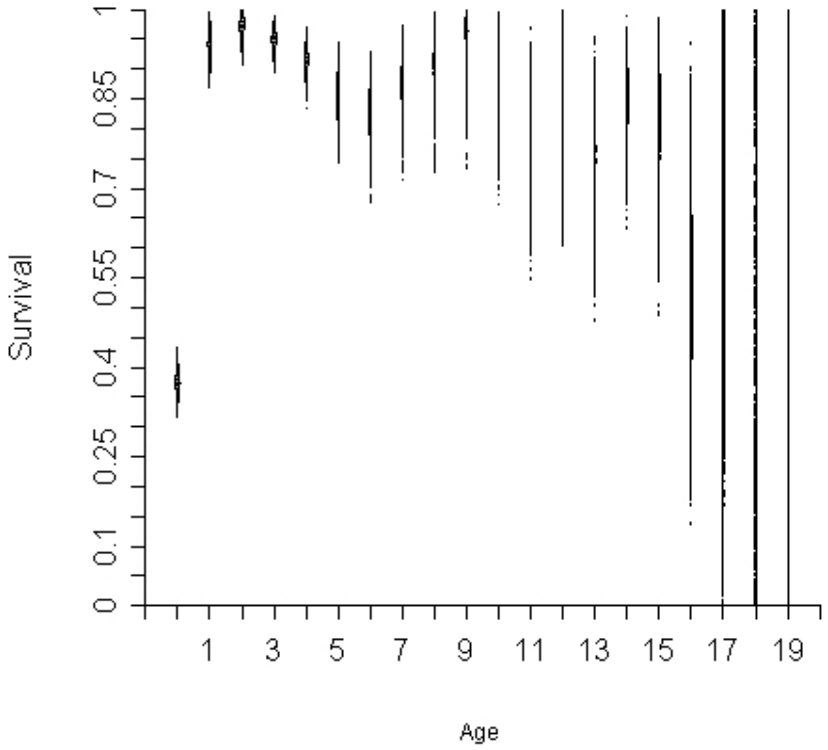


Figure 19: Posterior distributions for probability of survival from year *t* to *t*+1 by age for individuals that were breeders in year *t,* from full age-specific model, using the strict definition of breeder.

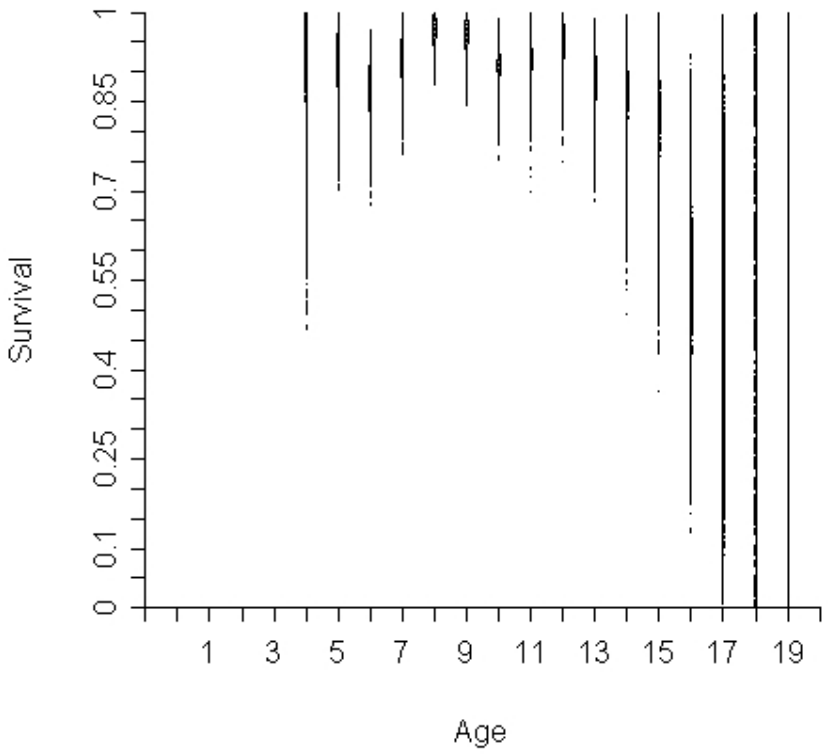


Figure 20: Posterior distributions for probability of breeding in year *t* by age group for individuals that were non-breeders in year *t*−1, from full age-specific model, using the strict definition of breeder.

