

Cam, E., Gimenez, O., Alpizar-Jara, R., Aubry, L. M., Authier, M., Cooch, E. G., Koons, D. N., Link, W. A., Monnat, J.-Y., Nichols, J. D., Rotella, J. J., Royle, J. A., and Pradel, R. 2013. Looking for a needle in a haystack: inference about individual fitness components in a heterogeneous population. – *Oikos* 122: 739–753.

Appendix A1

Methods. Estimation and model selection (Cam et al. 2013).

Bayesian estimation

Prior distributions. Fixed effects (i.e. slopes for age, age of first breeding ‘afr’, interactions between age and ‘afr’, previous breeding state) were assigned Normal prior distributions with mean 0 and precision 0.001, where “precision” refers to the inverse of the variance. Small precisions (e.g. 0.001 here) correspond to large variances. This means that investigators don’t want to favor specific values or a small interval: the range of possible values considered a priori is large (‘vague’ prior distribution). Year was treated as a random effect: the 22 levels of this variable represented in our dataset were assumed to come from a larger population of year effects. Instead of drawing inferences about the specific effect of each year (e.g. survival decreased in that year, increased in that other year), we were interested in the variance of the year effects (a summary of the temporal variability). We used a Normal random effect with mean 0 and precision τ . A common practice is to use a Gamma prior distribution for precision parameters of Normal distributions (because this distribution and the Normal distribution with known mean are conjugate). Gamma distributions are defined by two parameters: scale, and shape, and may range from 0 to infinity. The scale determines the practical range (the smaller the scale, the smaller the range, which means that a larger a priori probability is placed on small values of the precision of the individual random

effect). The shape determines the profile of the distribution (e.g., the kurtosis is inversely proportional to the shape). Here we used a $\Gamma(0.001, 0.001)$ for τ , a standard choice.

Individual random effects were considered either correlated or independent. For correlated random effects, a trivariate Normal distribution with mean 0 was assumed for the $d \times d$ ($d = 3$) variance-covariance matrix Σ

$$\Sigma = \begin{pmatrix} \sigma_{\phi}^2 & \rho_{\phi,\beta}\sigma_{\phi}\sigma_{\beta} & \rho_{\phi,\gamma}\sigma_{\phi}\sigma_{\gamma} \\ \rho_{\phi,\beta}\sigma_{\phi}\sigma_{\beta} & \sigma_{\beta}^2 & \rho_{\beta,\gamma}\sigma_{\beta}\sigma_{\gamma} \\ \rho_{\phi,\gamma}\sigma_{\phi}\sigma_{\gamma} & \rho_{\beta,\gamma}\sigma_{\beta}\sigma_{\gamma} & \sigma_{\gamma}^2 \end{pmatrix}$$

where σ_{ϕ}^2 , σ_{β}^2 , and σ_{γ}^2 are the variances of the individual random effects on survival, breeding and success probability, respectively. ρ stands for the correlation between two random effects

specified as subscripts. For multivariate Normal distributions, the classical prior distribution available in BUGS is the Wishart distribution placed on the inverse of the variance-covariance

matrix Σ (i.e. the precision matrix $\Sigma^{-1} = \Omega$). The Wishart distribution is a generalization of the

Gamma distribution; it is a conjugate prior distribution for multivariate Normal distributions with known means. It is defined by its number of degrees of freedom (ν) and scale matrix (Ω_0). The

expected value of the variance-covariance matrix for the individual random effects ($E[\Sigma]$) is

related to the number of degrees of freedom and the scale matrix of the Wishart distribution in

the following way: if $\Omega \sim \text{Wishart}_d(\nu, \Omega_0^{-1})$, then $E[\Sigma] = \frac{1}{\nu - d - 1} \Omega_0$, where d is the

number of individual random effects. Ω_0 can be interpreted as determining the 'location' of the

prior and ν as determining the spread of the distribution if ν is not too small (Rossi et al. 2005).

One of the difficulties with the Wishart prior is the choice of parameter values. We used $\nu = d +$

$1 = 4$ degrees of freedom, which implies a uniform distribution $U(-1,1)$ on the correlation

parameters (Gelman and Hill 2007). This reflects the lack of a priori knowledge concerning the

degree of association between individual random effects. In BUGS, we used the default values of 1 (Congdon 2006) for the diagonal elements of the scale matrix (the variance of individual random effects on the logit scale), and 0 for off-diagonal elements. For models with independent individual random effects, we used the same approach as for year effects: Normal random effects with mean 0 and precision τ , and a Gamma prior distribution $\Gamma(0.001, 0.001)$ for τ .

Convergence

As with other numerical estimation algorithms, inferences about parameter estimates should not be made before convergence is reached. To assess convergence in Markov chain Monte Carlo approaches, several chains can be used to check whether the magnitude of variability between chains isn't that different from the variability within chains. Here we ran three chains with different sets of initial values (e.g. mean of Normal random variables). To avoid the influence of initial values in our inferences, we discarded the first 5000 samples out of a total of 50000 samples. To reduce autocorrelation in the chains, we retained only 1 sample out of 3 (thin = 3). Models with independent random effects were more difficult to estimate (the autocorrelation in the chains was sometimes large). The first 10 000 samples were discarded, and 1 sample out of 6 was retained for inferences. Convergence was checked using the Brooks-Gelman-Rubin diagnostic \hat{R} for each model (Gelman and Rubin 1992). Values close to 1 indicate convergence. We used the R package CODA (Plummer et al. 2006) to analyze results reported in the Supplementary Material Appendix A6

Sensitivity analyses

Sensitivity analyses were performed using the lowest-DIC models. For models with correlated random effects, we focused on the prior distribution of the inverse of the variance-covariance matrix for individual random effects Σ . Following Hoff (2010), we used informative priors for

larger levels of variability of the logit-scale vital rates. Recall that if $\mathbf{\Omega} \sim \text{Wishart}_d(\nu, \mathbf{\Omega}_0^{-1})$,

then $E[\mathbf{\Sigma}] = \frac{1}{\nu - d - 1} \mathbf{\Omega}_0$. We set the number of degrees of freedom of the Wishart distribution

equal to 5 so that $E[\mathbf{\Sigma}] = \mathbf{\Omega}_0$, which makes it straightforward to choose values for $\mathbf{\Omega}_0$

corresponding to expected values of the variance–covariance matrix for random effects. Larger

numbers of degrees of freedom allow variances to be estimated more freely but constrain

correlations among individual random effects (Gelman and Hill 2007). We used prior values for

σ^2 (the variance of individual random effects on the logit scale) of 0.05, 0.5 and 5 (convergence

was questionable with the smallest value). These values were used to construct the diagonal scale

matrix $\mathbf{\Omega}_0$ specified in BUGS. For uncorrelated random effects, sensitivity to prior Gamma

distributions was assessed using 1 for the shape and scale parameters, or 10 for both parameters

(i.e. increased prior precision for the Normal individual random effects).

Model selection via inclusion variables

According to several authors, there are difficulties with inferences about random effects using

information criteria in the framework of generalized linear models in both the Frequentist and

the Bayesian paradigms (Spiegelhalter et al. 2002, Harry 2008, Plummer 2008, O'Hara and

Sillanpää 2009). Consequently, we also used inclusion variables (O'Hara and Sillanpää 2009) at

different steps of the model selection process to assess whether random effects were needed to

describe the process that gave rise to our data. An inclusion variable can be thought of as a

'switch' (indicator variable) taking two values (0 and 1) with a specified probability (e.g. 0.5); see

Royle (2008) for an example and BUGS codes. Here the indicator variable is associated with an

individual random effect. When the variable is equal to 1, the random effect is included in the

model and its variance estimated. If the model is estimated using a Bayesian approach, the

posterior probability of the inclusion variable is also estimated. If we set the prior probability of

inclusion of a random effect to 0.5, this means that investigators do not have any a priori idea about the relevance of the random effect for their data, and that they consider the hypotheses corresponding to the model with the random effect and the one without it as equally likely for the dataset. If the posterior probability of the indicator variable including the individual random effect is larger (say, 0.8), this means that the data have brought information useful to update knowledge about the relevance of the model with the random effect: there is evidence that the model including it is more consistent with the data than the model without it.

Our objective was to assign an inclusion variable to each individual random effect. We used two sets of prior probabilities of including individual random effects: 0.5, and 0.8. If the inclusion of a random effect is treated as a Bernoulli trial with probability 0.5, the prior probability of the three inclusion variables being simultaneously equal to 1.0 is 0.125. Prior probabilities of 0.8 for each inclusion variable resulted in prior probabilities of including all the random effects simultaneously in the model close to 0.5 (precisely, 0.512). When the individual random effects are independent and have independent prior Normal distributions, building a simplified version of a random effect model is straightforward (Royle 2008): an inclusion variable is used to include or remove variance terms from the model.

However, when individual random effects are not independent and are assumed to have a multivariate Normal distribution, investigators have to handle covariances among random effects: a covariance must be included in the model whenever two inclusion variables for two individual random effects take values of 1. This isn't possible if a Wishart prior is specified in BUGS for the precision matrix of a multivariate Normal distribution: the size of the scale matrix of the Wishart distribution and its number of degrees of freedom would change at each iteration according to the outcome of 3 Bernoulli trials. Consequently, we used the Cholesky decomposition of the variance-covariance matrix of correlated random effects introduced by Chen and Dunson (2003; see Authier et al. 2012 for BUGS codes). Chen and Dunson (2003) re-parameterized the variance-covariance matrix of a multivariate Normal distribution for random effects in a linear

mixed model so that the use of the Wishart distribution can be avoided. They suggested factorizing the variance-covariance matrix Σ as follows: $\Sigma = \Lambda \Gamma \Gamma' \Lambda$. Instead of considering directly a multivariate Normal distribution for individual random effects, the linear model is expressed as functions of independent standard Normal distributions (Chen and Dunson 2003).

In the framework of a linear mixed model, for n subjects contributing n_i observations, let y_i be the response variable of subject i at occasion j , \mathbf{x}_j a $p \times 1$ vector of predictors, and \mathbf{z}_j a $q \times 1$ vector of predictors (random effects). The linear mixed model for observations y_i from subject i is

$$\mathbf{y}_i = \mathbf{X}_i \boldsymbol{\alpha} + \mathbf{Z}_i \boldsymbol{\beta}_i + \boldsymbol{\varepsilon}_i$$

where $\mathbf{y}_i = (y_{i1}, \dots, y_{in_i})^T$, $\mathbf{X}_i = (\mathbf{X}_{i1}^T, \dots, \mathbf{X}_{in_i}^T)^T$, $\mathbf{Z}_i = (\mathbf{Z}_{i1}^T, \dots, \mathbf{Z}_{in_i}^T)^T$, $\boldsymbol{\alpha}$ is a $p \times 1$ vector of population parameters, $\boldsymbol{\beta}_i$ is a $q \times 1$ vector of individual random effects, with $\boldsymbol{\beta}_i \sim N(0, \Sigma)$, and the residuals $\boldsymbol{\varepsilon}_i$ are $N(0, \sigma^2 \mathbf{I})$. Let \mathbf{L} be the lower Cholesky decomposition of Σ . Given \mathbf{L} , the linear mixed model is expressed as follows

$$\mathbf{y}_i = \mathbf{X}_i \boldsymbol{\alpha} + \mathbf{Z}_i \mathbf{L} \mathbf{b}_i + \boldsymbol{\varepsilon}_i$$

where $\mathbf{b}_i = (b_{i1}, \dots, b_{iq})^T$ is a vector of independent standard Normal latent variables. Then we let $\mathbf{L} = \mathbf{\Lambda} \mathbf{\Gamma}$, where $\mathbf{\Lambda} = \text{diag}(\sigma_1, \dots, \sigma_q)$ with $\sigma_k \geq 0$ for $k = 1, \dots, q$, and $\mathbf{\Gamma}$ is a $q \times q$ triangular lower matrix (here, $q = 3$),

$$\begin{pmatrix} 1 & & \\ \gamma_{21} & 1 & \\ \gamma_{31} & \gamma_{32} & 1 \end{pmatrix}$$

The linear mixed model can then be expressed as follows:

$$\mathbf{y}_i = \mathbf{X}_i \boldsymbol{\alpha} + \mathbf{Z}_i \mathbf{\Lambda} \mathbf{\Gamma} \mathbf{b}_i + \boldsymbol{\varepsilon}_i$$

That is, a model with several individual random effects following a multivariable Normal distribution can be estimated by estimating the elements of the matrices $\mathbf{\Lambda}$ and $\mathbf{\Gamma}$ and

constructing Σ . When relevant (i.e. depending on whether a given individual random effect is relevant to individual i , as specified in \mathbf{Z}_i), each individual deviate (say a_{i1}, a_{i2}, a_{i3}) corresponding to random effects is estimated by multiplying a random value drawn from a standard Normal distribution (b_i) by Λ . For example, for $q = 3$ random effects, if all of them are relevant for individual i , the individual value corresponding to the first random effect a_{i1} will be equal to $\lambda_1 b_{i1}$, with b_{i1} drawn from a standard Normal distribution. The value corresponding to the second individual random effect a_{i2} will be equal to $\lambda_2(\gamma_{21}b_{i1} + b_{i2})$, with b_{i2} drawn from a standard Normal distribution. For the value corresponding to the third individual random effect: $a_{i3} = \lambda_3(\gamma_{31}b_{i1} + \gamma_{32}b_{i2} + b_{i3})$. This allows investigators to use several inclusion variables simultaneously. For example, the first indicator variable determined whether the first individual random effect was included in the model. If not, the same indicator variable excluded $\gamma_{21}b_{i1}$ from the formula used to estimate the value corresponding to the second random effect, as well as $\gamma_{31}b_{i1}$ from the formula used to estimate the individual value corresponding to the third random effect. That is, we didn't address covariances separately from variances. As in Authier et al. (2012) we used Half- Normal prior distribution for the elements of Λ with mean 0 and variance equal to 0.25, and Normal distributions with mean 0 and variances 2.25 for the elements of Σ . Such priors place a large probability mass on zero for variances. Most of the mass is between 0 and 5, and values exceeding 5 are still possible by far less likely: such a range is reasonable for variances on the logit scale. BUGS codes can be found in Authier et al. (2012), as well as illustrations of the characteristics of the priors placed on the Cholesky decomposition of the variance-covariance matrix Σ . Here we used a similar approach for a generalized linear mixed model with a logit link function (Cai and Dunson 2006).

The use of inclusion variables raised difficulties in some cases: the estimates of mean posterior probabilities of inclusion variables were equal to 1.00 and mixing in the Markov chains

stopped before discarding the first 5000 samples to avoid the influence of initial values. In these cases we also used prior probabilities of 0.2, which leads to a prior probability of simultaneous inclusion of all the individual random effects of 0.008. In the approach developed by Chen and Dunson (2003), when the variances of two random effects are included in a model, the correlation between them is also automatically included. In other words, the above-mentioned prior probabilities of inclusion of individual random effects corresponded to set of several parameters simultaneously (variances and correlations). In addition, theoretically, it should be possible to assess covariances between individual random effects using the approach developed by Chen and Dunson (2003), Cai and Dunson (2006), or Kinney and Dunson (2007). Indeed, in problems relying on complex variance-covariance matrices, some individual random effects may be correlated and others not. Investigators may even have specific a priori biological hypotheses about components of variance. As emphasized by O'Hara and Sillanpää (2009) some approaches require substantial tuning. In our case, this involved a substantial increase in computing time using OpenBUGS. Models were first run using the Cholesky decomposition of the variance-covariance matrix of individual random effects to obtain starting values (the decomposition itself slowed the process down with our dataset), and then re-run using inclusion variables. Future work with this data set may address more detailed hypotheses about the structure of the variance-covariance matrix of random effects. For a given Markov chain, we used identical initial values for the inclusion variables ; 0, 0, 0 for chains 1 and 2, and 1, 1, 1 for chain 3.

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Appendix A2

Inclusion variables (Chen and Dunson 2003).

Model		Prior probability of inclusion of Σ	Prior probability for each inclusion variable	Mean	Median	Quantiles 0.025 0.975	
Complete data set							
1	φ	0.50	0.80	0.79	1.0	0.0	1.0
	β			0.99	1.0	1.0	1.0
	γ			0.98	1.0	1.0	1.0
	φ	0.125	0.50	0.43	1.0	0.0	1.0
	β			0.98	1.0	1.0	1.0
	γ			0.93	1.0	0.0	1.0
9	φ	0.50	0.80	1	1.0	1.0	1.0
	β			1	1.0	1.0	1.0
	γ			1	1.0	1.0	1.0
	φ	0.125	0.50	1	1.0	0.0	1.0
	β			1	1.0	1.0	1.0
	γ			0.99	1.0	1.0	1.0
Males							
1	φ	0.50	0.80	0.81	1.0	0.0	1.0
	β			0.99	1.0	1.0	1.0
	γ			0.76	1.0	0.0	1.0
	φ			0.57	1.0	0.0	1.0

	β	0.125 \forall	0.50	0.96	1.0	0.0	1.0
	γ			0.46	1.0	0.0	1.0
Females							
1	φ	0.5	0.80	0.84	1.0	0.0	1.0
	β			0.99	1.0	1.0	1.0
	γ			0.97	1.0	0.0	1.0
	φ	0.125	0.50	0.52	1.0	0.0	1.0
	β			0.96	1.0	0.0	1.0
	γ			0.41	1.0	0.0	1.0

φ = survival probability. β = breeding probability. γ = probability of raising at least one chick to independence given that the individual attempted to breed. \forall Convergence was questionable.

Chen, Z. and Dunson, D. B. 2003. Random effects selection in linear mixed models. –
Biometrics 59: 762–769.

Appendix A3

Sensitivity analyses (complete data set).

