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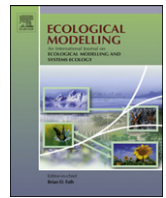
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Modelling environmental stochasticity in adult survival for a long-lived species

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ABSTRACT

Stochastic matrix population models are often used to help guide the management of animal populations. For a long-lived species, environmental stochasticity in adult survival will play an important role in determining outcomes from the model. One of the most common methods for modelling such stochasticity is to randomly select the value of adult survival for each year from a distribution with a specified mean and standard deviation. We consider four distributions that can provide realistic models for stochasticity in adult survival. For values of the mean and standard deviation that cover the range we would expect for long-lived species, all four distributions have similar shapes, with small differences in their skewness and kurtosis. This suggests that many of the outcomes from a population model will be insensitive to the choice of distribution, assuming that distribution provides a realistic model for environmental stochasticity in adult survival. For a generic age-structured model, the estimate of the long-run stochastic growth rate is almost identical for the four distributions, across this range of values for the mean and standard deviation. Model outcomes based on short-term projections, such as the probability of a decline over a 20-year period, are more sensitive to the choice of distribution.

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1. Introduction

Matrix models are often used to help guide the management of animal populations (Boyce, 1992; Beissinger and Westphal, 1998; Caswell, 2001). When there is environmental stochasticity (hereafter referred to simply as *stochasticity*) in one or more of the demographic parameters, use of a stochastic model will be preferable to use of a deterministic one (Shaffer, 1987; Soulé, 1987; Burgman et al., 1993; Caswell, 2001; Engen et al., 2001).

For the population model we consider later (Section 3), preliminary analysis suggested that the results obtained from incorporating stochasticity in one of the parameters (such as adult survival) would not depend greatly on the values of the other parameters. This implied that we could therefore focus on modelling stochasticity in adult survival alone, with all other parameters fixed, as this is the parameter for which a specified amount of stochasticity has the largest impact on the stochastic growth rate for a long-lived species (Tuljapurkar, 1982). Stochasticity in adult survival can be modelled in a number of ways, one of the most common methods being to randomly select the value of adult survival for each year from a statistical distribution (Fieberg and Ellner, 2001; Kaye and Pyke, 2003; Dias et al., 2008). The distribution will often be specified in terms of its mean (μ) and

standard deviation (σ). For long-lived species, these values might come from an analysis of mark-recapture data (Gould and Nichols, 1998; Burnham and White, 2002), or from fitting the population model directly to census and mark-recapture data (Buckland et al., 2004, 2007; Thomas et al., 2005). Whatever methods are used, estimation of σ can be prone to problems if there are only a few annual estimates and/or these are poorly estimated. In such cases σ may need to be arbitrarily specified, perhaps using information from other long-lived species (Breen et al., 2003).

However we determine appropriate values for μ and σ , there is some choice as to the form of the distribution to use to model the stochasticity. The purpose of this paper is to consider the extent to which the form of this distribution has an impact on the results from the population model. If two distributions have the same shape they will obviously provide the same results from the population model. If they have the same mean and standard deviation, any difference between the model results will be due to differences in their higher-order moments, particularly skewness and kurtosis (Slade and Levenson, 1984; Tuljapurkar, 1990; Wiener and Tuljapurkar, 1994). It is therefore of interest to compare the skewness and kurtosis of distributions that might provide realistic models of environmental stochasticity in adult survival.

Previous work in this area has focussed on distributions that were either similar or markedly different in shape (and therefore in higher-order moments), and the results reported seem to reflect this. Thus Fieberg and Ellner (2001) found that the choice of distribution had little effect on the results they obtained from a population model that incorporated stochasticity in all the parameters,

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and noted that this was not surprising as the distributions they considered were either symmetric or close to symmetric. Conversely, Slade and Levenson (1984) found that using two distributions with quite different shapes (symmetric or negatively skewed) to model stochasticity in juvenile survival had an effect on the results from their population model. Likewise, Nakaoka (1997) found that use of a truncated-normal or a lognormal distribution to model stochasticity in recruitment led to quite different results. Kaye and Pyke (2003) also found that distributions with quite different shapes could lead to different estimates of stochastic population growth rate and population viability.