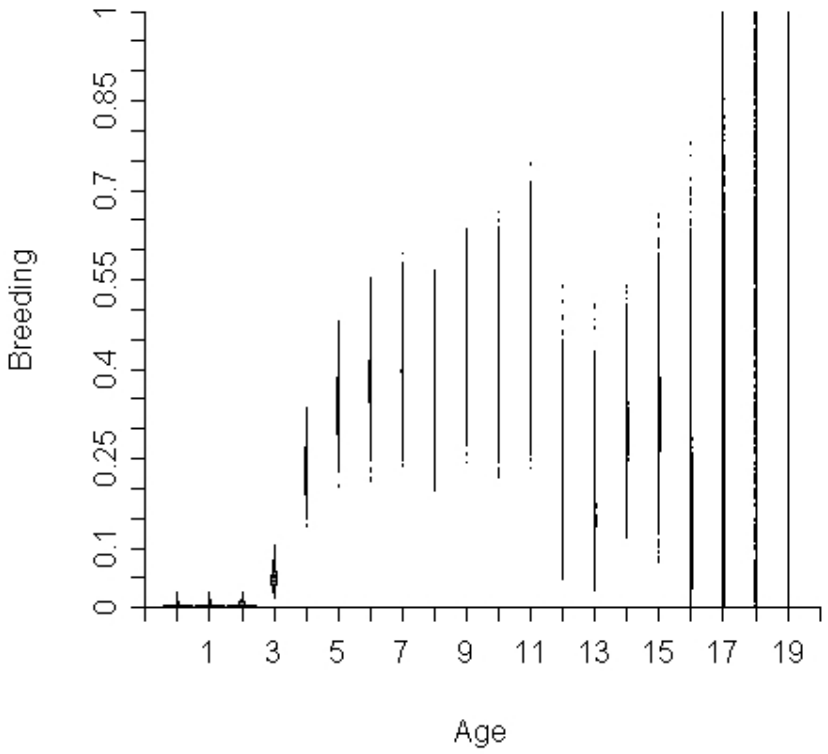


Figure 21: Posterior distributions for probability of breeding in year *t* by age group for individuals that were breeders in year *t*−1, from full age-specific model, using the strict definition of breeder.

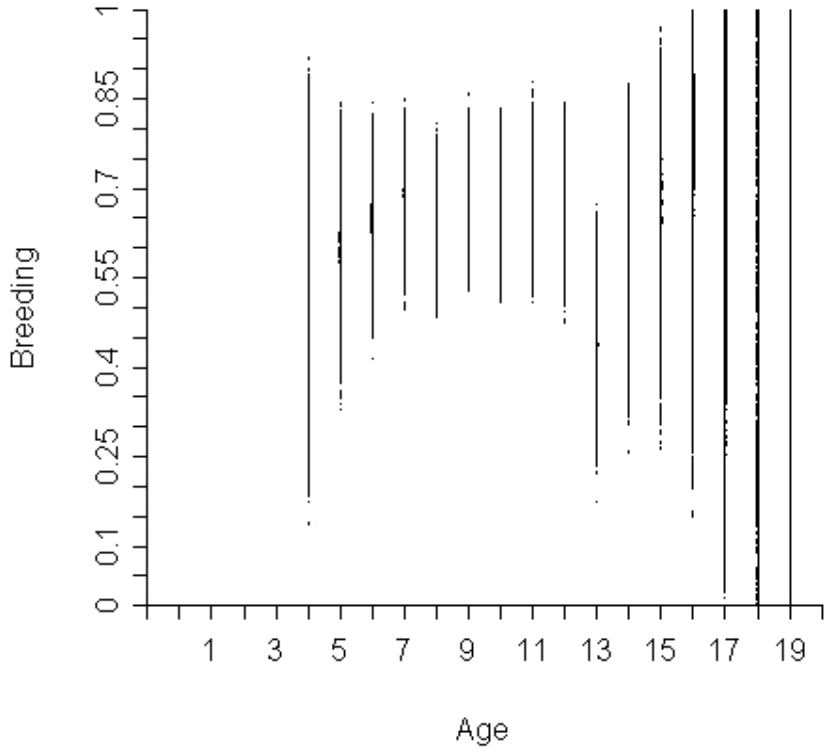


Figure 22: Posterior distributions for probability of survival from year *t* to *t*+1 by age for individuals that were non-breeders in year *t*, from full age-specific model, using the liberal definition of breeder.