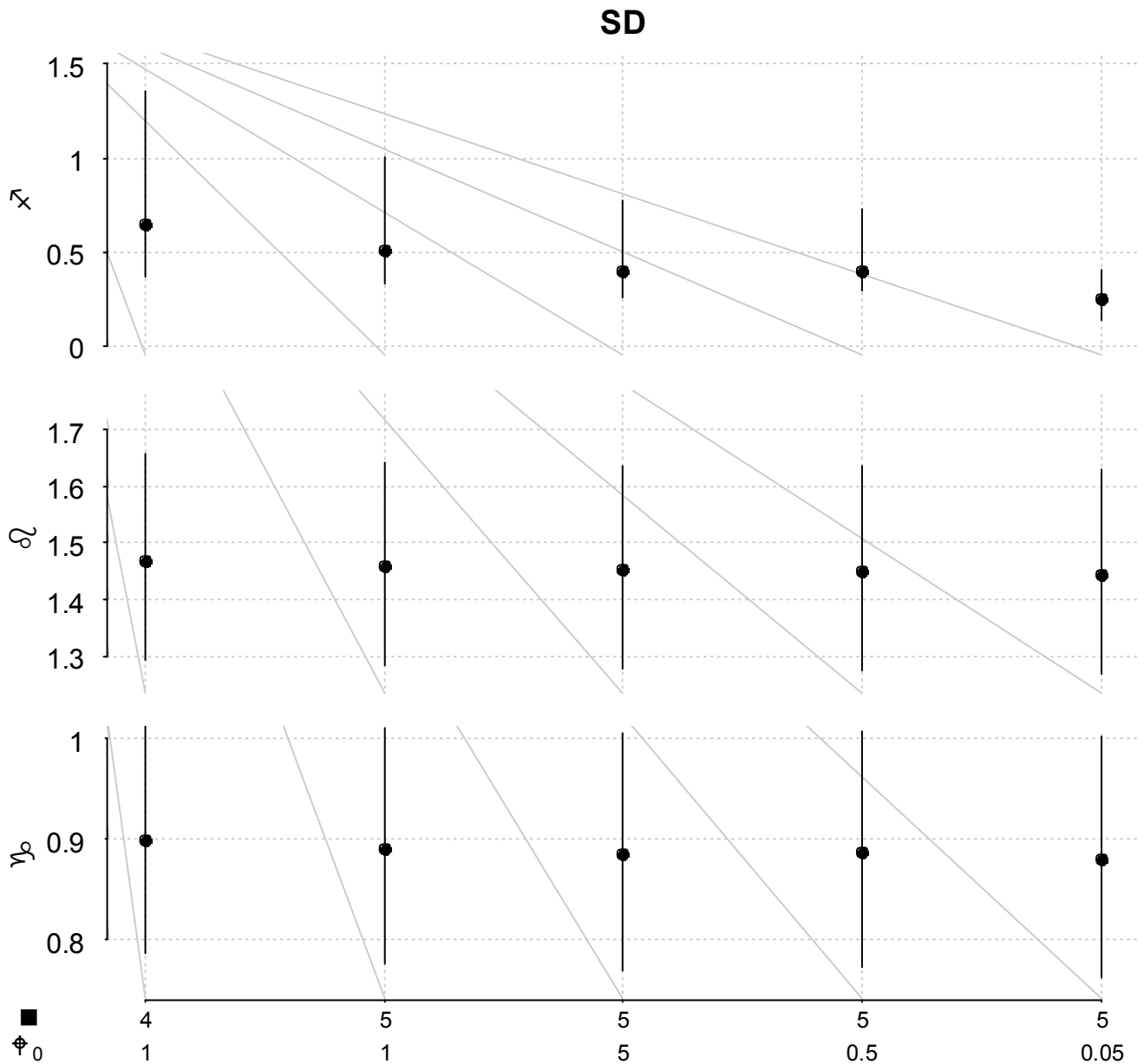


Figure A1a. Posterior distributions of individual random effects according to the number of degrees of freedom (ν) and scale matrix (Ω_0) of the Wishart distribution. Dot: median. Extremes: 2.25% and 97.5% quantiles. SD = standard deviation. φ : survival probability. β : breeding

probability. γ : success probability. For small a priori variances in the scale matrix ($\mathbf{\Omega}_0 = \text{diag}(0.05, 0.05, 0.05)$) convergence was questionable.

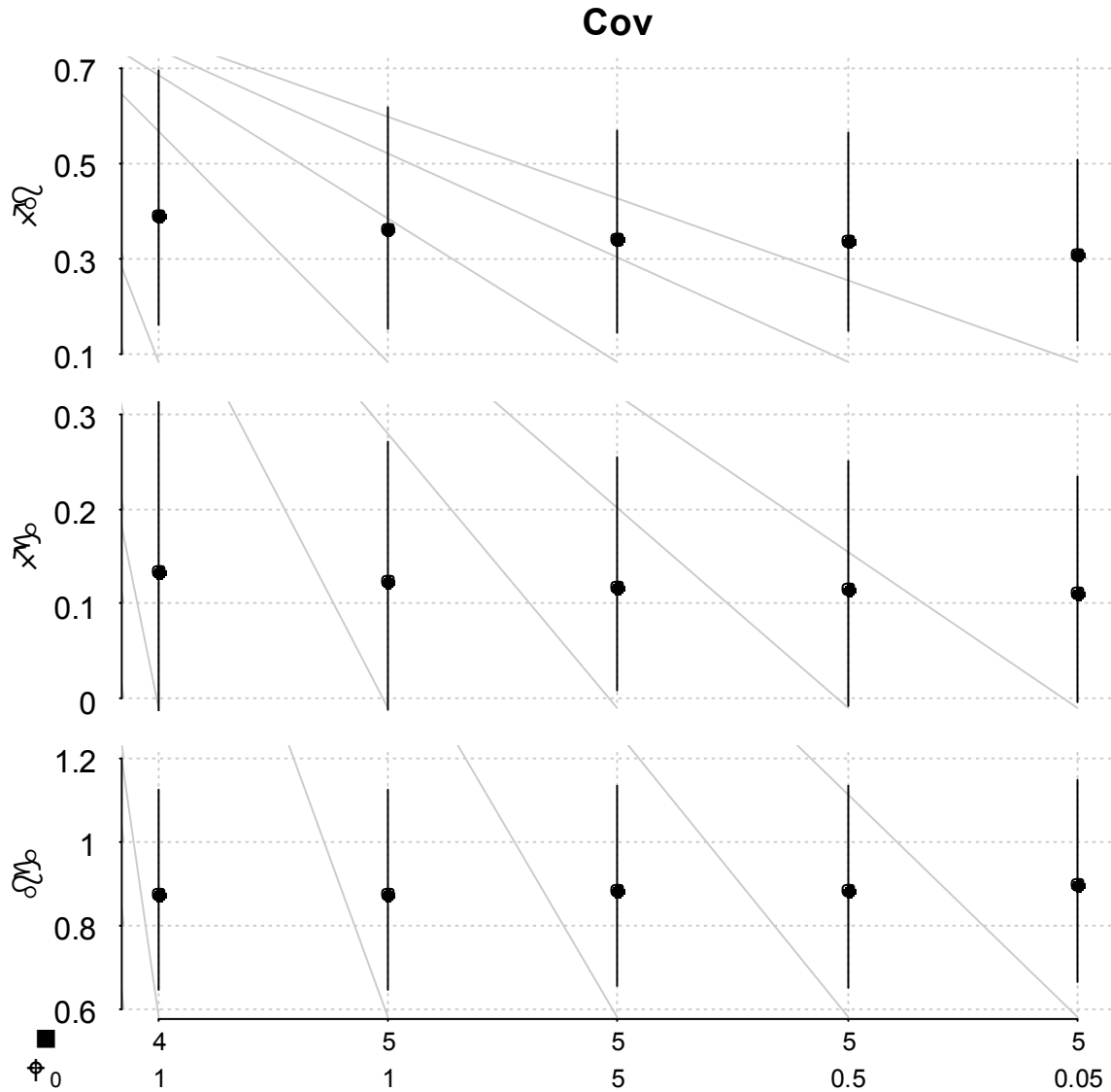


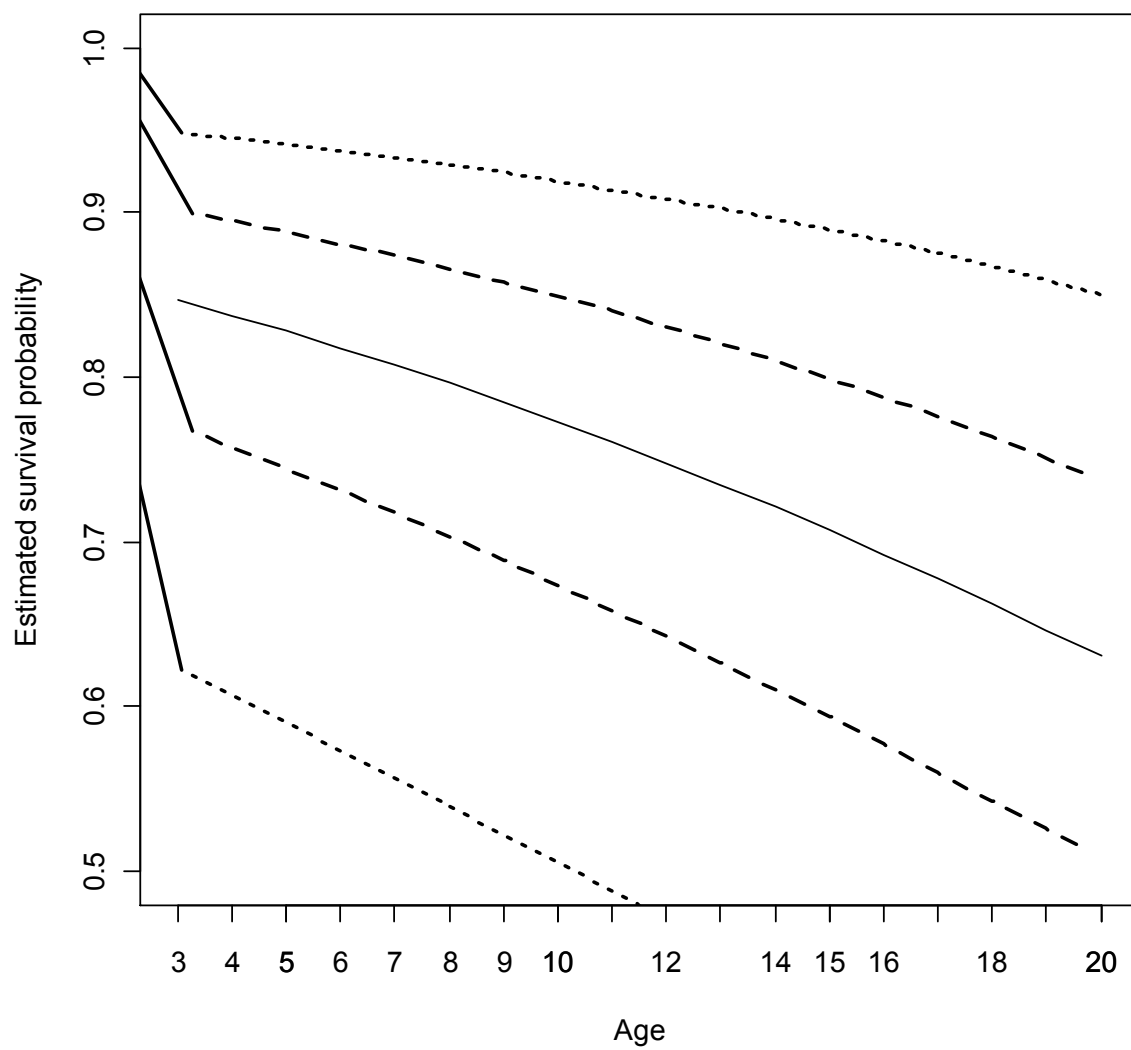
Figure A1b. Posterior distributions of individual random effects according to the number of degrees of freedom (ν) and scale matrix ($\mathbf{\Omega}_0$) of the Wishart distribution. Dot: median. Extremes: 2.25% and 97.5% quantiles. Cov = covariance. φ : survival probability. β : breeding probability. γ : success probability. For small a priori variances in the scale matrix ($\mathbf{\Omega}_0 = \text{diag}(0.05, 0.05, 0.05)$) convergence was questionable.

When increasing the number of degrees of freedom (i.e. constraining correlations but estimating variances more freely), the posterior standard deviation of the individual random effect for survival decreased. The difference in the median was not so marked. The variance of this individual random effect was influenced by the scale matrix of the Wishart distribution. Concerning the individual random effects on breeding and success probability, results were not sensitive to the number of degrees of freedom or the scale matrix of the Wishart distribution.

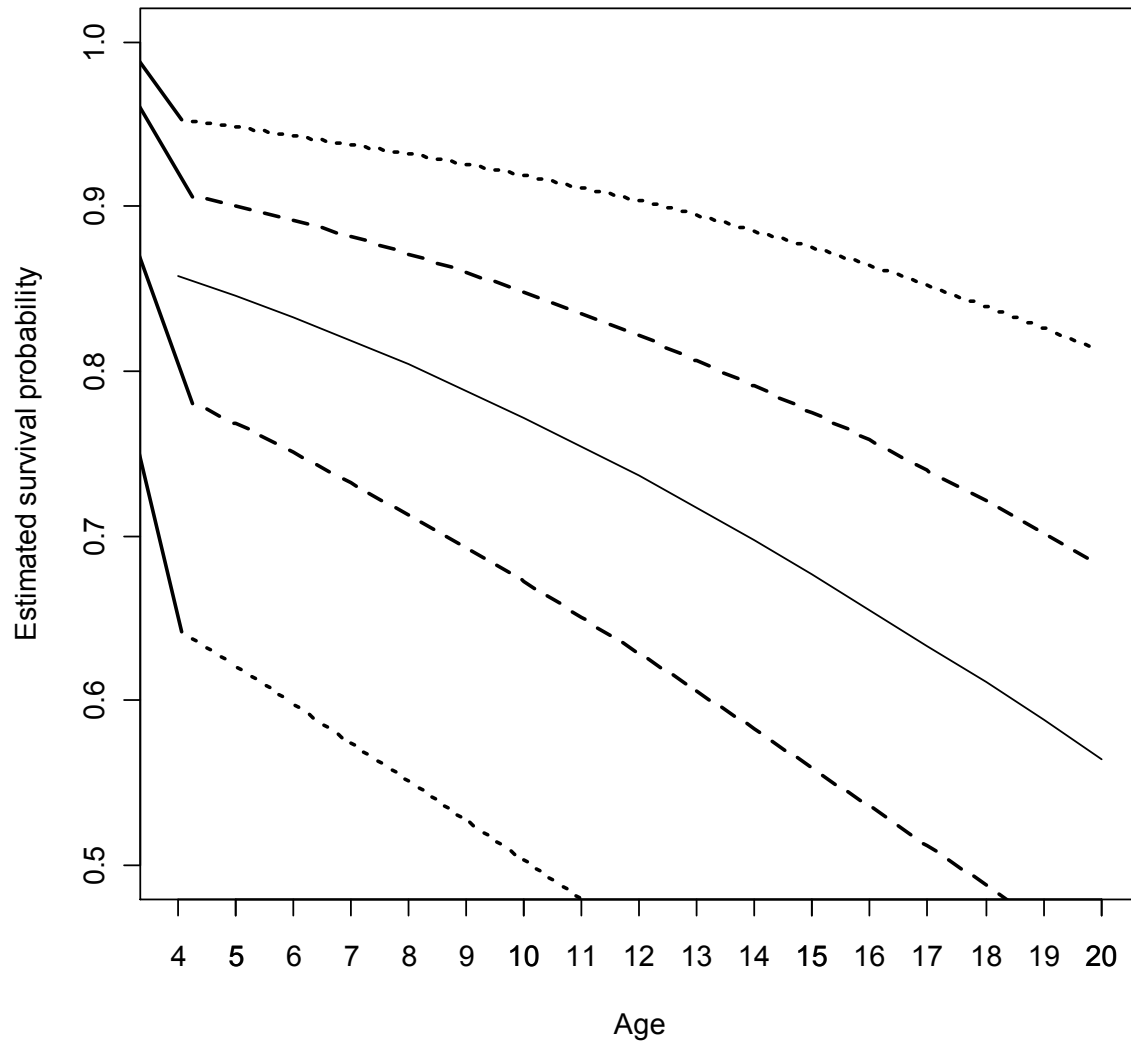
Appendix A4a

Relationship between age and survival probability (complete data set): mean individual. Dashed lines: quartiles. Dotted lines: quantiles (0.05 and 0.95).