We argue that any comparison between distributions should involve only those that have the ability to match the shape of the distribution of annual estimates of the relevant parameter, or a shape that is considered appropriate for the population. In the case of adult survival, Dias et al. (2008) suggest that a unimodal distribution will usually be appropriate, and that a J-shaped or U-shaped distribution may sometimes be considered. Although they have been used in the past, it is clear that a truncated distribution cannot provide a realistic model for stochasticity in a demographic parameter (Nakaoka, 1997; Wade, 1998; Higgins et al., 2000). In addition naïve use of truncation can lead to the distribution differing markedly from what was intended (Caswell, 2001; Fieberg and Ellner, 2001; Todd and Ng, 2001; Kaye and Pyke, 2003; Dias et al., 2008).

In comparing the effects of two distributions, it is also important to consider the type of outcome from the population model. A natural outcome to consider is the stochastic growth rate, defined as

$$\log \lambda_s = \lim_{t \rightarrow \infty} \frac{1}{t} \log N_t$$

where N_t is the population size in year t (Caswell, 2001). It is common to estimate $\log \lambda_s$ by calculating the mean annual growth rate over a suitably long period (T years), i.e. by

$$\frac{1}{T} \sum_{t=0}^{T-1} r_t$$

where $r_t = \log(N_{t+1}/N_t)$. Estimation of $\log \lambda_s$ therefore involves use of a sample of size T from the distribution for adult survival, where T is very large. If two distributions for adult survival have similar shapes, the two samples of values for adult survival will be similar, thereby leading to the two estimates of $\log \lambda_s$ being close. Another way of seeing this is to consider a standard approximation to $\log \lambda_s$ (Caswell, 2001, p. 398). For the population model we consider in Section 3, this approximation can be written as

$$\log \lambda_s \approx \log \lambda - \frac{1}{2} \left(\frac{\sigma}{5\lambda - 4\mu} \right)^2$$

where λ is the population growth rate for the corresponding deterministic model (i.e. with $\sigma = 0$). This result suggests that two distributions with the same values for μ and σ will lead to similar estimates of $\log \lambda_s$, any differences being related to the terms missing from this approximation, which involve higher-order moments such as skewness and kurtosis (Tuljapurkar, 1990; Wiener and Tuljapurkar, 1994).

An alternative type of outcome to consider is one based on short-term projections, such as the probability of a population decline over a 20-year period. This can be estimated by projecting the population for 20 years a large number of times and calculating the proportion of these replicate projections for which the population size declined. In this context, the “sample size” taken from the distribution for adult survival is relatively small for each projection, but the overall “sample size” will usually be large, due to the number of replicate projections used in the estimation.

Regardless of the type of model outcome considered, little is currently known about how close such outcomes might be for two realistic distributions for modelling stochasticity in adult survival for a long-lived species. In Section 2 we describe four such distributions, and compare their skewness and kurtosis over a range of values for μ and σ that are relevant to long-lived species. In Section 3 we compare the effect they have on the results from a generic population model for such a species. Section 4 contain the results and discussion.

2. Candidate distributions

As we have argued above, a realistic distribution for adult survival should allow one to specify a unimodal, J-shaped or U-shaped distribution (the latter corresponding to the case where we wish to use a distribution to model the occurrence of “catastrophic” years). In addition, it is clear that use of a truncated distribution is not appropriate. Dias et al. (2008) make a strong case for the beta distribution as the default choice for modelling stochasticity in any demographic parameter. This has the following probability density function (pdf) on the (0,1) interval:

$$f(s) = \frac{s^{\alpha-1}(1-s)^{\beta-1}}{B(\alpha, \beta)} \quad (0 < s < 1; \alpha, \beta > 0)$$

where α and β are the parameters and $B(\alpha, \beta)$ is the beta function (Johnson et al., 1994). There are many examples of this distribution being used to model stochasticity (e.g. Kendall, 1998; Grevstad, 1999). For the purposes of this paper, we consider the beta distribution as a benchmark against which the others are compared. A natural alternative to the beta distribution is the logit-normal distribution, as its use implies that adult survival has a normal distribution on the logit-scale, an assumption that is often made when analysing mark-recapture data, especially when modelling survival in terms of covariates (Newman, 2003). Using this distribution means that the survival rate S can be generated using $S = (1 + e^{-X})^{-1}$, where $X \sim N(\mu_X, \sigma_X^2)$, and the pdf for S is given by

$$f(s) = \frac{1}{(2\pi)^{1/2}s(1-s)\sigma_X} \exp\left(-\frac{(\log it(s) - \mu_X)^2}{2\sigma_X^2}\right) \quad (0 < s < 1; \sigma > 0)$$