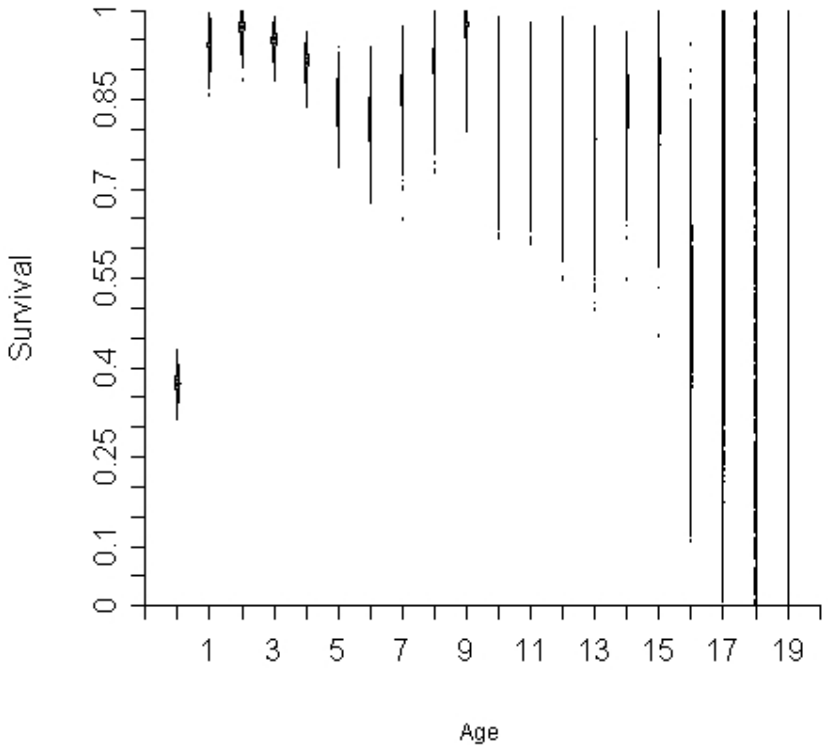


Figure 23: Posterior distributions for probability of survival from year *t* to *t*+1 by age for individuals that were breeders in year *t,* from full age-specific model, using the liberal definition of breeder.

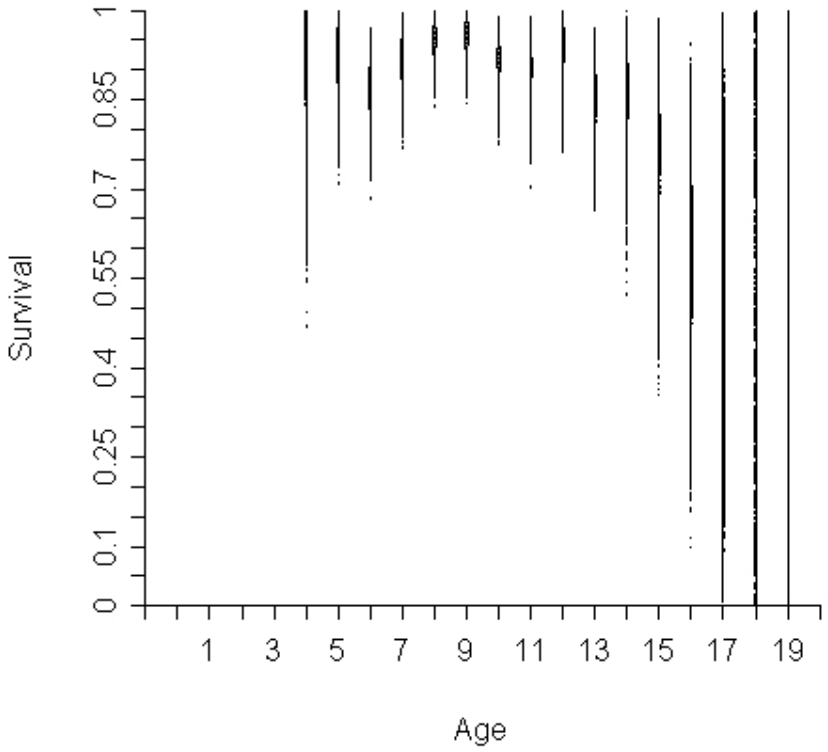


Figure 24: Posterior distributions for probability of breeding in year *t* by age group for individuals that were non-breeders in year *t*−1, from full age-specific model, using the liberal definition of breeder.