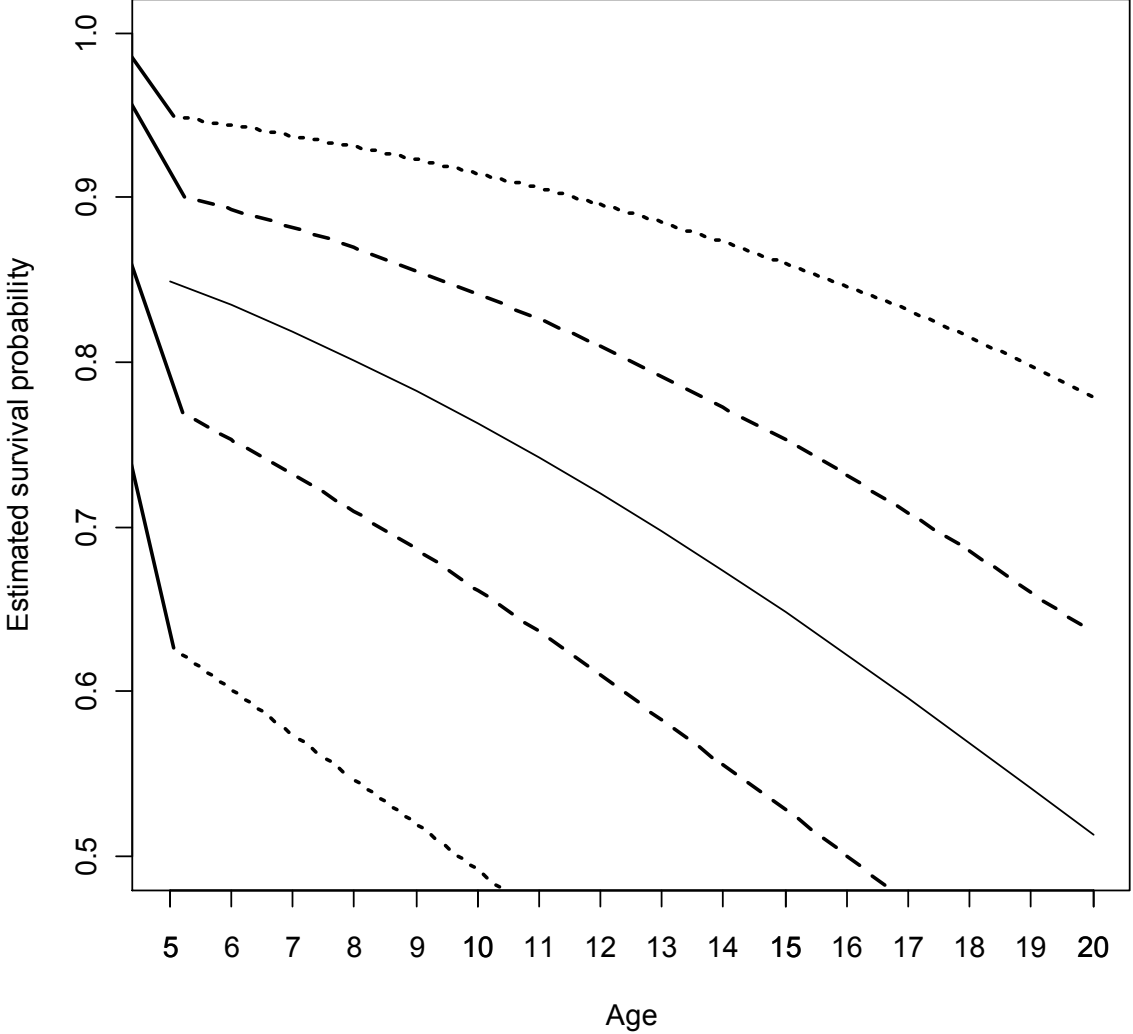
Age of first breeding ≤ 3 years old



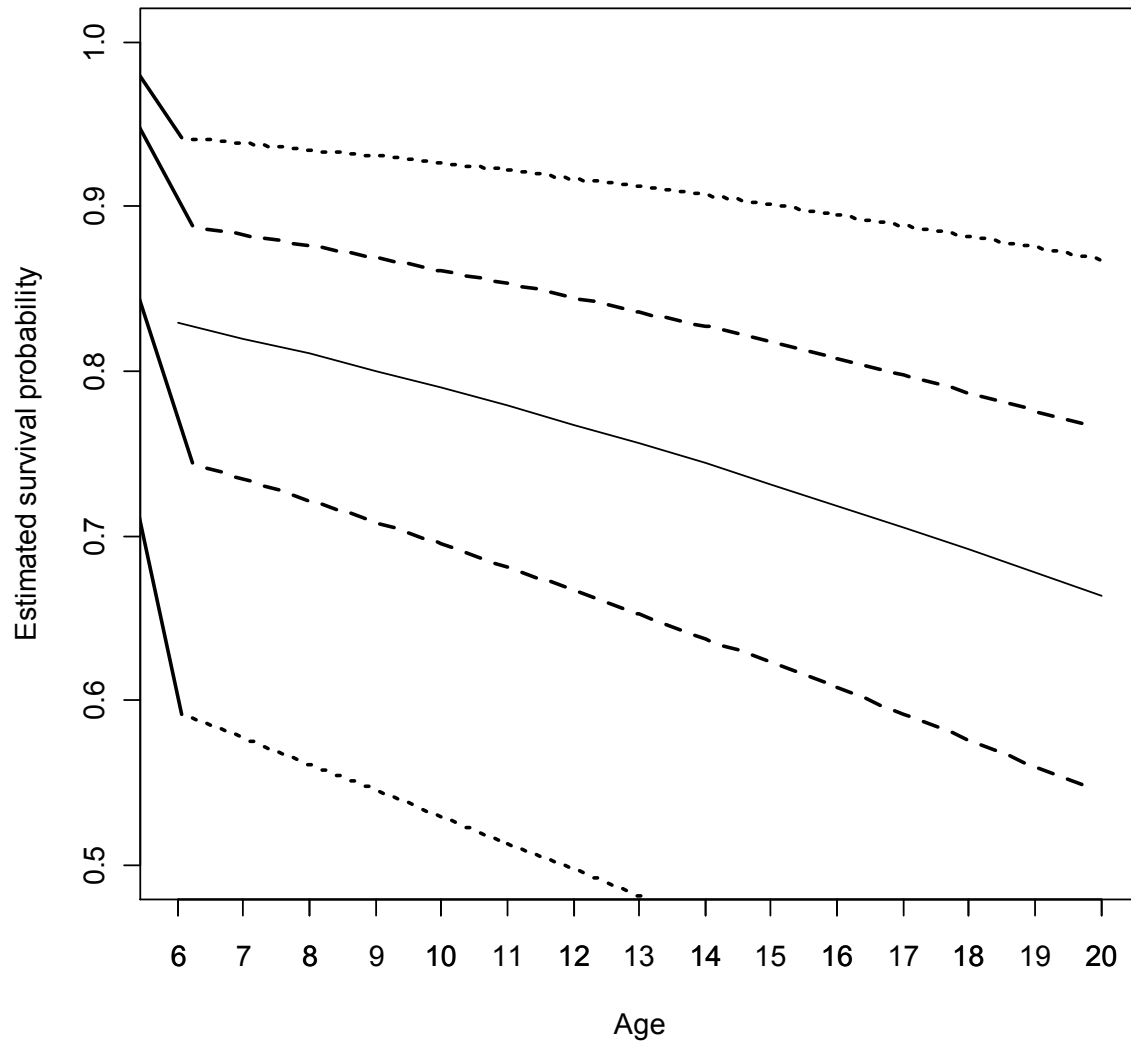
Age of first breeding = 4 years old



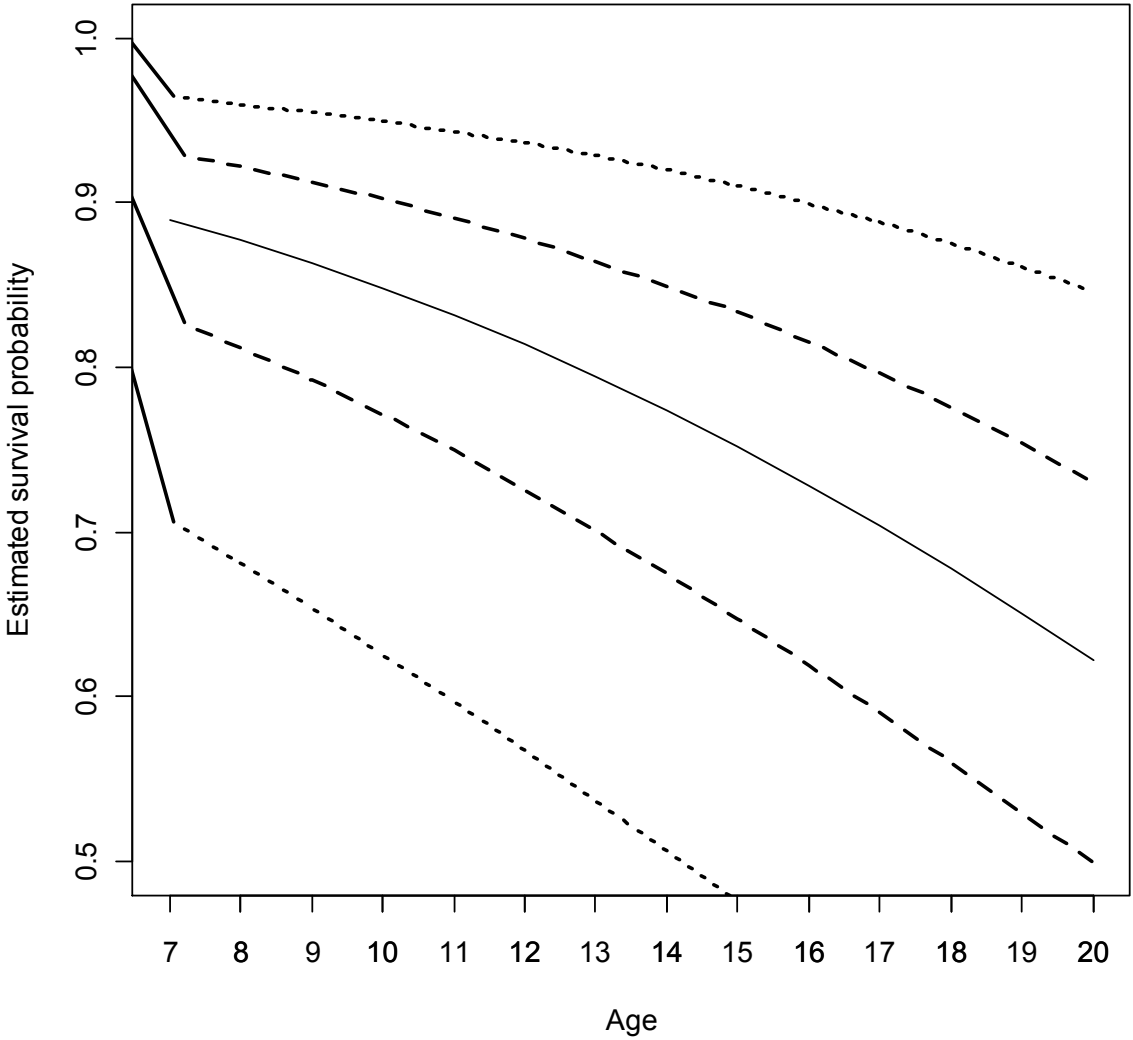
Age of first breeding = 5 years old



Age of first breeding = 6 years old



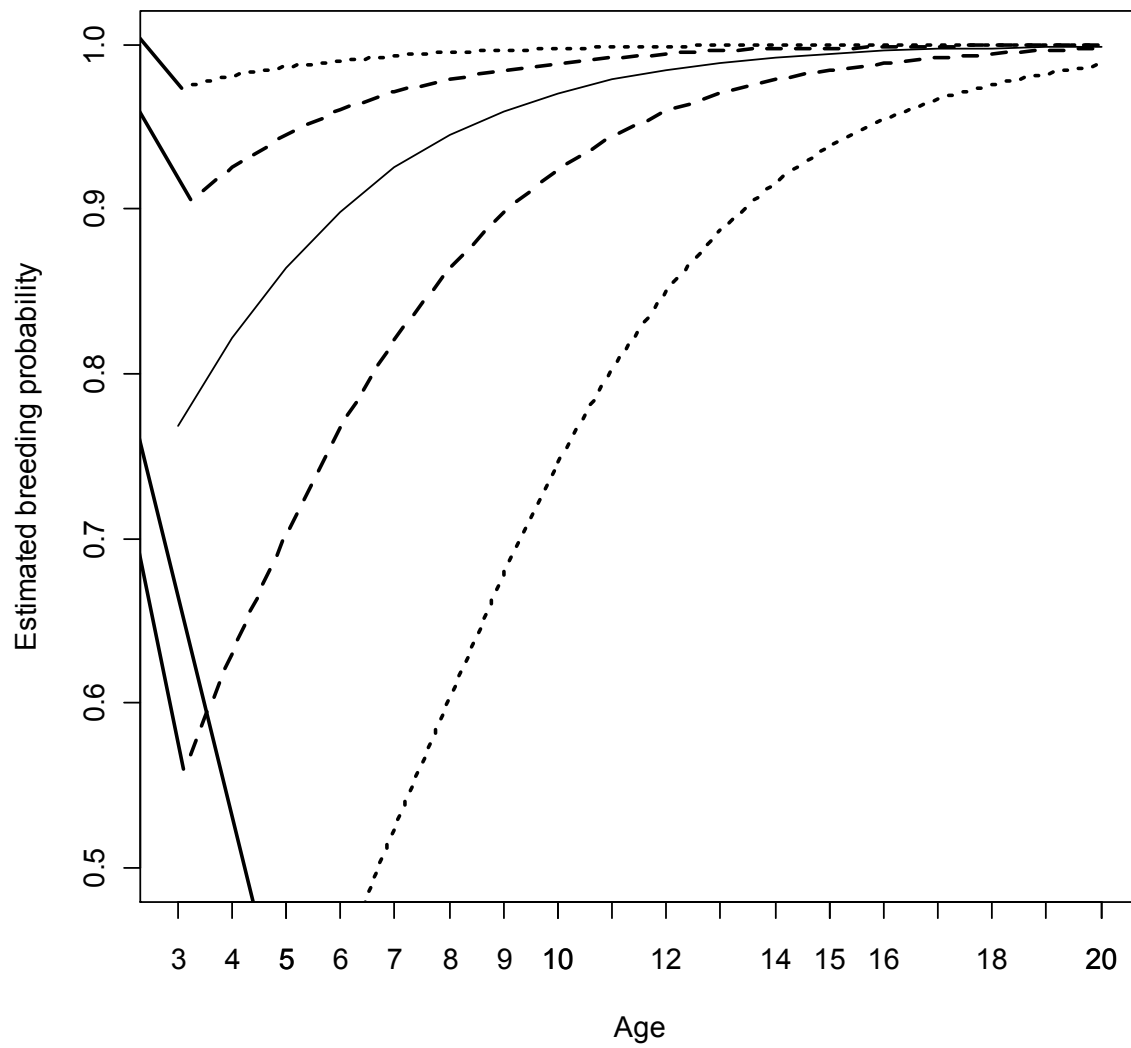
Age of first breeding ≥ 7 years old



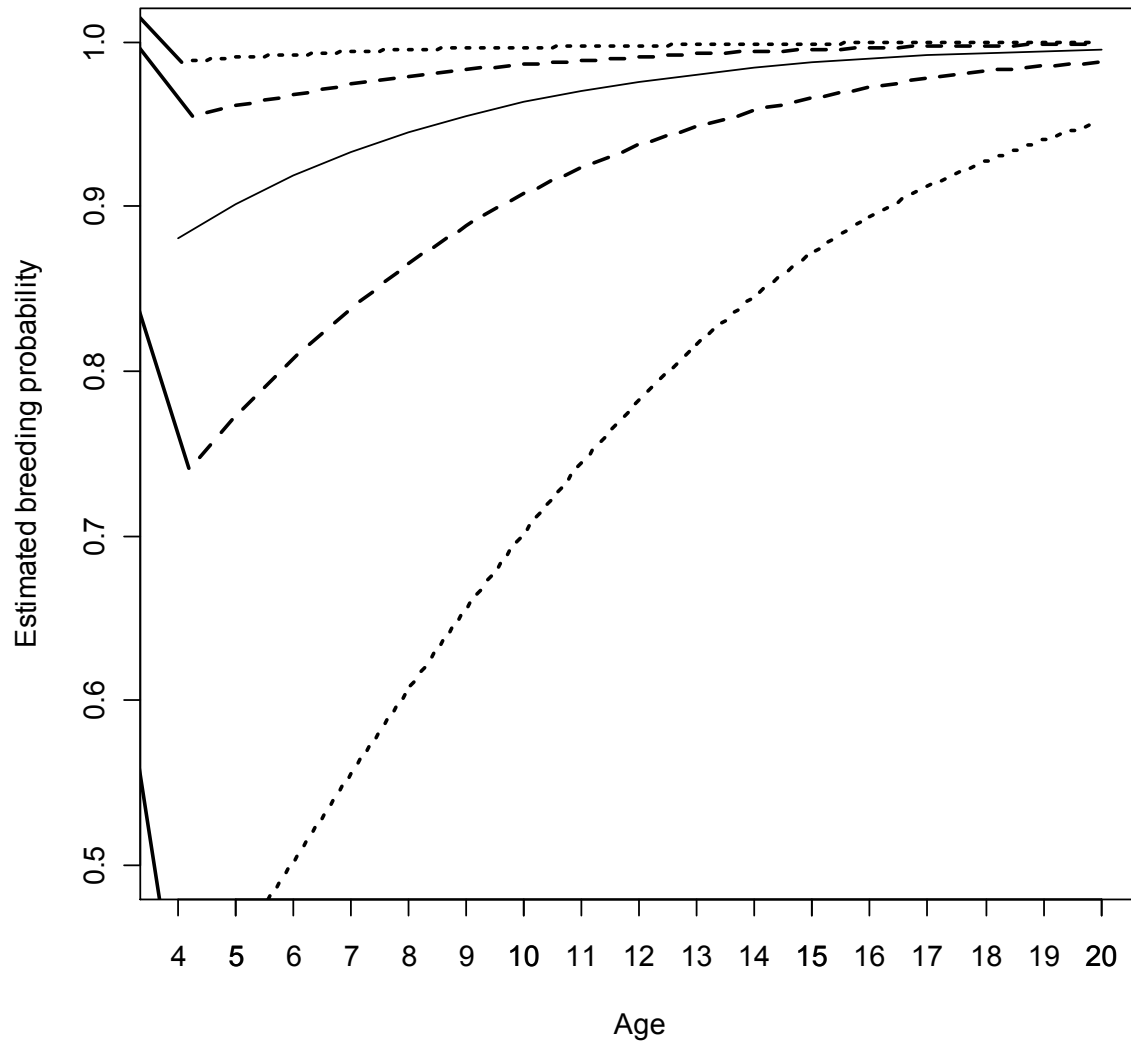
Appendix A4b

Relationship between age and breeding probability (complete dataset): mean individual. Dashed lines: quartiles. Dotted lines: quantiles (0.05 and 0.95).