A distribution that is closely related to the logit-normal is the probit-normal. Todd and Ng (2001) promoted use of this distribution in the case where one wants to incorporate cross-correlation amongst different demographic parameters. Recently, however, Dias et al. (2008) have shown that the beta distribution can also be used when there is a need to model such correlation, potentially obviating the need for the probit-normal. We include it here for the sake of completeness. The probit-normal is based on the assumption that survival will have a normal distribution on the probit-scale, i.e. the survival rate S can be generated using $S = \Phi(X)$, where $X \sim N(\mu_X, \sigma_X^2)$ and $\Phi(\cdot)$ is the cumulative distribution function for the standard normal distribution. The pdf for S is given by

$$f(s) = \frac{1}{\sigma_X \phi\left(\Phi^{-1}(s)\right)} \phi\left(\frac{\Phi^{-1}(s) - \mu_X}{\sigma_X}\right) \quad (0 < s < 1; \sigma_X > 0)$$

where $\phi(\cdot)$ is the pdf for the standard normal distribution. Finally, we consider a distribution that is sometimes used by fisheries modellers (e.g. Breen et al., 2003). We refer to it as the “lognormal-power distribution”. The survival rate S is generated using $S = \psi^{\exp(X)}$,

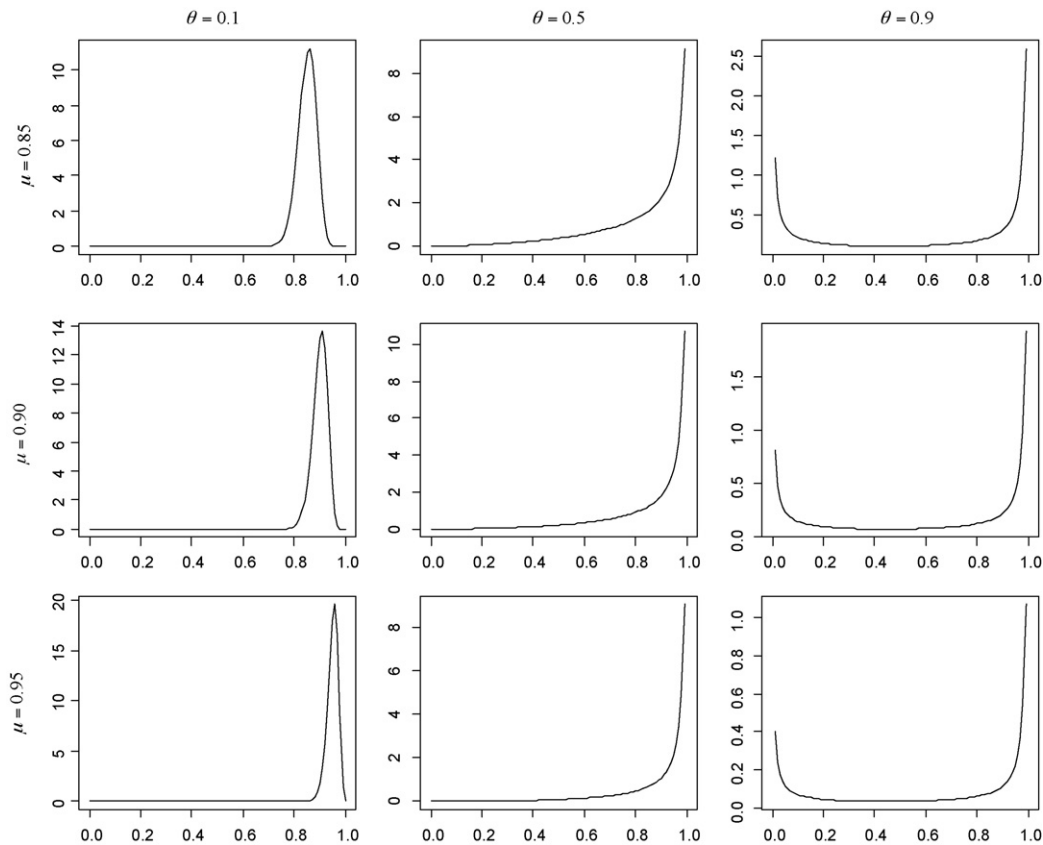


Fig. 1. The beta probability density function, for nine combinations of the mean (μ) and $\theta = \sigma / \sqrt{\mu(1-\mu)}$, where σ is the standard deviation.

where $X \sim N(0, \sigma_X^2)$ and $0 < \psi < 1$, and the pdf for S is given by

$$f(s) = \frac{1}{(2\pi)^{1/2} s \ln(s^{-1}) \sigma_X} \exp\left(\frac{-1}{2\sigma_X^2} \left(\ln\left(\frac{\ln(s)}{\ln(\psi)}\right)\right)^2\right)$$