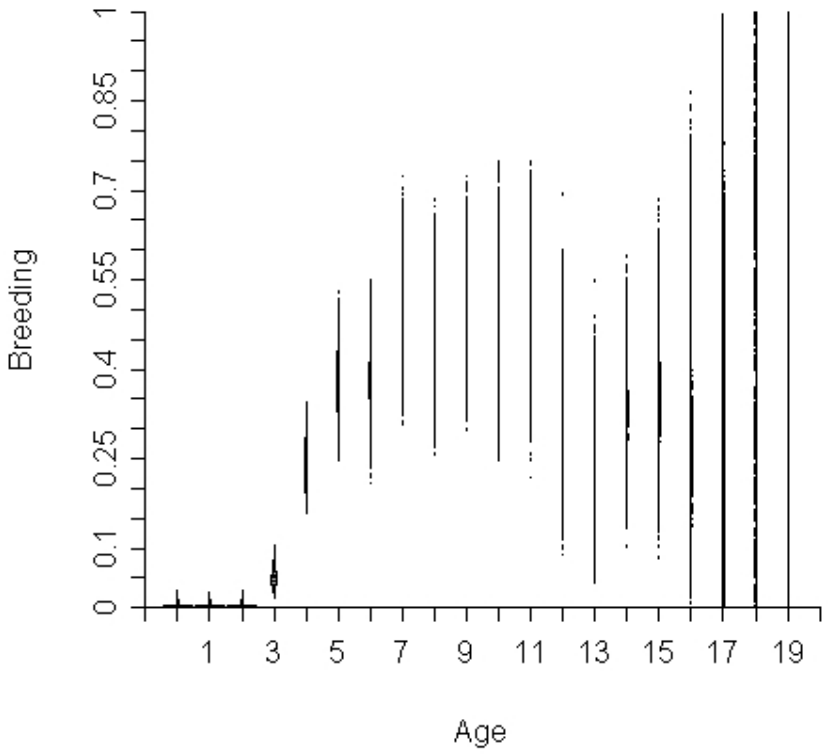
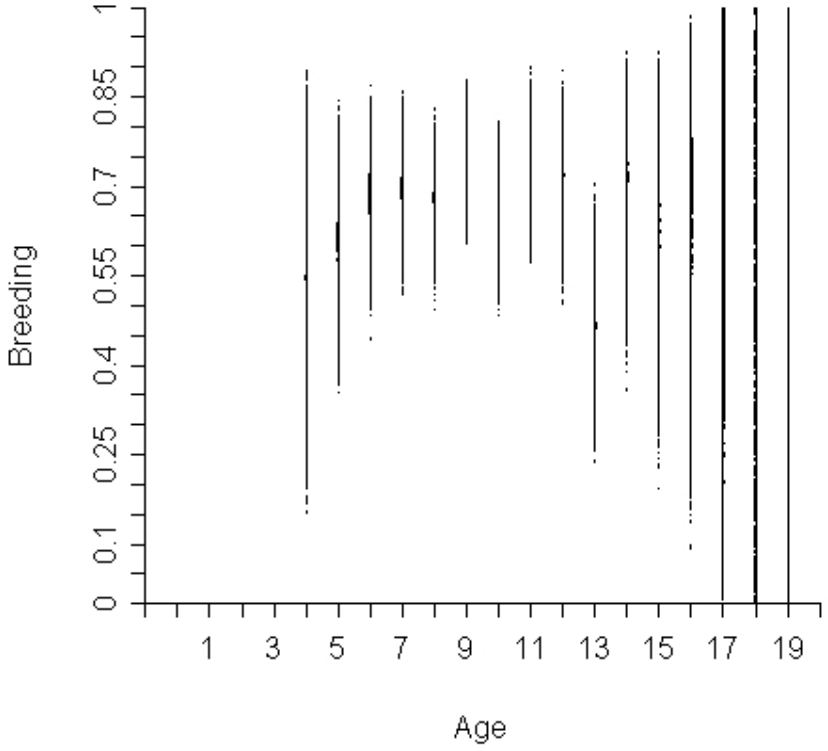


Figure 25: Posterior distributions for probability of breeding in year *t* by age group for individuals that were breeders in year *t*−1, from full age-specific model, using the liberal definition of breeder.