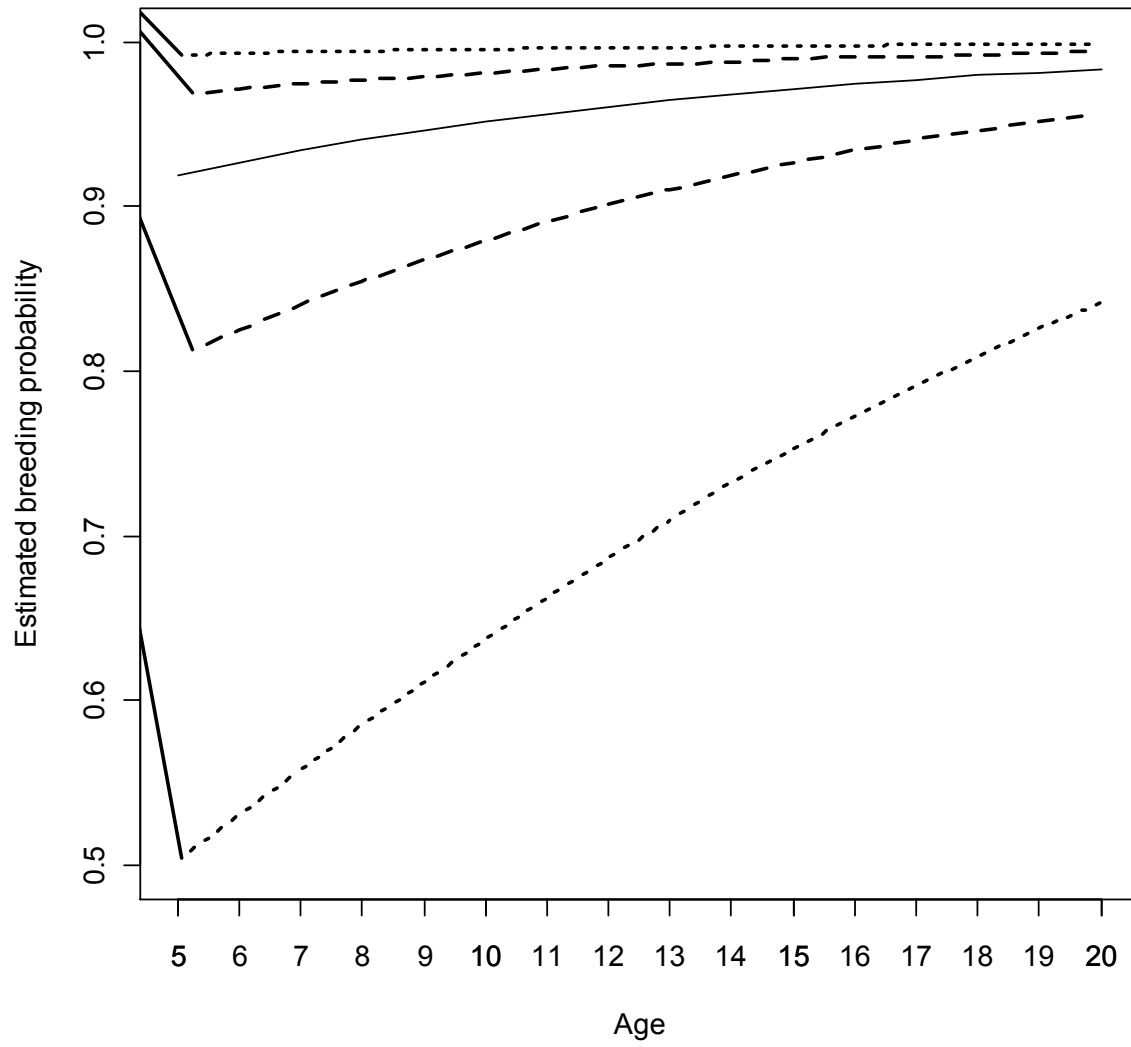
Age of first breeding ≤ 3 years old



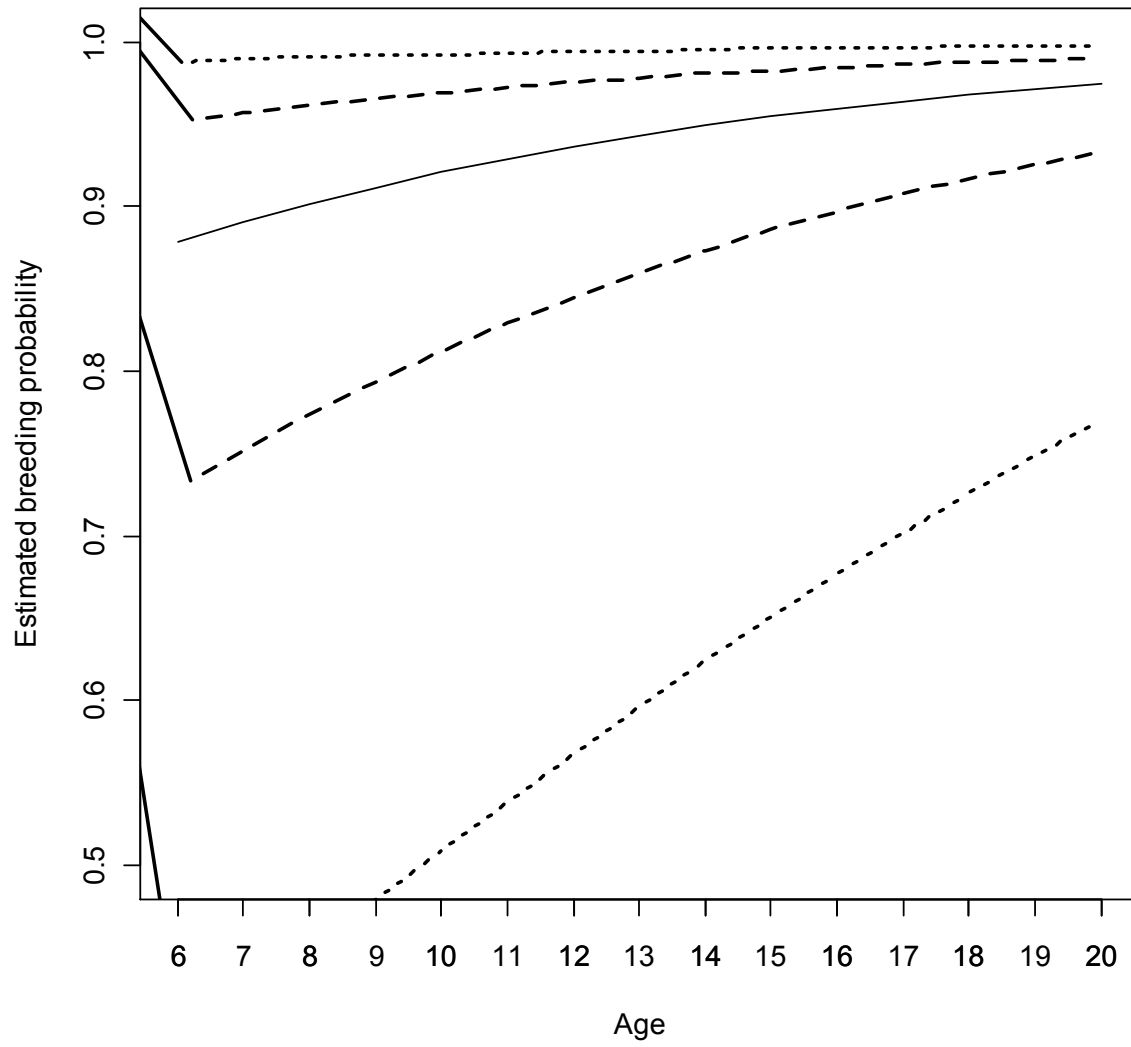
Age of first breeding = 4 years old



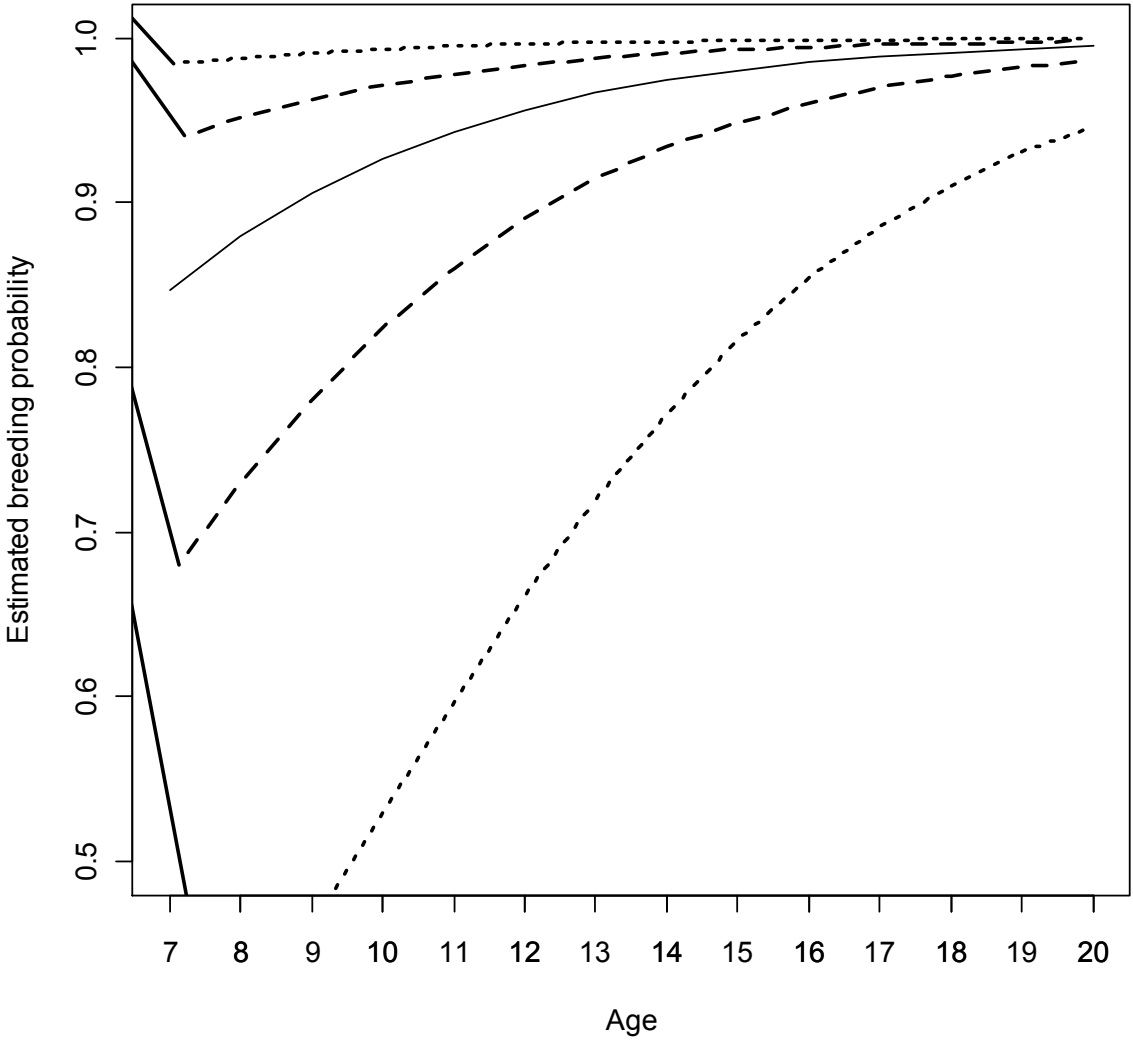
Age of first breeding = 5 years old



Age of first breeding = 6 years old



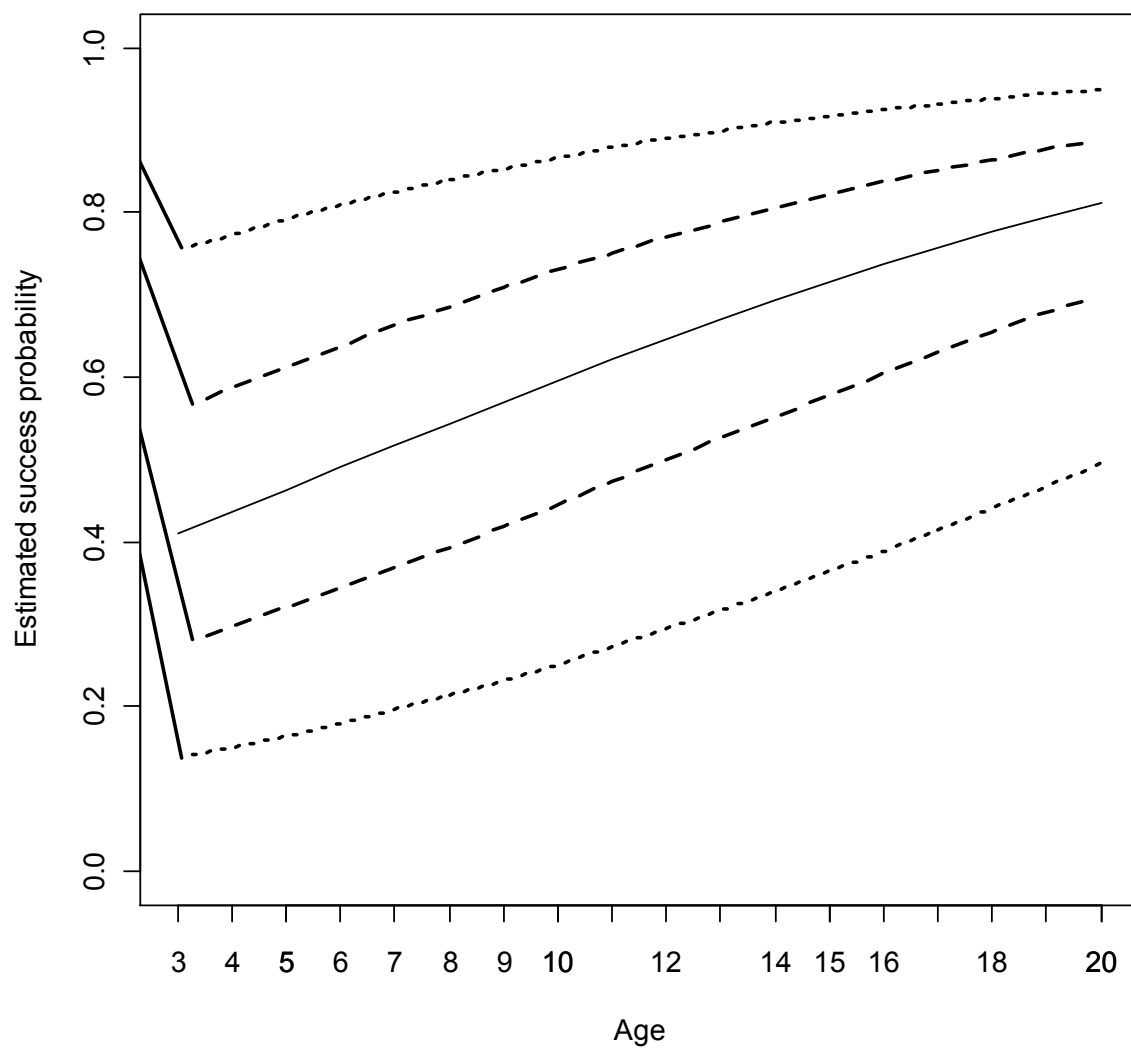
Age of first breeding ≥ 7 years old



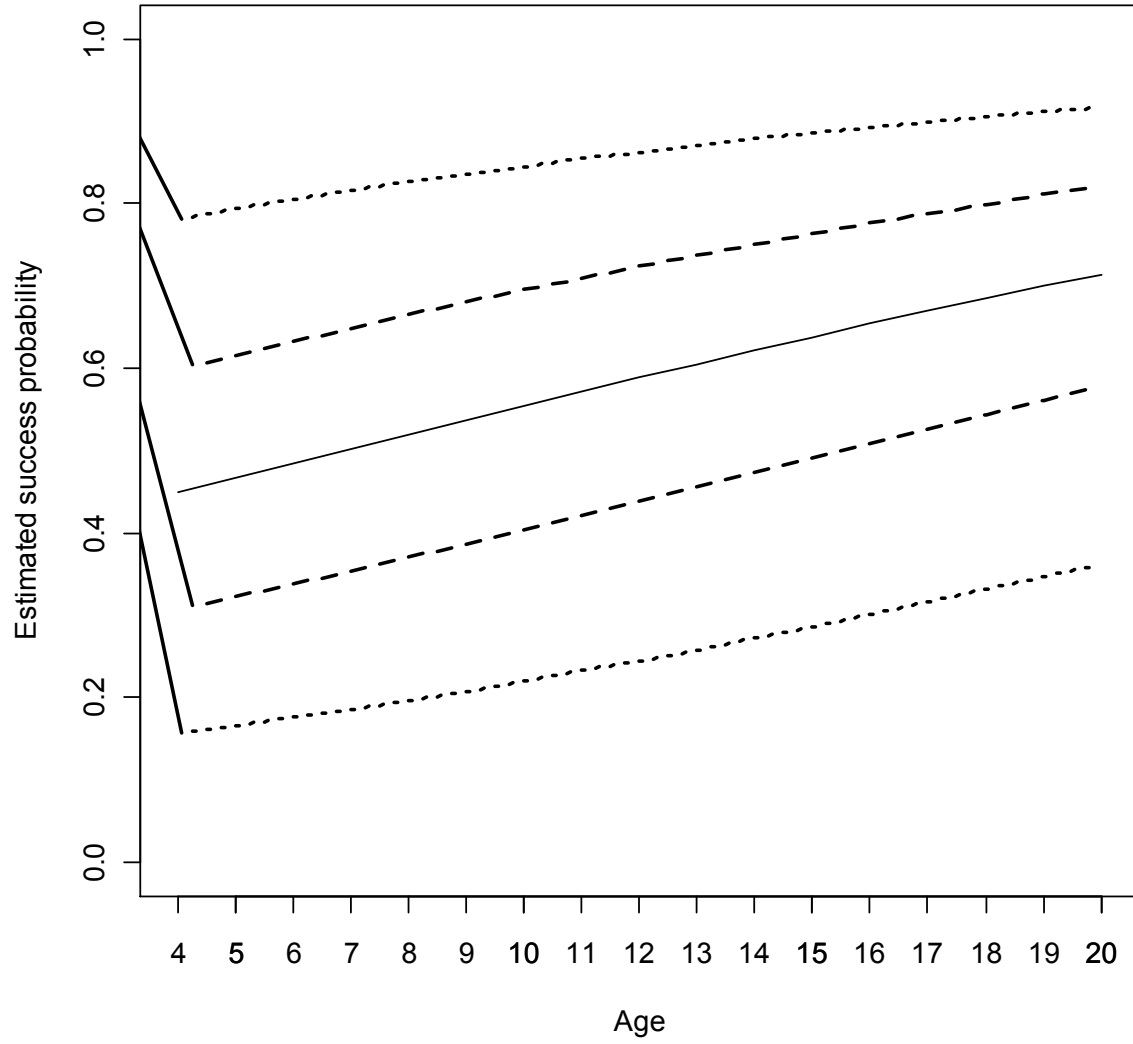
Appendix A4c

Relationship between age and success probability (complete dataset): mean individual. Dashed lines: quartiles. Dotted lines: quantiles (0.05 and 0.95).