($0 < s < 1$; $\sigma_X > 0$)

Suppose we estimate μ and σ in a preliminary analysis, i.e. we do not fit a population model directly to data (Section 1). Use of the beta distribution then has the advantage that we can specify the parameters directly in terms of μ and σ :

$$\alpha = \mu \left(\frac{\mu(1-\mu)}{\sigma^2} - 1 \right), \quad \beta = \frac{(1-\mu)\alpha}{\mu}$$

For the logit-normal, probit-normal and lognormal-power, there are no exact expressions for μ and σ (nor for any higher-order moments). Note that it might sometimes be convenient to specify μ and σ on the logit-scale, in which case calculation of the parameters for the logit-normal would be exact, while those for the beta would not. We used the following numerical procedure to calculate the parameter values, given target values (μ_T and σ_T) for μ and σ :

- (1) Specify initial values for the parameters of the distribution (see below)
- (2) Randomly select 10^6 observations from the specified distribution, and calculate their mean (m) and standard deviation (S)
- (3) Calculate the sum of the absolute relative errors in μ and σ , i.e.

$$e = \left| \frac{m - \mu_T}{\mu_T} \right| + \left| \frac{S - \sigma_T}{\sigma_T} \right|$$

- (4) Repeat Steps 2 and 3 until e is suitably small, using an optimisation algorithm to vary the values of μ and σ .

All calculations were carried out in R Version 2.8.0 (2008), and we implemented the procedure using the *optim* command. This command makes use of the Nelder–Mead simplex method for optimisation (Nelder and Mead, 1965). In order to speed up convergence, we used the same random seed each time Step 2 was invoked. We used Taylor series approximations to specify the initial values for the parameters (Samaranayaka, 2005). For each distribution and for each pair of values (μ_T, σ_T), we replicated the procedure ten times and used the mean estimate for each parameter.

3. Comparison of model outcomes

We considered an age-classified population model that is applicable to many long-lived species. It is based on a pre-breeding census, and age at first reproduction is a for all individuals, i.e. there are $a - 1$ juvenile stages, and one adult stage. Adults that survive remain in the final stage, and both fertility and adult survival are assumed to be independent of age. Preliminary analysis suggested that our results would be robust to the choice of a , which we arbitrarily set to 5 years. All parameters other than adult survival were assumed to be constant. The projection matrix associated with this model is given by

$$\begin{bmatrix} 0 & 0 & 0 & 0 & f s_0 \\ s_1 & 0 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 & 0 \\ 0 & 0 & s_3 & 0 & 0 \\ 0 & 0 & 0 & s_4 & s_A(t) \end{bmatrix}$$

Table 1
Estimates of the probability of a population decline over 20, 50 or 100 years for a population model, using four distributions to model stochasticity in adult survival. Each estimate has a standard error of less than 0.002.

μ	θ	Beta	Logit-normal	Probit-normal	Lognormal-power
20 years					
0.85	0.1	1.000	1.000	1.000	1.000
0.85	0.5	0.972	0.972	0.973	0.974
0.85	0.9	0.915	0.914	0.916	0.917
0.90	0.1	0.987	0.988	0.987	0.988
0.90	0.5	0.711	0.703	0.706	0.690
0.90	0.9	0.766	0.766	0.765	0.773
0.95	0.1	0.000	0.000	0.000	0.000
0.95	0.5	0.144	0.158	0.151	0.182
0.95	0.9	0.453	0.454	0.457	0.478
50 years					
0.85	0.1	1.000	1.000	1.000	1.000
0.85	0.5	0.999	0.999	0.999	0.999
0.85	0.9	0.984	0.984	0.984	0.984
0.90	0.1	1.000	1.000	1.000	1.000
0.90	0.5	0.838	0.832	0.835	0.827
0.90	0.9	0.860	0.861	0.862	0.863
0.95	0.1	0.000	0.000	0.000	0.000
0.95	0.5	0.059	0.071	0.068	0.104
0.95	0.9	0.374	0.378	0.377	0.380
100 years					
0.85	0.1	1.000	1.000	1.000	1.000
0.85	0.5	1.000	1.000	1.000	1.000
0.85	0.9	0.999	0.999	0.999	0.999
0.90	0.1	1.000	1.000	1.000	1.000
0.90	0.5	0.924	0.923	0.923	0.919
0.90	0.9	0.943	0.945	0.942	0.943
0.95	0.1	0.000	0.000	0.000	0.000
0.95	0.5	0.016	0.024	0.020	0.045
0.95	0.9	0.351	0.356	0.357	0.364

where f is the reproductive rate (newborns per adult), S_i is the survival rate from age i to $i+1$ ($i=0, 1, 2, 3, 4$), and $S_A(t)$ is the adult survival rate from year t to $t+1$ ($t=0, 1, 2, \dots$).