Tables

Table 1: Summary of the posterior distribution for the deviance values from each model and the associated deviance-based Bayesian p-value, using the strict definition of breeder.

	Age Classes in Model		
	Single	3	4
Mean	257719.3	258874.7	258864.0
2.5%ile	257352.9	258570.8	258561.2
97.5%ile	258088.2	259163.7	259160.9
min	256971.5	258268.0	258156.4
max	258529.4	259413.4	259463.4
p-value	0.9999	0.2151	0.2206

Table 2: Mean and central 95% credible interval from each model for the probability of survival from year *t* to *t*+1 by age group for individuals that were non-breeders in year *t*, using the strict definition of breeder.

	Age Classes in Model		
	Single	3	4
0-3	0.72 (0.70, 0.74)	0.72 (0.70, 0.74)	0.72 (0.70, 0.74)
4-7	0.72 (0.70, 0.74)	0.88 (0.85, 0.89)	0.88 (0.86, 0.90)
8-14	0.72 (0.70, 0.74)	0.88 (0.85, 0.89)	0.86 (0.83, 0.90)
15+	0.72 (0.70, 0.74)	0.72 (0.59, 0.84)	0.72 (0.59, 0.84)

Table 3: Mean and central 95% credible interval from each model for the probability of survival from year *t* to *t*+1 by age group for individuals that were breeders in year *t*, using the strict definition of breeder.

	Age Classes in Model		
	Single	3	4
0-3	-	-	-
4-7	0.90 (0.88, 0.92)	0.93 (0.90, 0.94)	0.90 (0.86, 0.94)
8-14	0.90 (0.88, 0.92)	0.93 (0.90, 0.94)	0.93 (0.91, 0.95)
15+	0.90 (0.88, 0.92)	0.68 (0.51, 0.83)	0.68 (0.51, 0.83)

Table 4: Mean and central 95% credible interval from each model for the probability of breeding in year *t* by age group for individuals that were non-breeders in year *t*−1, using the strict definition of breeder.

	Age Classes in Model		
	Single	3	4

0-3	0.43 (0.41, 0.46)	0.01 (0.01, 0.01)	0.01 (0.01, 0.01)
4-7	0.43 (0.41, 0.46)	0.32 (0.29, 0.35)	0.30 (0.27, 0.34)
8-14	0.43 (0.41, 0.46)	0.32 (0.29, 0.35)	0.35 (0.30, 0.39)
15+	0.43 (0.41, 0.46)	0.29 (0.16, 0.43)	0.29 (0.16, 0.43)

Table 5: Mean and central 95% credible interval from each model for the probability of breeding in year *t* by age group for individuals that were breeders in year *t*−1, using the strict definition of breeder.

	Age Classes in Model		
	Single	3	4
0-3	-	-	-
4-7	0.59 (0.57, 0.62)	0.65 (0.62, 0.69)	0.65 (0.59, 0.72)
8-14	0.59 (0.57, 0.62)	0.65 (0.62, 0.69)	0.66 (0.62, 0.69)
15+	0.59 (0.57, 0.62)	0.71 (0.52, 0.87)	0.71 (0.52, 0.87)

Table 6: Mean 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.

		Age Classes in Model		
Tags at *t*-1	Tags at *t*	Single	3	4
1	0	0.08 (0.06, 0.10)	0.09 (0.07, 0.11)	0.09 (0.07, 0.11)
	1	0.92 (0.90, 0.94)	0.91 (0.89, 0.93)	0.91 (0.89, 0.93)
2	0	0.07 (0.05, 0.08)	0.07 (0.06, 0.09)	0.07 (0.06, 0.09)
	1	0.16 (0.15, 0.18)	0.17 (0.15, 0.19)	0.17 (0.15, 0.19)
	2	0.77 (0.75, 0.79)	0.76 (0.73, 0.78)	0.76 (0.73, 0.78)

Table 7: Summary of the posterior distribution for the deviance values from each model and the associated deviance-based Bayesian p-value, using the liberal definition of breeder.