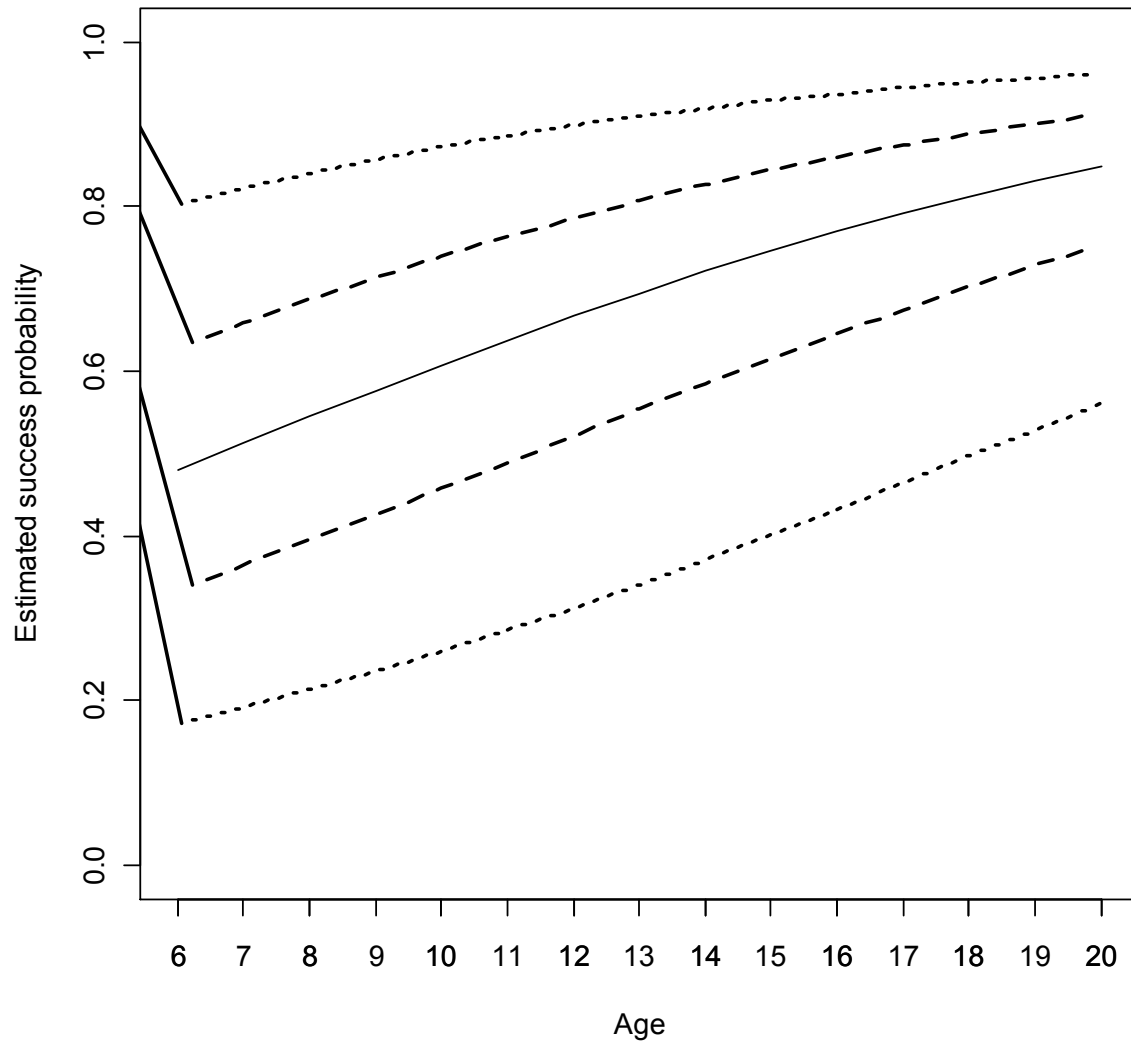
Age of first breeding ≤ 3 years old



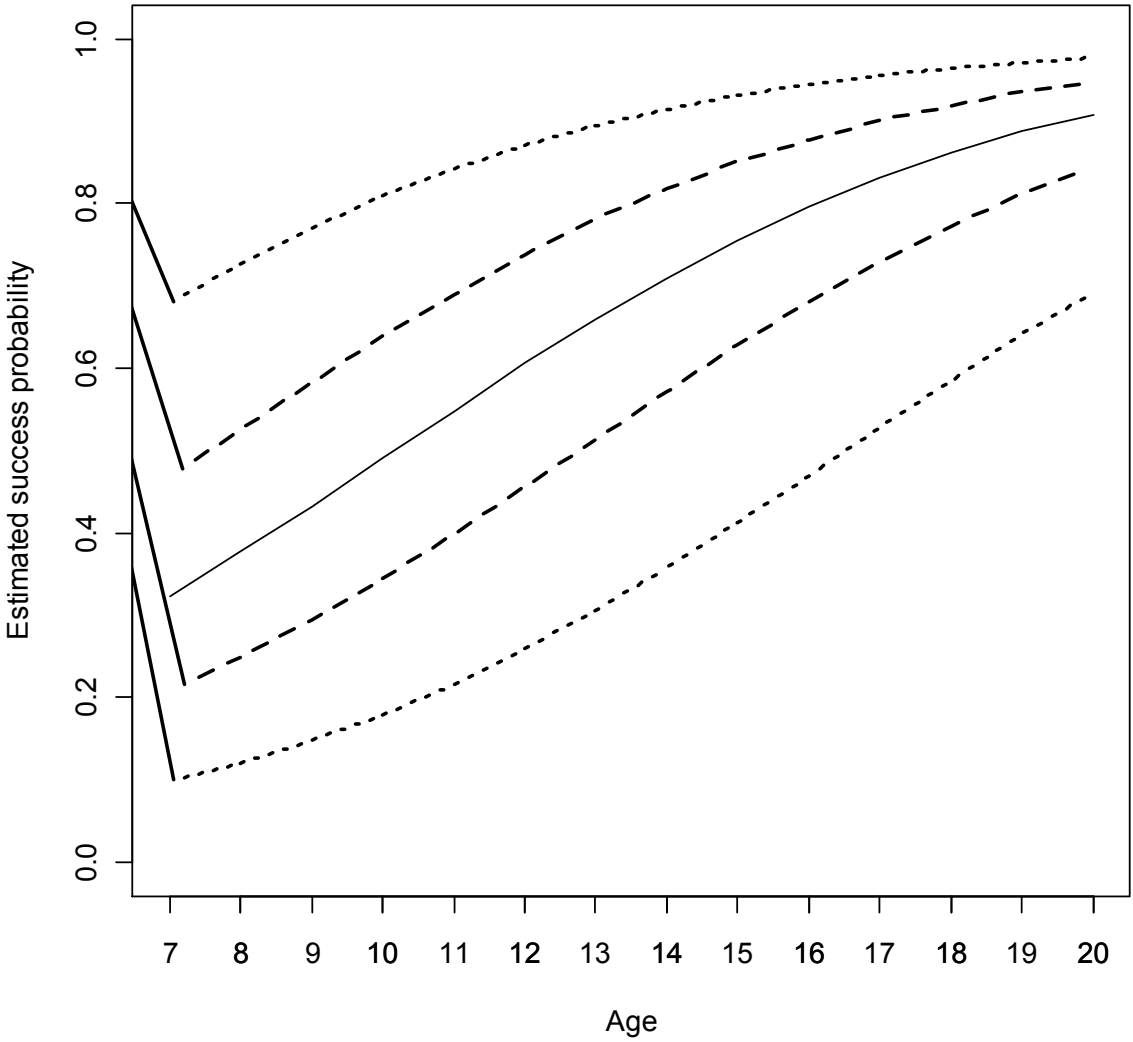
Age of first breeding = 4 years old



Age of first breeding = 6 years old

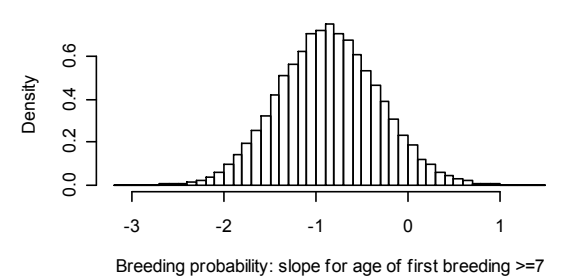
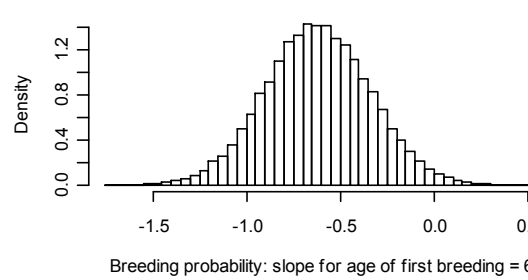
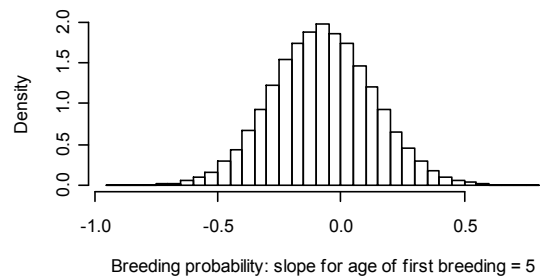
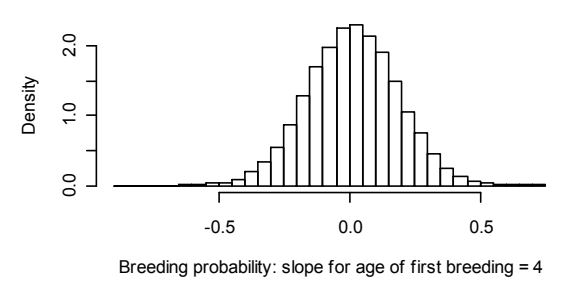
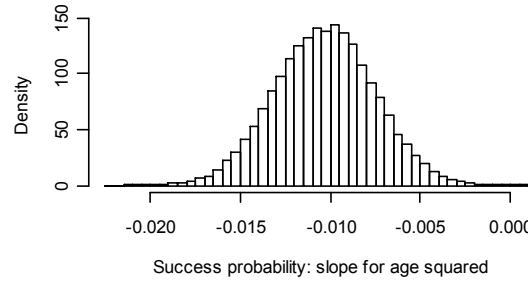
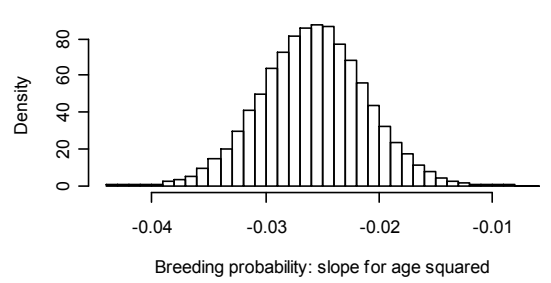
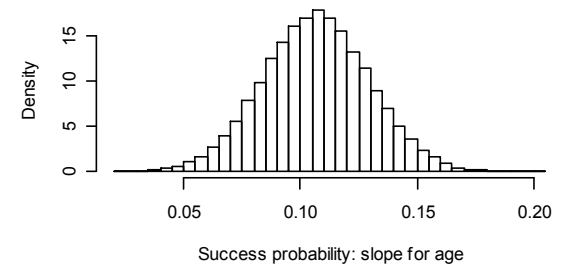
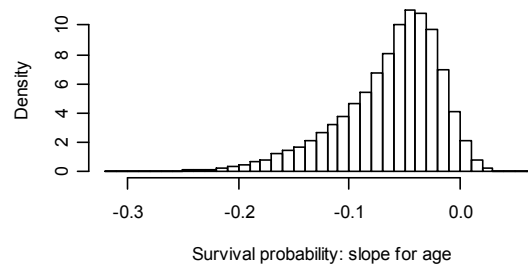
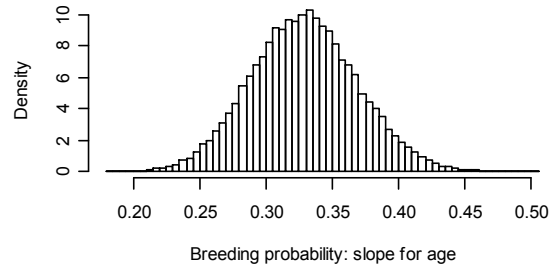


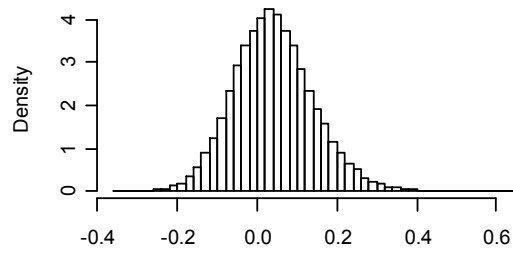
Age of first breeding ≥ 7 years old



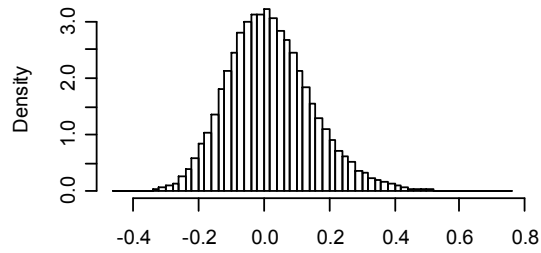
Appendix A5a

Posterior densities (model 9, main text Table 1, complete data set)

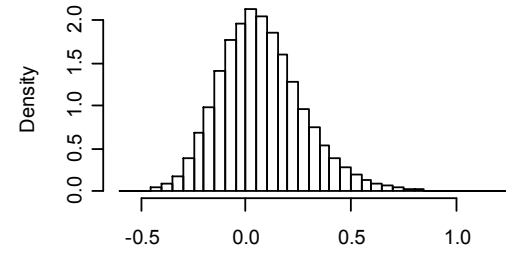




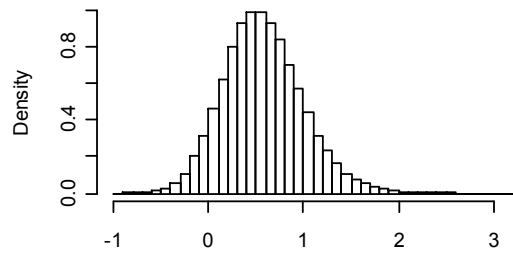
Survival probability: slope for age of first breeding = 4



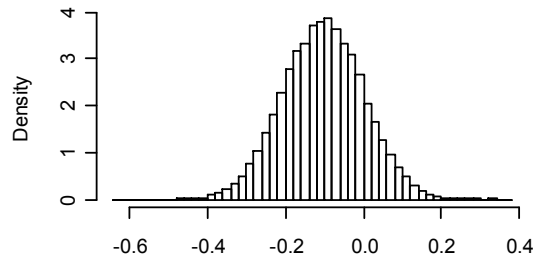
Survival probability: slope for age of first breeding = 5



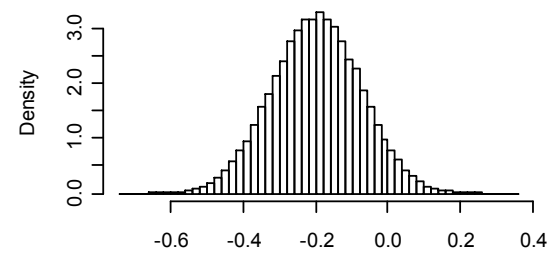
Survival probability: slope for age of first breeding = 6



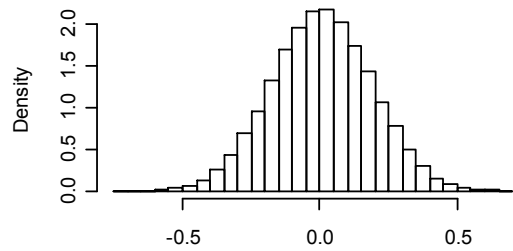
Survival probability: slope for age of first breeding >=7



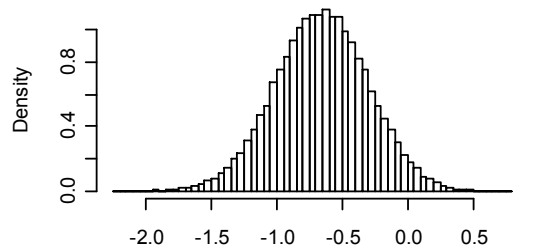
Success probability: slope of age of first breeding = 4



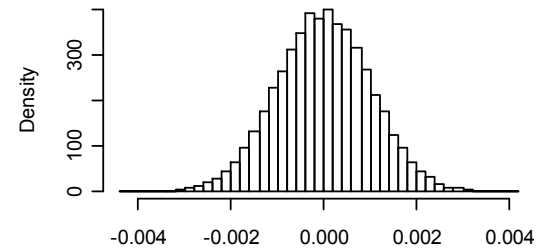
Success probability: slope for age of first breeding = 5



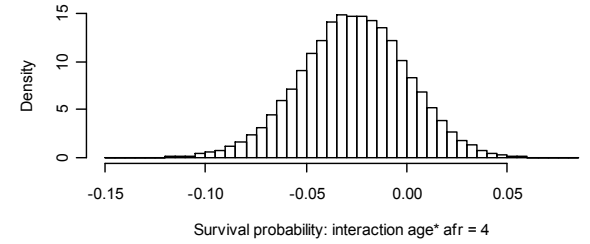
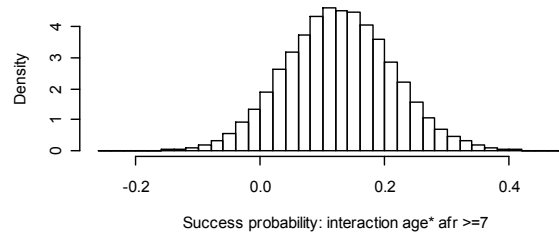
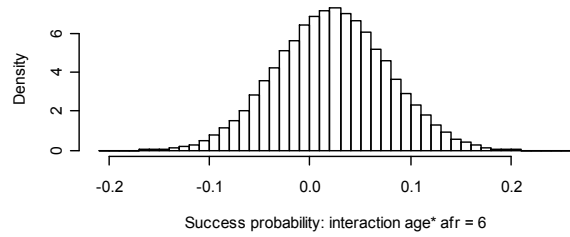
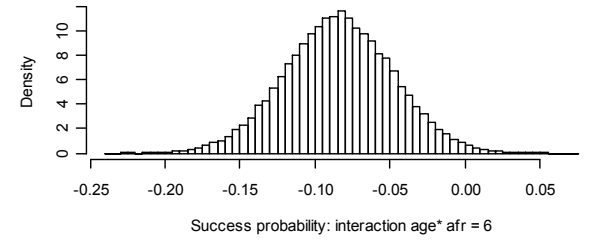
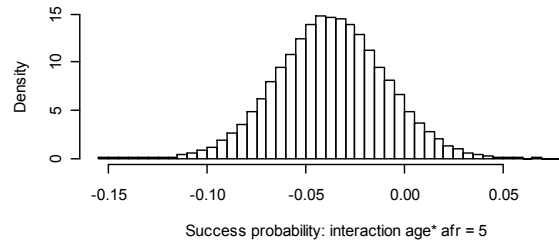
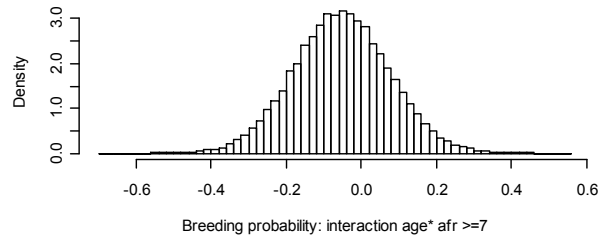
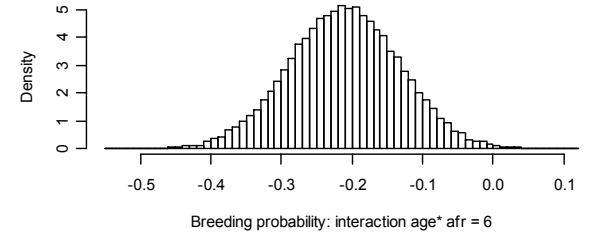
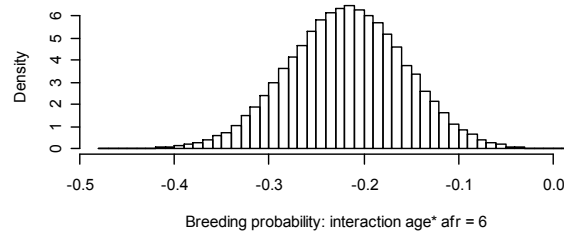
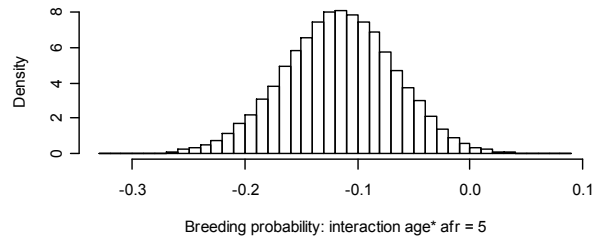
Success probability: slope for age of first breeding = 6