The preliminary analysis referred to earlier (Section 1) suggested that our results would be robust to the choices of f and S_i ($i=0, 1, 2, 3, 4$), so we arbitrarily set $f=0.3$, $S_0=0.7$ and $S_i=0.8$ ($i=1, 2, 3, 4$). We considered three values for the mean of the adult survival rate (μ), covering the range we would expect for long-lived species: 0.85, 0.90 and 0.95. In choosing suitable values for the standard deviation of the survival rate (σ), we used the fact that it cannot exceed $\sqrt{\mu(1-\mu)}$ (Dias et al., 2008). Thus we set $\sigma = \theta \sqrt{\mu(1-\mu)}$ with $\theta=0.1, 0.5$ or 0.9 , corresponding to low, medium and high levels of stochasticity, respectively. These three values of θ lead to the beta distribution being unimodal, “J-shaped” and “U-shaped”, respectively.

We considered two types of outcome from the population model. The first was the long-run stochastic growth rate, $\log \lambda_s$, defined in Section 1. The standard error of the estimate of $\log \lambda_s$ was calculated as $\sqrt{V/T}$, where V is the sample variance of the r_t ($t=0, 1, \dots, T-1$) (Caswell, 2001). We used $T=10^6$, as this led to the standard error being less than 0.0001 for each of the scenarios we considered. We arbitrarily set $N_0=1$, and the initial age distribution was set equal to the stable age distribution for the corresponding deterministic model. The second type of outcome we considered was the probability of a decline in population size in the short-term, i.e. after 20, 50 and 100 years. We estimated these probabilities by repeatedly projecting the model over the relevant time period, using the same initial conditions as for estimation of the long-run growth rate. We chose to use 10^5 replicates for this purpose, in order to ensure that the binomial standard error of the estimated probability would be less than 0.002.

4. Results and conclusions

For the range of values considered for μ and θ , the four distributions have similar shapes. For all four distributions, $\theta=0.1, 0.5$ and 0.9 correspond to unimodal, “J-shaped” and “U-shaped” distributions, respectively. Fig. 1 shows the beta distribution for each combination of μ and θ : the other three distributions are close enough in shape to the beta that we have not plotted them, for ease of presentation. The degree of similarity across the four distributions can be gauged by considering the relative absolute difference between the first four moments of the beta distribution and those for the other three distributions, using the samples of size 10^6 that were generated in order to estimate $\log \lambda_s$: across the range of values considered for μ and θ , these relative differences are all less than 0.0005.

For each of the nine combinations of μ and θ , the estimates of the long-run stochastic growth rate ($\log \lambda_s$) were identical for the four distributions (to three decimal places). As predicted, this estimate is thus extremely robust to the choice of distribution. The differences between the distributions might be explained by differences in their higher-order moments, but could also be due to numerical differences in their means and standard deviations, as a result of the numerical procedure used to estimate the parameters for the logit-normal, probit-normal and lognormal-power distributions. A general linear model for the estimate of $\log \lambda_s$ in terms of the realised mean and standard deviation of the corresponding distribution (i.e. from the sample of size 10^6) fitted better than one involving all of the first four moments (the difference in AIC being 2.25). This implies that differences in the mean and standard deviation, caused by errors in estimating the parameters for the logit-normal, probit-normal and lognormal-power, were more influential than differences in skewness and kurtosis (c.f. Tuljapurkar, 1990; Wiener and Tuljapurkar, 1994).

Estimates of the probability of population decline over 20, 50 and 100 years are given in Table 1. These are also fairly robust to the choice of distribution, with the estimates for the logit-normal, probit-normal and lognormal-power all being within five percentage points of the corresponding estimate for the beta distribution. The largest differences are for the lognormal-power, especially when the distribution is J-shaped or U-shaped ($\theta=0.5$ or 0.9). If the distribution is unimodal ($\theta=0.1$) the differences are negligible.

Overall, our results suggest the outcomes from a stochastic matrix population model for a long-lived species will be robust to the choice of distribution used to represent stochasticity in adult survival, as long as that distribution provides a realistic model for such stochasticity. As adult survival is the parameter for which a specified amount of stochasticity has the largest impact on the stochastic growth rate, we would expect similar results for the survival rates of other age classes.

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