	Age Classes in Model		
	Single	3	4
Mean	260086.5	259192.2	259196.7
2.5%ile	259784.9	258895.1	258898.4
97.5%ile	260375.2	259485.1	259491.5
min	259444.5	258602.1	258563.4
max	260681.8	259771.8	259840.5
p-value	0.4274	0.2230	0.2322

Table 8: Mean and central 95% credible interval from each model for the probability of survival from year *t* to *t*+1 by age group for individuals that were non-breeders in year *t*, using the liberal definition of breeder.

	Age Classes in Model		
	Single	3	4
0-3	0.89 (0.87, 0.90)	0.72 (0.70, 0.74)	0.72 (0.70, 0.74)
4-7	0.89 (0.87, 0.90)	0.87 (0.85, 0.89)	0.88 (0.85, 0.90)
8-14	0.89 (0.87, 0.90)	0.87 (0.85, 0.89)	0.87 (0.83, 0.90)
15+	0.89 (0.87, 0.90)	0.72 (0.59, 0.84)	0.72 (0.59, 0.84)

Table 9: Mean and central 95% credible interval from each model for the probability of survival from year *t* to *t*+1 by age group for individuals that were breeders in year *t*, using the liberal definition of breeder.

	Age Classes in Model		
	Single	3	4
0-3	-	-	-
4-7	0.91 (0.89, 0.93)	0.92 (0.89, 0.94)	0.90 (0.86, 0.94)
8-14	0.91 (0.89, 0.93)	0.92 (0.89, 0.94)	0.92 (0.90, 0.94)
15+	0.91 (0.89, 0.93)	0.67 (0.52, 0.81)	0.67 (0.52, 0.82)

Table 10: Mean and central 95% credible interval from each model for the probability of breeding in year *t* by age group for individuals that were non-breeders in year *t*−1, using the liberal definition of breeder.

	Age Classes in Model		
	Single	3	4
0-3	0.26 (0.24, 0.28)	0.01 (0.01, 0.01)	0.01 (0.01, 0.01)
4-7	0.26 (0.24, 0.28)	0.36 (0.33, 0.39)	0.33 (0.29, 0.36)
8-14	0.26 (0.24, 0.28)	0.36 (0.33, 0.39)	0.41 (0.36, 0.46)
15+	0.26 (0.24, 0.28)	0.33 (0.19, 0.48)	0.33 (0.19, 0.48)

Table 11: Mean and central 95% credible interval from each model for the probability of breeding in year *t* by age group for individuals that were breeders in year *t*−1, using the liberal definition of breeder.

	Age Classes in Model		
	Single	3	4
0-3	-	-	-
4-7	0.69 (0.66, 0.72)	0.69 (0.66, 0.72)	0.68 (0.61, 0.73)
8-14	0.69 (0.66, 0.72)	0.69 (0.66, 0.72)	0.69 (0.65, 0.73)

15+		0.69 (0.66, 0.72)	0.65 (0.46, 0.81)	0.65 (0.46, 0.81)

Table 12: Mean and central 95% credible interval from each model for the probability of number of tags in year *t* given the number of tags in year *t*−1, using the liberal definition of breeder.

		Age Classes in Model		
Tags at *t*-1	Tags at *t*	Single	3	4
1	0	0.09 (0.08, 0.11)	0.09 (0.07, 0.11)	0.09 (0.07, 0.11)
	1	0.91 (0.89, 0.92)	0.91 (0.89, 0.93)	0.91 (0.89, 0.93)
2	0	0.05 (0.04, 0.07)	0.07 (0.06, 0.09)	0.07 (0.06, 0.09)
	1	0.18 (0.16, 0.20)	0.17 (0.15, 0.19)	0.17 (0.15, 0.19)
	2	0.77 (0.75, 0.79)	0.76 (0.73, 0.78)	0.75 (0.73, 0.78)