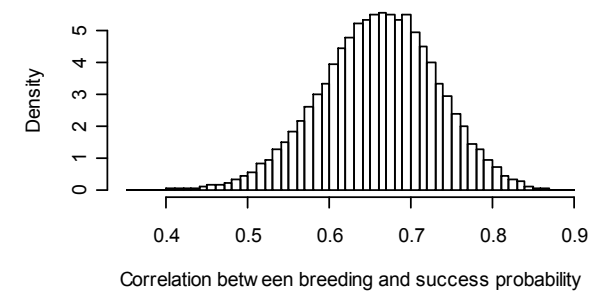
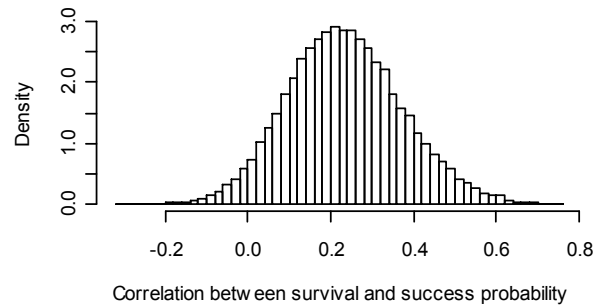
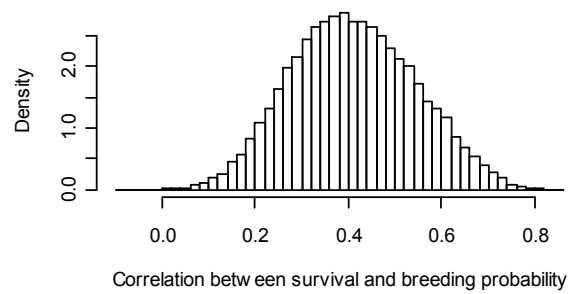
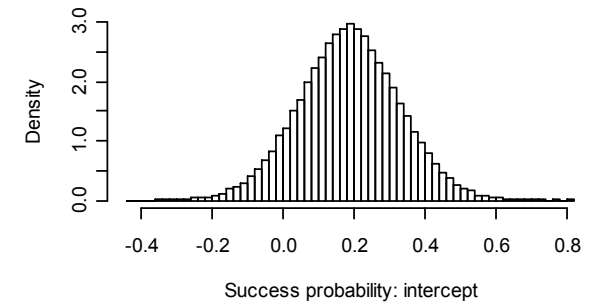
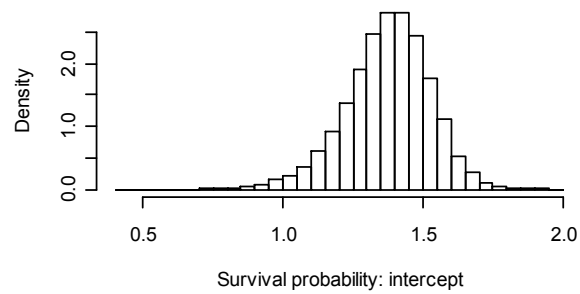
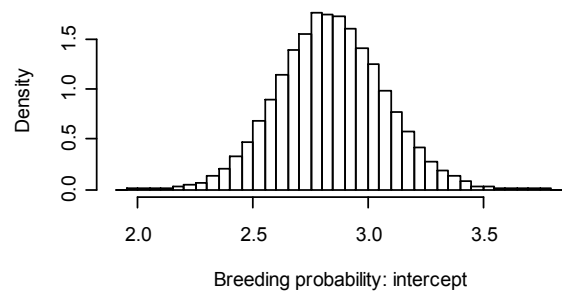
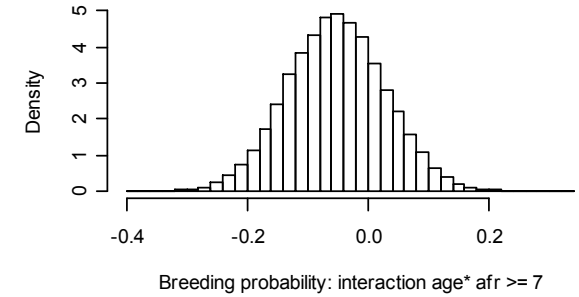
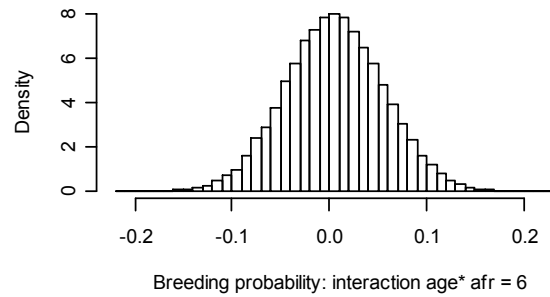
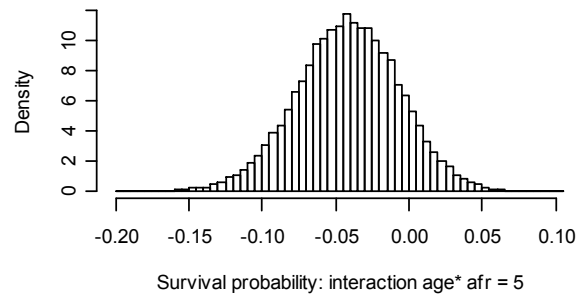


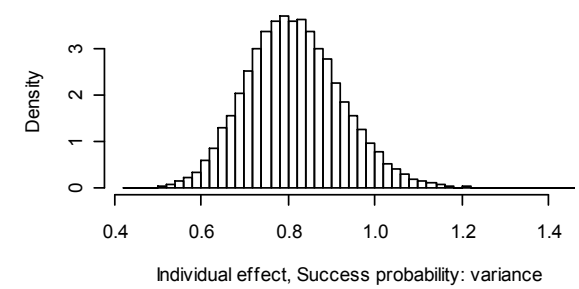
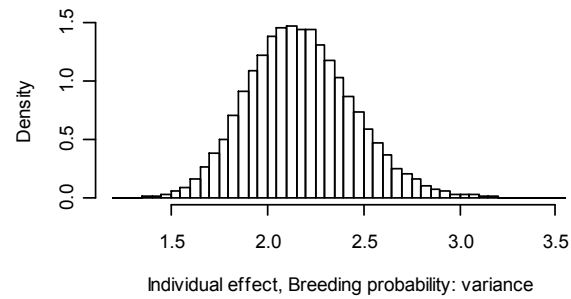
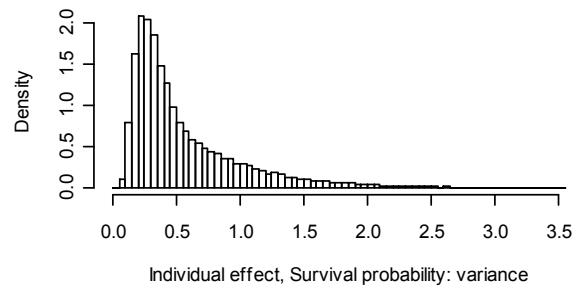
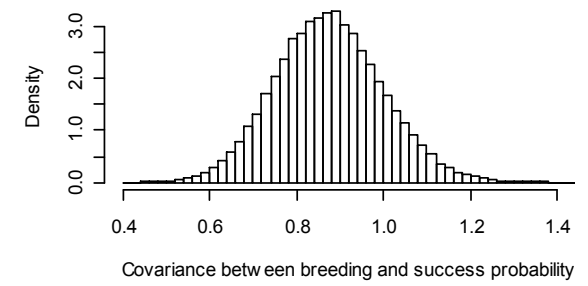
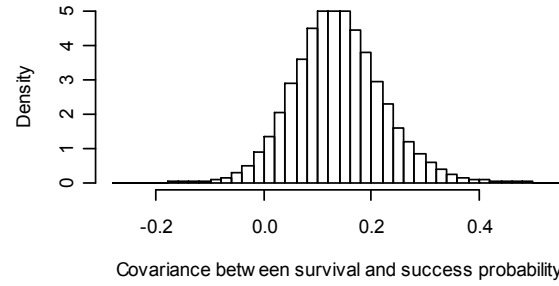
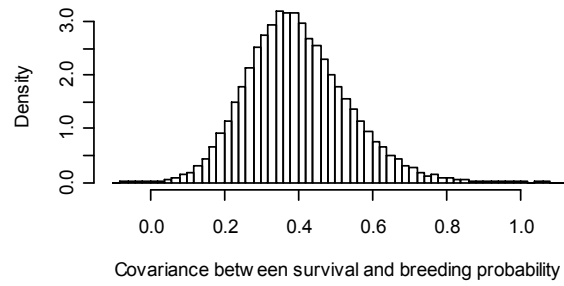
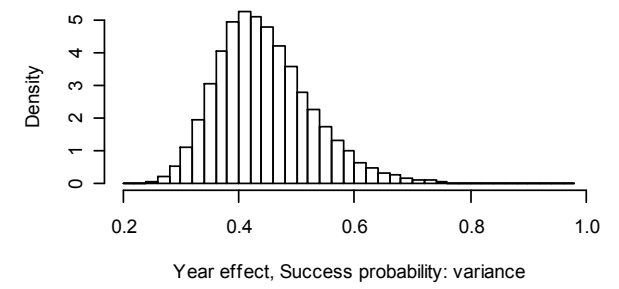
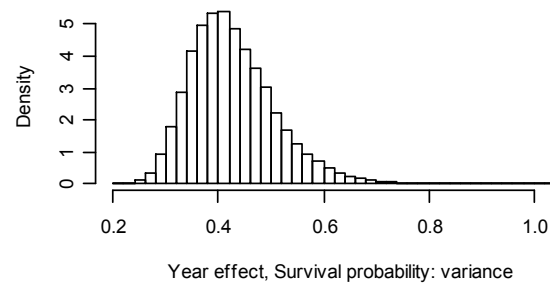
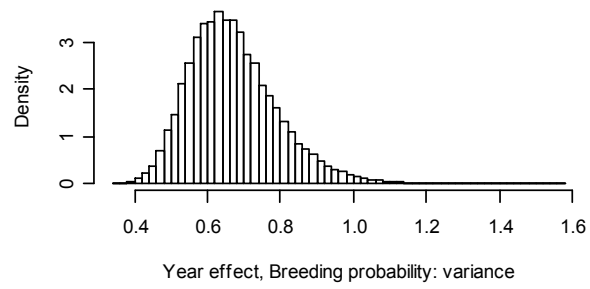
Success probability: slope for age of first breeding >=7



Breeding probability: interaction age* afr =4

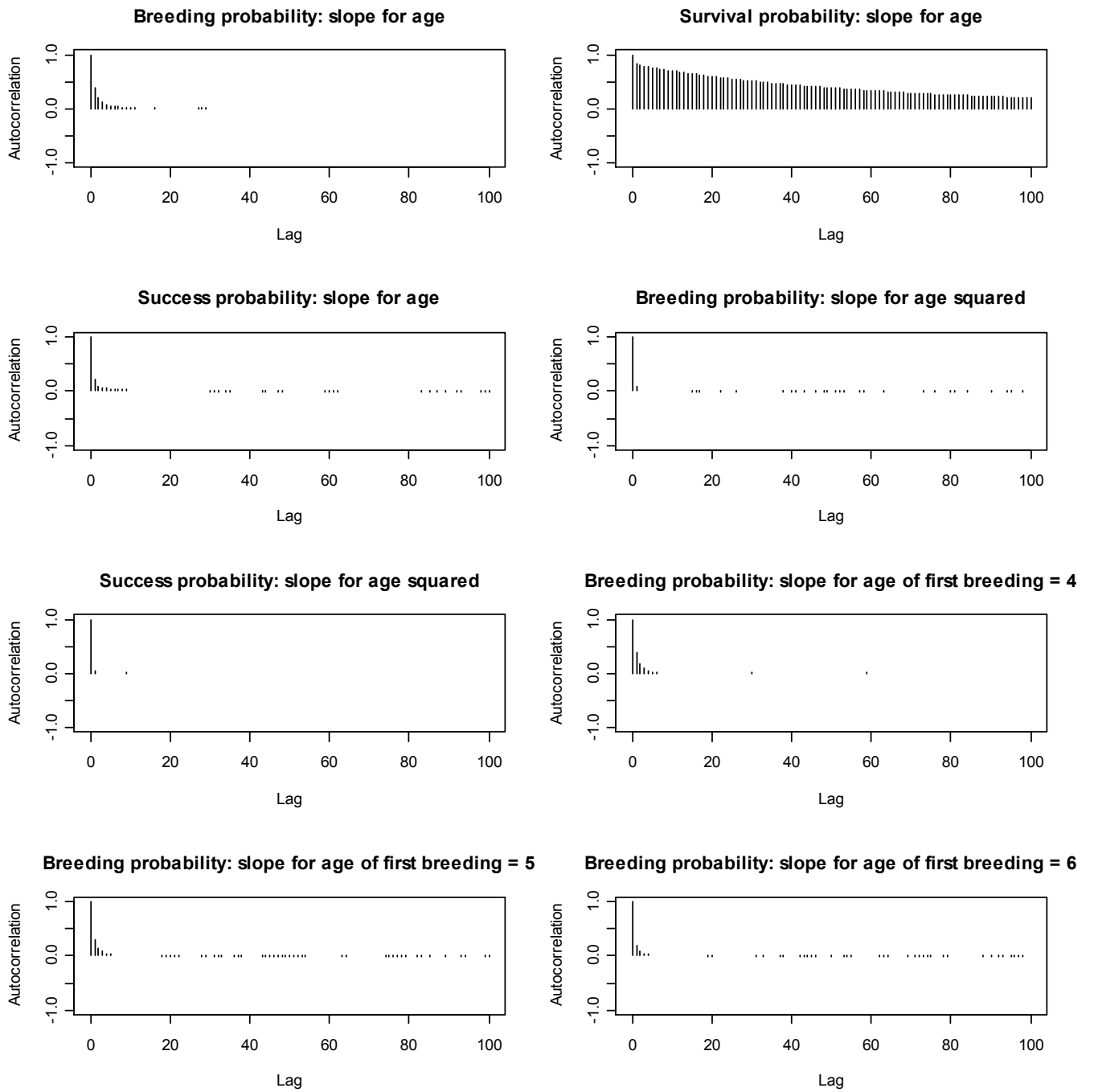




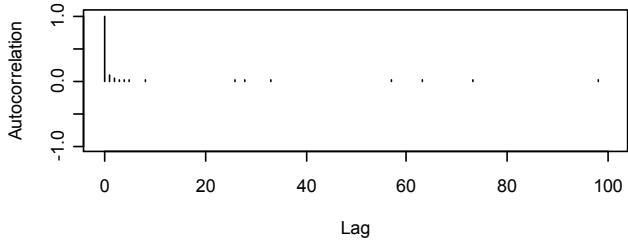


Appendix A5b

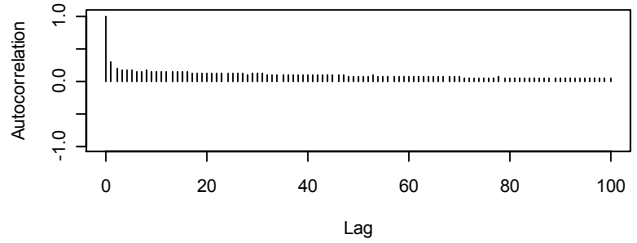
Autocorrelation (model 9, main text Table 1, complete data set)



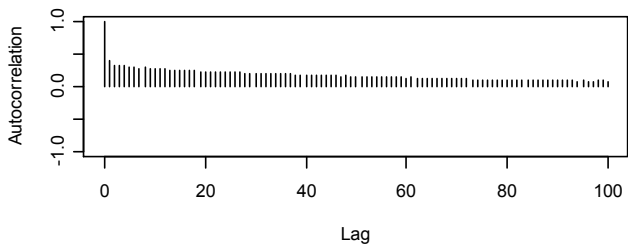
Breeding probability: slope for age of first breeding ≥ 7



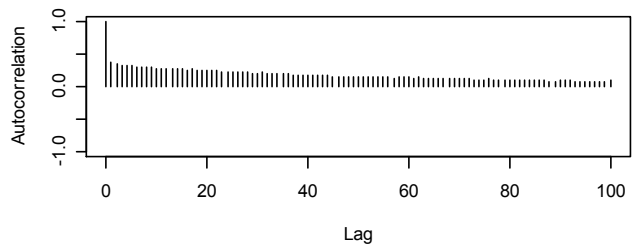
Survival probability: slope for age of first breeding = 4



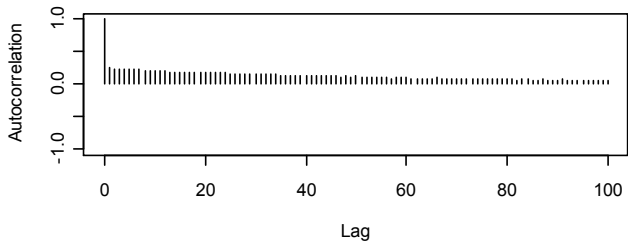
Survival probability: slope for age of first breeding = 5



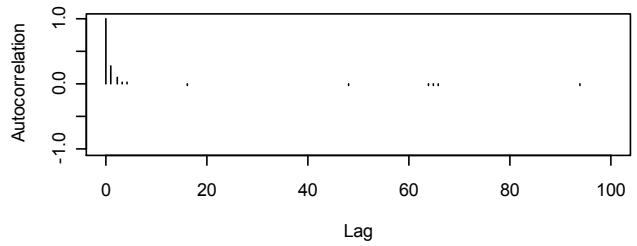
Survival probability: slope for age of first breeding = 6



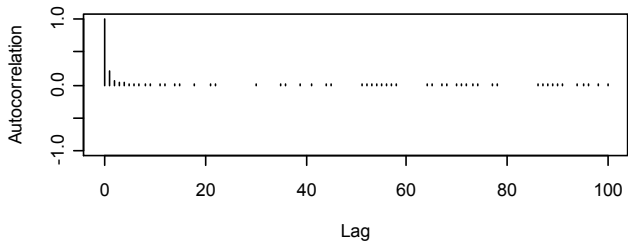
Survival probability: slope for age of first breeding ≥ 7



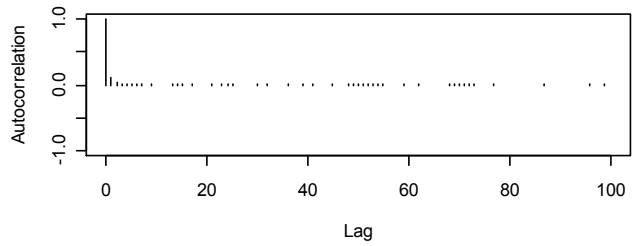
Success probability: slope of age of first breeding = 4

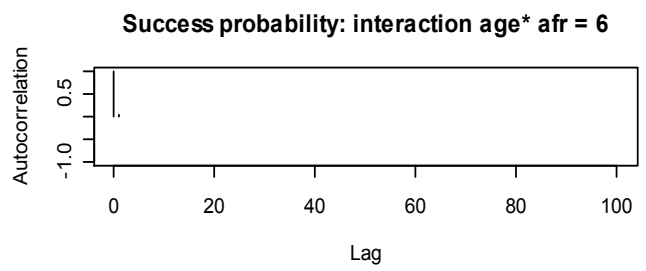
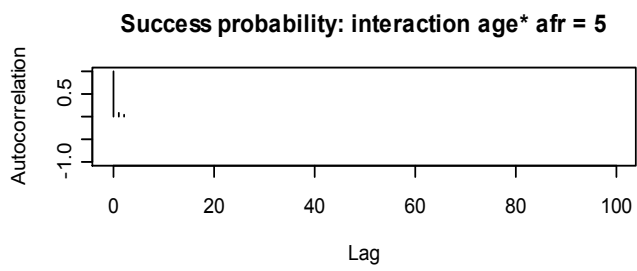
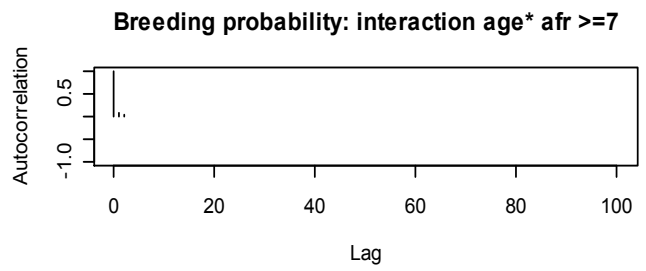
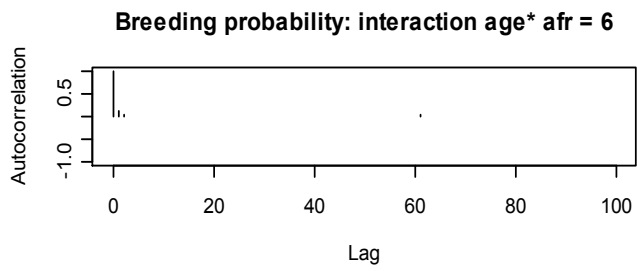
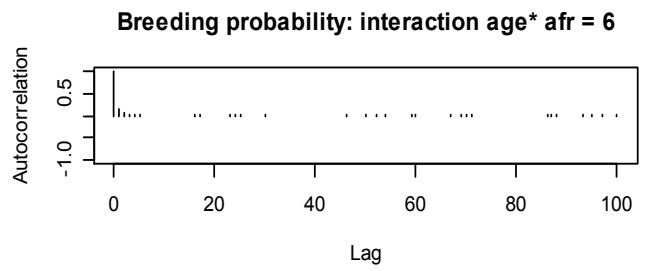
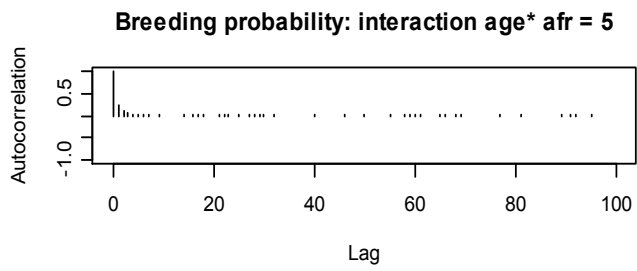
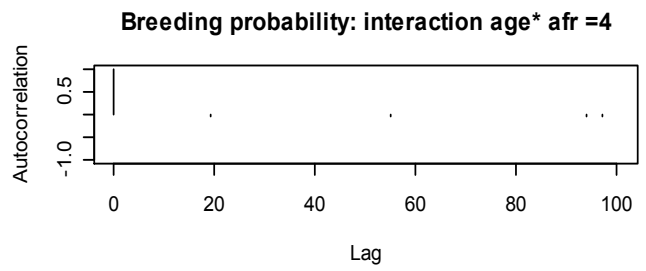
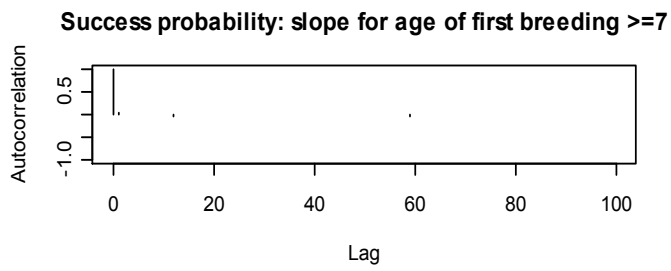


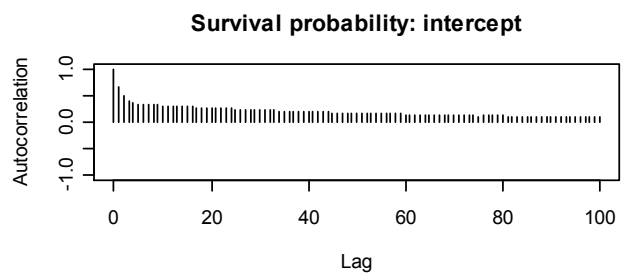
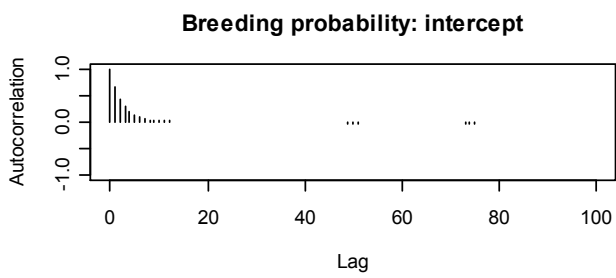
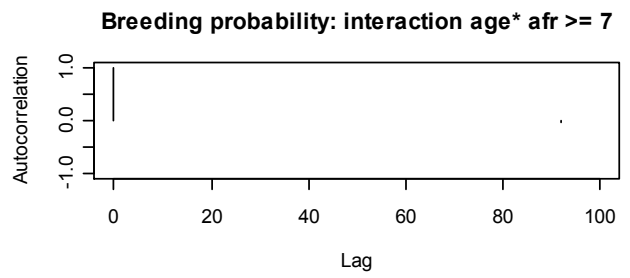
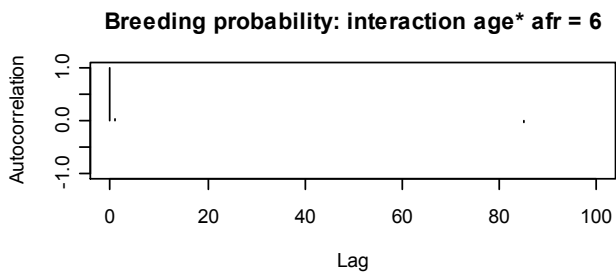
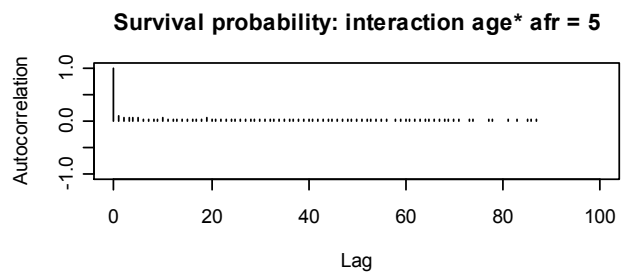
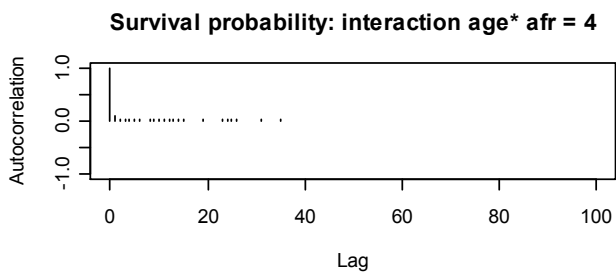
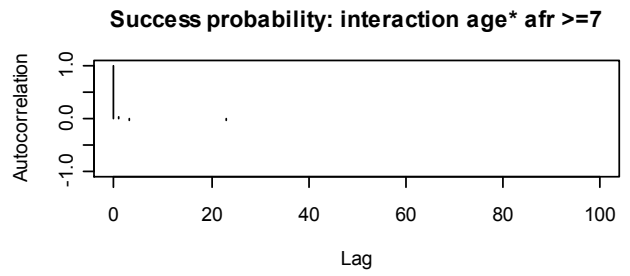
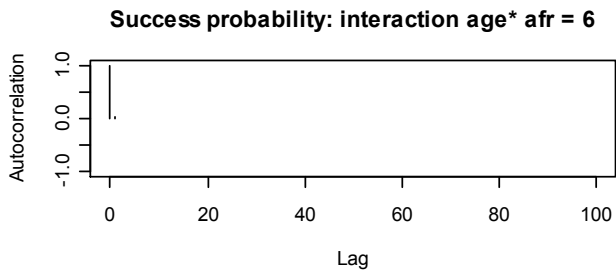
Success probability: slope for age of first breeding = 5



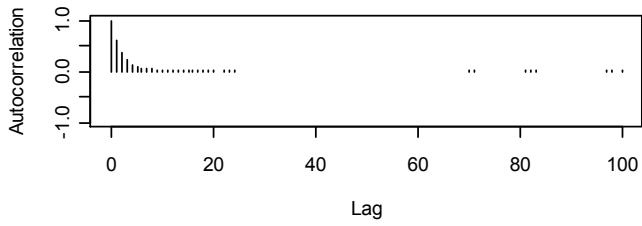
Success probability: slope for age of first breeding = 6



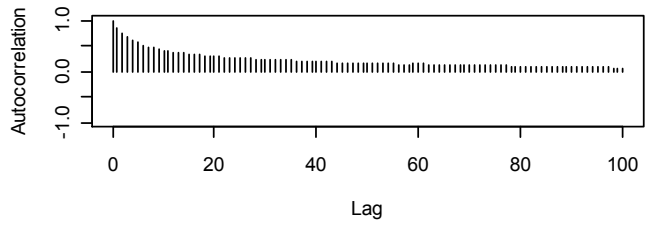




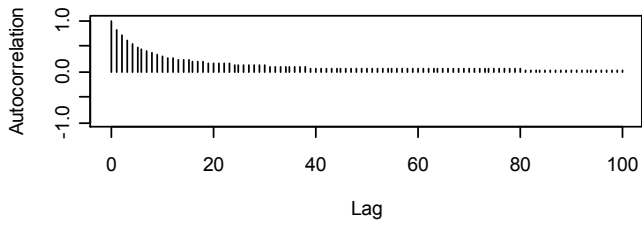
Success probability: intercept



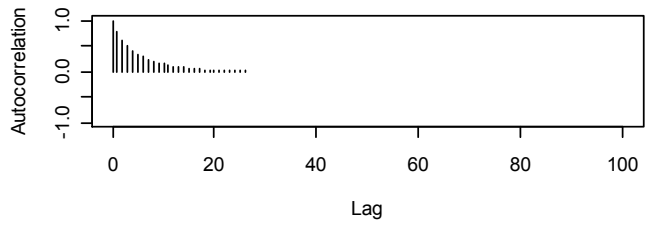
Correlation between survival and breeding probability



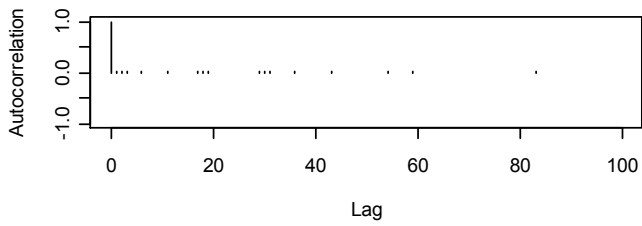
Correlation between survival and success probability



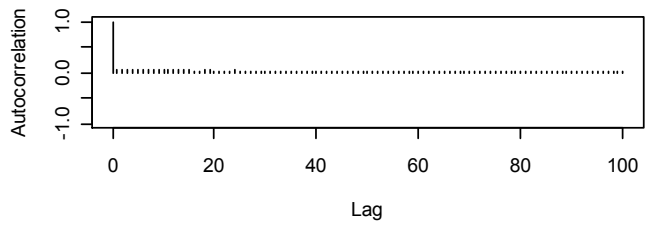
Correlation between breeding and success probability



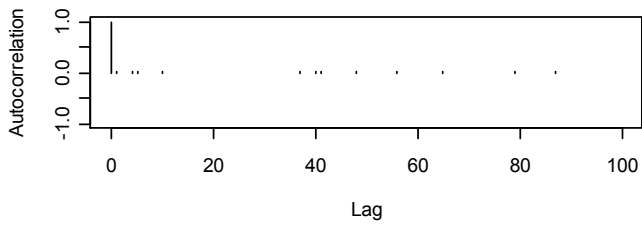
Year effect, Breeding probability: variance



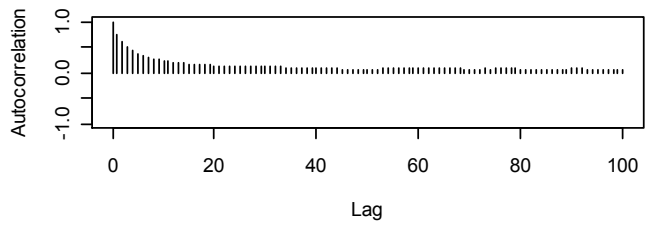
Year effect, Survival probability: variance



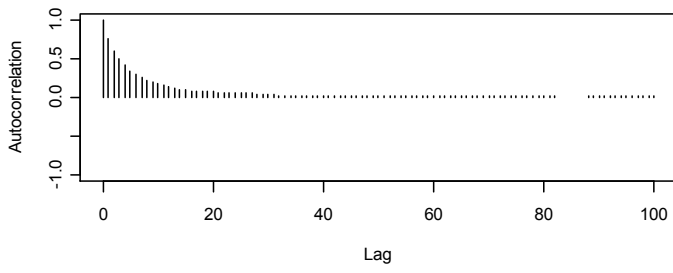
Year effect, Success probability: variance



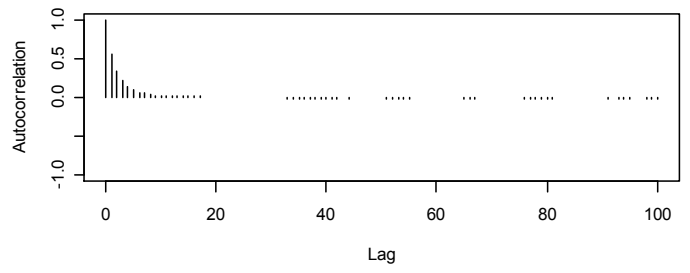
Covariance between survival and breeding probability



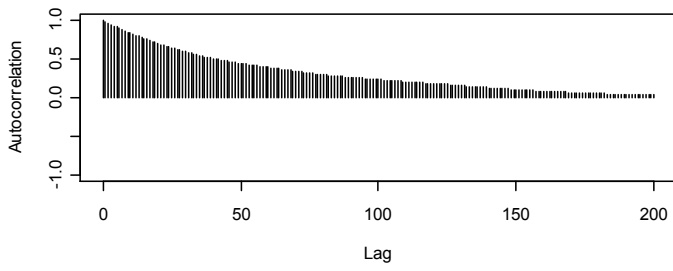
Covariance between survival and success probability



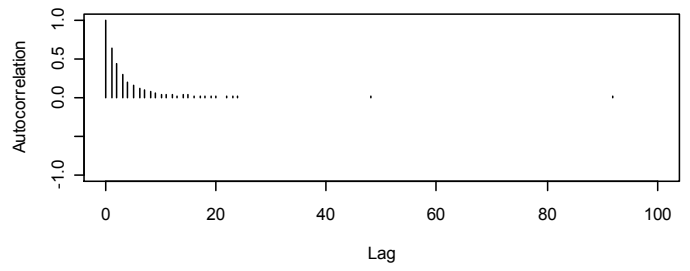
Covariance between breeding and success probability



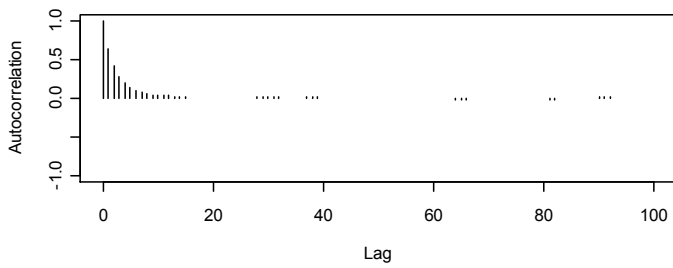
Individual effect, Survival probability: variance



Individual effect, Breeding probability: variance



Individual effect, Success probability: variance



Appendix A6

Excluding location-years with massive predation on eggs

We selected data from location-years ('cliffs'; Naves et al. 2006) without sign of substantial predation on eggs by corvids. Once started, such predation events occurred in consecutive years and, when massive, led to complete desertion of two colonies over the period considered here (Cam et al. 2004, Bled et al. 2011). Substantial predation on eggs in a location was identified by synchronous early failure at the egg stage in May in clusters of nests in colonies, and numerous egg shells found at the top of cliffs. When 20% or more of the active nests of a location were concerned, data from that location–year were excluded. This does not exclude all predation cases, but excludes situations of typical systematic predation by corvids. In addition, observations did not correspond to consecutive years in some individual histories because high predation at the egg stage in the location led to exclusion of some location–years. Data were assumed to be missing at random (Lu and Copas 2004). Imputation to deal with missing data is beyond the scope of this paper. Data from 1873 individuals were used (5277 alive/dead events, 3809 breeding/nonbreeding events, and 3379 success/failure events).

Results

Based on DIC, there was no evidence of correlations among random effects (Supplementary Material Appendix A6 Table A1). Here the quadratic effect of age on survival probability was included in the lowest-DIC model (model 8). Apart from that, results were consistent with those obtained using the complete data set (Cam et al. 2013). We used inclusion variables with model 8 by setting the terms standing for the correlations among individual random effects in the Cholesky decomposition equal to 0 (i.e. independent random effects). With prior probabilities of inclusion variables of 0.2, 0.8 and 0.5, estimates of mean posterior probabilities were systematically 1.0 and mixing had stopped before the end of the burn-in period (results not

presented). Concerning inclusion variables used with the most general model (model 1), results were sensitive to prior probability of inclusion of individual random effects, mostly for success probability (Supplementary Material Appendix A6 Table A2). The smallest posterior mean probabilities of inclusion variables concerned the individual random effect on success probability when strongly penalizing the random-effects model a priori. The estimates of posterior probabilities of the corresponding inclusion variables (the mean) were very close to 1.00 and mixing occurred at the beginning of the analysis (when the Markov chains may be influenced by initial values), but stopped before 5000 samples were drawn from the posterior distribution (burn-in period). Results concerning inclusion of the individual random effect on success probability with this data subset were definitely different from those obtained using data collected during both heavy predation and outside predation episodes (Cam et al. 2013). The data may be less informative concerning individual random effects for success probability in favorable environment.

We also addressed post hoc hypotheses about the quadratic effect of age on each fitness component. Model without age^2 on survival: DIC = 11751.7 (effective number of parameters = 1645.1); model without age^2 on breeding probability: DIC = 11773.1 (effective number of parameters = 1640.8); model without age^2 on success probability: DIC = 11752.1 (effective number of parameters = 1646.0). These results provided evidence that the quadratic effect of age on survival wasn't necessary to account for the process that gave rise to our data, neither was it for success probability (which wasn't the case with the complete data set). Conversely, the model incorporating age^2 on breeding probability received larger support than the model without it. Estimates made under the model with a single quadratic relationship with age (breeding probability) are reported in Supplementary Material Appendix A6 Table A3. The negative relationship between age and survival was more marked using this subset of the data compared to the complete data set (Cam et al. 2013). The autocorrelation in the Markov chains was substantially smaller than with the complete data set (Supplementary Material Appendix A5) for

the variance of the individual random effect on survival and the slope of the relationship between age and survival (results not presented here). The variances of the individual random effects on survival and breeding probability were sensitive to the parameters of the prior Gamma distribution on the precision τ : the larger the precision, the smaller the posterior variance (Supplementary Material Appendix A6 Table A4). This relationship was not observed for the variance of the individual random effect on success probability.

Discussion

As expected (Cam et al. 2013), inclusion variables indicated that heterogeneity in individual success probability received smaller support when data from massive predation periods were excluded (see also Cam et al. 2004). This suggests that part of the heterogeneity in success probability among individuals in the complete data set results from contrasted environmental conditions experienced by individuals. Similarly, one of the main differences between the two analyses (these analyses are not independent because this one was conducted using a subset of the complete dataset) is that the correlations between individual random effects were not selected here when excluding data collected during predation events. A possible interpretation is that these correlations partly reflect behavioral responses to environmental conditions, namely a relationship between failed breeding attempts, dispersal, nonbreeding (Danchin et al. 2002), and divorce (Naves et al. 2006). Danchin et al. (1998) have provided evidence of a relationship between dispersal within the study area and breeding success. In addition, our estimates of survival probability are restricted to the study area; emigration out of the study area cannot be assessed yet because of the large distribution area of the species and insufficient effort to collect data in a large part of this area. However, anecdotal observations of breeding individuals in the UK (and Ireland) show that emigration exists. Part of the individuals deserting heavily predated locations may enter a 'failure vicious cycle' that would translate into a positive relationship between breeding performance and local survival, and between breeding and success probability

(unsuccessful individuals disperse and fail again after moving to another location, or don't breed; if they disperse out of the study area, this translates into apparent death in our data).

To assess whether local conditions are responsible for heterogeneity in success probability among individuals, analyses should be conducted at a different spatial scale (Bled et al. 2011). Local conditions in the study area are unlikely to create heterogeneity in overwinter survival among individuals (this species migrates and we have no reason to think that feeding areas are specific to colonies or 'cliffs' in summer). However, these conditions may create some heterogeneity in breeding probability among individuals if some of the individuals have to face several predation episodes consecutively in different locations. Investigating this question will require joint consideration of habitat features, dispersal within the study area, and fitness components in this fragmented population. In addition, it is interesting to note that posterior probabilities of inclusion of the individual random effect on survival were larger when focusing on favorable environmental conditions (at least for predation on eggs) compared to the complete data set (main text, Table 2; Cam et al. 2013). The estimated standard deviation of the individual random effect on survival probability (Supplementary material Appendix A6 Table A3) was also larger than with the complete data set (main text, Table 4; Cam et al. 2013). A formal comparison of variances would require building a model with heterogeneous variance. As explained above, our survival estimates are confounded with fidelity to the study area. Under the hypothesis of differences in individual potential for survival, massive predation on eggs and subsequent dispersal out of the study area will concern any individual regardless of its baseline mortality risk. External causes of failure are expected to homogenize local survival probabilities in the concerned location-year. In contrast, the variance among individuals is expected to be large in situations where external causes of failure do not lead to permanent emigration.

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Table A1. Model selection for survival, breeding, and success probability: inferences about age, age of first breeding, year, previous breeding activity and success and random individual effects. Data from locations–years without heavy predation at the egg stage by corvids.

Model	Life history trait	Age	Age ²	Afr	Afr*Age	Pbs	Year (random effect)	Individual random effects	Correlation between individual random effects	Deviance information criterion	Effective number of parameters	Deviance information criterion weight
1*	φ	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	11813.5	1189.8	0.00
	β	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes			
	γ	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes			
2	φ	Yes	Yes	Yes	Yes	Yes	Yes	No	NA	12180.0	82.6	0.00
	β	Yes	Yes	Yes	Yes	Yes	Yes	No	NA			
	γ	Yes	Yes	Yes	Yes	Yes	Yes	No	NA			
3	φ	Yes	Yes	Yes	Yes	No	Yes	Yes	Yes	11771.8	1565.1	0.00
	β	Yes	Yes	Yes	Yes	No	Yes	Yes	Yes			
	γ	Yes	Yes	Yes	Yes	No	Yes	Yes	Yes			
4	φ	Yes	Yes	Yes	Yes	No	Yes	No	NA	12562.7	75.8	0.00
	β	Yes	Yes	Yes	Yes	No	Yes	No	NA			

	γ	Yes	Yes	Yes	Yes	No	Yes	No	NA			
5	φ	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No	11776.7	1180.3	0.00
	β	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No			
	γ	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No			
6	φ	Yes	Yes	Yes	No	No	Yes	Yes	Yes	11821.1	1504.2	0.00
	β	Yes	Yes	Yes	No	No	Yes	Yes	Yes			
	γ	Yes	Yes	Yes	No	No	Yes	Yes	Yes			
7	φ	Yes	Yes	Yes	No	No	Yes	Yes	No	11810.8	1583.6	0.00
	β	Yes	Yes	Yes	No	No	Yes	Yes	No			
	γ	Yes	Yes	Yes	No	No	Yes	Yes	No			
8 *	φ	Yes	Yes	Yes	Yes	No	Yes	Yes	No	11755.8	1644.2	1.00
	β	Yes	Yes	Yes	Yes	No	Yes	Yes	No			
	γ	Yes	Yes	Yes	Yes	No	Yes	Yes	No			
9	φ	Yes	No	Yes	Yes	No	Yes	Yes	No	11777.3	1639.3	0.00
	β	Yes	No	Yes	Yes	No	Yes	Yes	No			
	γ	Yes	No	Yes	Yes	No	Yes	Yes	No			
	φ	Yes	Yes	Yes	Yes	No	No	Yes	No			

10	β	Yes	Yes	Yes	Yes	No	No	Yes	No	11954.2	1848.0	0.00
	γ	Yes	Yes	Yes	Yes	No	No	Yes	No			

φ = survival probability. β = breeding probability. γ = probability of raising at least one chick to independence given that the individual attempted to breed. Age^2 = quadratic effect of age on survival, breeding, and success probability. Afr = age of first breeding. Pbs = previous breeding activity and success. In bold: lowest-AIC model. * Models used with inclusion variables (Chen and Dunson 2003). Chen, Z. and Dunson, D. B. 2003. Random effects selection in linear mixed models. – *Biometrics* 59: 762–769.

Table A2. Inclusion variables (Chen and Dunson 2003).

Model		Prior probability of inclusion of Σ	Prior probability for inclusion variables	Mean	Median	Quantiles	
						0.025	0.975
1	φ	0.50	0.80	1.0	1.0	1.0	1.0
	β			0.97	1.0	0.0	1.0
	γ			0.73	1.0	0.0	1.0
	φ	0.125	0.50	1.0	1.0	1.0	1.0
	β			0.92	1.0	0.0	1.0
	γ			0.40	0.0	0.0	1.0
	φ	0.008	0.20	1.0	1.0	1.0	1.0
	β			0.76	1.0	0.0	1.0
	γ			0.14	0.0	0.0	1.0

φ = survival probability. β = breeding probability. γ = probability of raising at least one chick to

independence given that the individual attempted to breed. Chen, Z. and Dunson, D. B. 2003.

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Table A3. Estimates of coefficients and components of variance of the selected model (exclusion of locations-years with massive predation on eggs).

Covariate		Life history trait	Mean	Standard deviation	Median	Quantiles	
						0.025	0.975
Intercept		φ	0.1533	0.2583	0.1581	-0.3707	0.6474
		β	4.358	0.3769	4.346	3.652	5.136
		γ	0.8188	0.1017	0.818	0.6219	1.021
Age		φ	-0.2448	0.0468	-0.2432	-0.3409	-0.1573
		β	0.4817	0.0670	0.4798	0.3564	0.6194
		γ	0.149	0.0287	0.1486	0.0935	0.2062
Age ²		β	-0.0337	0.0071	-0.0337	-0.0475	-0.0198
Age of first breeding	4	φ	0.2342	0.1583	0.2318	-0.0715	0.5514
	5	φ	0.4303	0.1946	0.4254	0.0606	0.8228
	6	φ	0.7448	0.2853	0.738	0.2043	1.325
	>6	φ	1.832	0.5611	1.817	0.7782	2.979
	4	β	-0.2155	0.2751	-0.2133	-0.7599	0.3182
	5	β	-0.2749	0.3177	-0.2759	-0.8958	0.3489
	6	β	-1.286	0.3956	-1.285	-2.06	-0.511
	>6	β	-1.206	0.7563	-1.218	-2.648	0.3159
	4	γ	-0.1197	0.1198	-0.1193	-0.356	0.1127
	5	γ	-0.2025	0.1286	-0.2028	-0.4752	0.0685
	6	γ	0.0	0.2049	0.0	-0.4	0.4065
	>6	γ	-0.8483	0.3719	-0.8472	-1.58	-0.1169
	4	φ	-0.0489	0.0391	-0.0487	-0.1265	0.0268
	5	φ	-0.1149	0.0525	-0.1142	-0.2198	0.1236

Interaction	6	φ	-0.0205	0.0742	-0.0200	-0.1678	0.1053	
	>6	φ	-0.0607	0.1107	-0.0601	-0.2803	0.1555	
	4	β	-0.1352	0.0829	-0.1334	-0.3032	0.0223	
	5	β	-0.3349	0.1002	-0.3329	-0.5374	-0.1429	
	6	β	-0.2469	0.1208	-0.2455	-0.4873	-0.0136	
	>6	β	-0.1452	0.1754	-0.1447	-0.4903	0.1976	
	4	γ	-0.1135	0.0360	0.0	-0.0019	0.0019	
	5	γ	-0.0971	0.0467	-0.0971	-0.1887	-0.0473	
	6	γ	-0.0421	0.0744	-0.0429	-0.1862	0.1063	
	>6	γ	0.0100	0.101	0.0081	-0.1842	0.2123	
			SD φ	1.839	0.2067	1.832	1.452	2.261
			SD β	1.761	0.1605	1.757	1.461	2.089
			SD γ	0.6722	0.0854	0.673	0.5039	0.8379
Year effects		SD φ	1.16	0.3976	1.109	0.5337	2.076	
		SD β	1.147	0.5332	1.047	0.4152	2.462	
		SD γ	0.1155	0.0597	0.1075	0.0287	0.2508	

φ = survival probability. β = breeding probability. γ = probability of raising at least one chick to independence given that the individual attempted to breed. Age^2 = quadratic effect of age on breeding probability. SD =standard deviation. Burn-in = 10 000, 1 every 6 samples retained for inferences, total number of samples =50 000.

Table A4. Sensitivity analyses.

Prior distribution			Mean		Median	Quantiles 0.025 0.975	
τ_ϕ'	$\Gamma(0.001,0.001)$		SD ϕ	1.842	1.832	1.421	2.321
	$\Gamma(1,1)$		SD ϕ	1.818	1.811	1.439	2.236
	$\Gamma(10,10)$		SD ϕ	1.563	1.556	1.235	1.925
τ_β'	$\Gamma(0.001,0.001)$		SD β	1.761	1.757	1.461	2.089
	$\Gamma(1,1)$		SD β	1.747	1.742	1.451	2.071
	$\Gamma(10,10)$		SD β	1.592	1.587	1.332	1.878
τ_γ'	$\Gamma(0.001,0.001)$		SD γ	0.6722	0.673	0.5039	0.8379
	$\Gamma(1,1)$		SD γ	0.6966	0.6959	0.5447	0.8518
	$\Gamma(10,10)$		SD γ	0.7909	0.7891	0.6756	0.9163

Appendix A7

BUGS codes (main text, Table 1, model 1).

```
model
{

# survival probability
for( i in 1 : 7893) {
sur[i] ~ dbern(phi[i])
logit(phi[i]) <- muphi+ beta1phi * (surage[i]-meansurage) + beta2phi * pow((surage[i]-
meansurage),2)+ betafs[ageftsur[i]]+ alpha[surid[i],1]
+year.phi[suryr[i]]+intsur[ageftsur[i]]*(surage[i]-meansurage)+bsurav[avsur[i]]
}

#breeding probability
for( j in 1 : 6425) {
breed[j] ~ dbern(br[j])
logit(br[j]) <- mubreed+ beta1breed * (breedage[j]-meanbreedage) + beta2breed *
pow((breedage[j]-meanbreedage),2)+ alpha[breedid[j],2] +year.breed[breedyr[j]]
+betafr[ageftrep[j]] +intbreed[ageftrep[j]]*(breedage[j]-meanbreedage) +brepav[avrep[j]]
}

#success probability
for( g in 1 : 5541) {
success[g] ~ dbern(suc[g])
logit(suc[g]) <- musuc+ beta1suc * (sucage[g]-meansucage) + beta2suc * pow((sucage[g]-
meansucage),2)+ alpha[sucid[g],3] +year.suc[sucyr[g]] +betasc[ageftsuc[g]]
+intsuc[ageftsuc[g]]*(sucage[g]-meansucage) +betasucav[avsuc[g]]
}

#individual random effects
for( k in 1 : 1971) {
alpha[k, 1:3]~dmnorm(muvec[], R[,])
}

#year effects
for( n in 1 : 22) {
year.phi[n] ~ dnorm(0.0,year.tau.phi)
year.breed[n] ~ dnorm(0.0,year.tau.breed)
year.suc[n] ~ dnorm(0.0,year.tau.suc)
}

#prior distributions for year effects
year.tau.phi ~ dgamma(0.001,0.001)
sigmaphi <- 1 / sqrt(year.tau.phi)
year.tau.breed ~ dgamma(0.001,0.001)
sigmabreed <- 1 / sqrt(year.tau.breed)
year.tau.suc ~ dgamma(0.001,0.001)
sigmasuc <- 1 / sqrt(year.tau.suc)
```

#prior distributions for age of first breeding: survival probability

betafs[1] ~ dnorm(0.0,1.0E06)

betafs[2] ~ dnorm(0.0,0.001)

betafs[3] ~ dnorm(0.0,0.001)

betafs[4] ~ dnorm(0.0,0.001)

betafs[5] ~ dnorm(0.0,0.001)

#prior distributions for age of first breeding: breeding probability

betafr[1] ~ dnorm(0.0,1.0E06)

betafr[2] ~ dnorm(0.0,0.001)

betafr[3] ~ dnorm(0.0,0.001)

betafr[4] ~ dnorm(0.0,0.001)

betafr[5] ~ dnorm(0.0,0.001)

#prior distributions for age of first breeding: probability of breeding successfully

betasc[1] ~ dnorm(0.0,1.0E06)

betasc[2] ~ dnorm(0.0,0.001)

betasc[3] ~ dnorm(0.0,0.001)

betasc[4] ~ dnorm(0.0,0.001)

betasc[5] ~ dnorm(0.0,0.001)

#prior distribution for the interaction between age of first breeding and previous breeding state:

survival probability

intsur[1] ~ dnorm(0.0,1.0E06)

intsur[2] ~ dnorm(0.0,0.001)

intsur[3] ~ dnorm(0.0,0.001)

intsur[4] ~ dnorm(0.0,0.001)

intsur[5] ~ dnorm(0.0,0.001)

#prior distribution for the interaction between age of first breeding and previous breeding state:

breeding probability

intbreed[1] ~ dnorm(0.0,1.0E06)

intbreed[2] ~ dnorm(0.0,0.001)

intbreed[3] ~ dnorm(0.0,0.001)

intbreed[4] ~ dnorm(0.0,0.001)

intbreed[5] ~ dnorm(0.0,0.001)

#prior distribution for the interaction between age of first breeding and previous breeding state:

probability of breeding successfully

intsuc[1] ~ dnorm(0.0,1.0E06)

intsuc[2] ~ dnorm(0.0,0.001)

intsuc[3] ~ dnorm(0.0,0.001)

intsuc[4] ~ dnorm(0.0,0.001)

intsuc[5] ~ dnorm(0.0,0.001)

#prior distributions for age effect: survival probability

beta1phi ~ dnorm(0.0,0.001)

beta2phi ~ dnorm(0.0,0.001)

#prior distributions for age effect: breeding probability

beta1breed ~ dnorm(0.0,0.001)

```

beta2breed ~ dnorm(0.0,0.001)

#prior distributions for age effect: probability of breeding successfully
beta1suc ~ dnorm(0.0,0.001)
beta2suc ~ dnorm(0.0,0.001)

#prior distributions for intercepts
mubreed ~ dnorm(0.0,0.001)
muphi ~ dnorm(0.0,0.001)
musuc ~ dnorm(0.0,0.001)

#prior distributions for previous breeding state: survival probability
bsurav[3]~dnorm(0.0,1.0E06)
bsurav[2]~dnorm(0.0,0.001)
bsurav[1]~dnorm(0.0,0.001)

#prior distributions for previous breeding state: breeding probability
brepav[3]~dnorm(0.0,1.0E06 )
brepav[2]~dnorm(0.0,0.001)
brepav[1]~dnorm(0.0,0.001)

#prior distributions for previous breeding state: probability of breeding successfully
betasucav[3]~dnorm(0.0,1.0E06)
betasucav[2]~dnorm(0.0,0.001)
betasucav[1]~dnorm(0.0,0.001)

meansurage<-mean(surage[1:7893])
meanbreedage<-mean(breedage[1:6425])
meansucage<-mean(sucage[1:5541])

#variance-covariance matrix for individual random effects
R[1:3 , 1:3]~dwish(Omega[ , ],4)
mv[1:3, 1:3] <- inverse(R[ , ])
v1<-mv[1,1]
v2<-mv[2,2]
v3<-mv[3,3]
s1<-sqrt(v1)
s2<-sqrt(v2)
s3<-sqrt(v3)
v12<-mv[1,2]
v13<-mv[1,3]
v23<-mv[2,3]
rho12<- v12/(sqrt(v1)*sqrt(v2))
rho13<- v13/(sqrt(v1)*sqrt(v3))
rho23<- v23/(sqrt(v2)*sqrt(v3))

}

#####
# Example of initial values for 1 chain

```


ageftrep=age of first breeding corresponding to breed (numbering starts at 1; vector length
#=6425)
ageftsuc=age of first breeding corresponding to success (numbering starts at 1; vector length
#=5541)
avsur=previous breeding state corresponding to sur (numbering starts at 1; vector length
#=7893)
avrep=previous breeding state corresponding to breed (numbering starts at 1; vector length
#=6425)
avsuc=previous breeding state corresponding to success (numbering starts at 1; vector length
#=5541)