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Estimating the variance of survival rates and fecundities

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Abstract

Estimating the risk of extinction or decline requires estimates of the variability in vital rates, such as survival and fecundity. This paper describes a method for estimating variance of survivals and fecundities from census data. The method involves calculating an estimate of the variance in survival and fecundity due to demographic stochasticity and subtracting this estimate from an estimate of total variance. The method is demonstrated by applying it to the data set on acorn woodpeckers by Stacey & Taper (1992), and tested in a series of simulations. The results show that the method can estimate the environmental variance with no bias. The main advantages of this method are its simplicity, its independence of the underlying distribution, and its applicability to estimating the variance of fecundity as well as of survival.

INTRODUCTION

Estimating the risk of extinction or decline of a population in a population viability analysis often requires estimates of the variability in vital rates, such as survival and fecundity. A common type of data used in such estimates consists of regular censuses of a population at which individuals in different age classes or stages are counted. Such data are used to calculate survival rates and fecundities. Repeated estimates of these rates in time allow estimating the temporal variance of these rates. However, this observed variance includes variance due to demographic stochasticity and measurement error. These components must be removed from the observed variance to estimate the variance due to environmental stochasticity. Otherwise, the variances, and hence risks of decline and extinction, may be overestimated.

Several previous studies have focused on the related problem of removing sampling variance from estimates of abundance (e.g. Link & Nichols, 1994; McArdle & Gaston, 1995), rather than survival rate or fecundity. Burnham *et al.* (1987), Gould and Nichols (1998) and White, Franklin & Shenk (2002) addressed the problem of removing sampling variance from survival rate estimates in analysis of data from marked individuals. However, these methods are not directly applicable to data from censuses, in which organisms are not individually marked or followed.

The only study that directly addressed this issue for census data was by Kendall (1998). The method for estimating environmental variance of survival rates described by Kendall (1998) involved fitting a maximum likelihood function that assumed an underlying distribution of environmental stochasticity (e.g. beta distribution). In this paper, an alternative, simpler method is described that is applicable to both survival rates and fecundities.

The method is simply to subtract an estimate of variance due to demographic stochasticity from the total observed variance. A similar approach was mentioned in an unpublished report by Mirande, Lacy & Seal (1991). In this paper, I extend this method by applying it to both survivals and fecundities, and by basing it on weighted statistics. I validate the method by a series of simulations, and demonstrate its use with an example based on data from Stacey & Taper (1992).

METHODS

The variance due to demographic stochasticity in survival is based on the variance of the binomial distribution, which is

$$p_t\,(1 - p_t)\,N_t$$

where p_t is the survival rate and N_t is the number of individuals at time step t. This formula gives the variance of the number of survivors. The variance of the survival rate is*

$$p_t\,(1 - p_t)\,N_t\;/\;N_t^2 = p_t\,(1 - p_t)\;/\;N_t \qquad (1)$$

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*The variance of the product of a constant c and a random variable x, $\mathrm{var}(c\,x) = c^2\,\mathrm{var}(x)$

Because N_t and p_t are different at each time step, the demographic variance can be calculated for each time step and averaged over the time steps:

$$\frac{\sum_{t=1}^{Y} p_t(1-p_t)/N_t}{Y} \tag{2}$$

where Y is the number of years (time steps). A weighted average of demographic variance can be calculated by

$$\frac{\sum_{t=1}^{Y} p_t(1-p_t)}{\sum_{t=1}^{Y} N_t} \tag{3}$$

The average demographic variance is then subtracted from the total observed variance to obtain an estimate of the environmental variance.

This method can be directly applied to fecundities if fecundities range between 0 and 1 (i.e. the maximum number of offspring per time step is 1). For other cases, the method can be generalized by estimating demographic variance based on Poisson (or another discrete probability distribution) rather than binomial variance. If the number of offspring follows a Poisson distribution, its variance will be the same as the mean, i.e. $f_t\, N_t$, where f_t is fecundity (e.g. number of surviving daughters per female) at time step t. Thus, the demographic variance of f can be estimated as (f_t / N_t) for each time step, and averaged over the time steps:

$$\frac{\sum_{t=1}^{Y} f_t/N_t}{Y} \tag{4}$$

A weighted average of demographic variance can be calculated as

$$\frac{\sum_{t=1}^{Y} f_t}{\sum_{t=1}^{Y} N_t} \tag{5}$$

To test the method, I created simulated time series of abundances using RAMAS Metapop (Akçakaya, 2002). The program first samples survival rate and fecundity from random distributions, and then simulates demographic stochasticity by sampling the number of survivors from a binomial distribution and number of offspring from a Poisson distribution. In the simulations, survival rate had a mean of 0.2, 0.5 or 0.8, and a standard deviation of 0.05, 0.10 or 0.15. The survival distributions were normal, lognormal, or mirrored lognormal (i.e. lognormally distributed mortality). These nine combinations of mean and standard deviation correspond to coefficients of variation (CV) ranging from 6% to 75%. Fecundity had a mean of 2.0 and a CV of 20%, and was normally distributed. The length of time series ranged from 10 to 50. The stage abundance (on which the variance estimates are based) ranged from 50 to 200 at the start of the simulation. For an abundance of 200 individuals, the proportion of demographic variance ranges from 3% to 33% of the total variance, with the means and standard deviations used in the simulations. The abundance varied during the 10-to-50 time step stochastic simulations, ranging from nought to several thousands, with a median of about 113. The time steps in which the stage abundance was 0 were omitted from the calculation of variances (because the vital rate would be undefined).

The abundances predicted by the simulations were output to text files, and then analyzed with a separate program. The analysis involved using abundance data to calculate the total variance and to estimate the demographic variance using equations (2) and (4). The difference was recorded as an estimate of environmental variance for each replication. The arithmetic average of environmental variance estimates was then compared to the variance used in the simulations. Thus, the results consisted of estimated environmental variance of survival and fecundity for each of the 10,000 simulated time series. The distribution of these estimated variances was summarized with its mean, quartiles and 90% confidence interval. This was repeated for each different length and input mean and standard deviation of survival.

Kendall (1998) demonstrated his method using the data on juvenile and adult acorn woodpeckers from Stacey & Taper (1992). This is an ideal data set for this purpose because of the wide ranges of sample sizes (1 to 59) and survival rates (0 to over 0.6) for juveniles. To demonstrate the method proposed here, and to compare it to Kendall's method, I applied it to the same data set.

RESULTS

The results of the simulations showed that the estimated environmental variance was close to the true variance (Table 1). There was no bias in the estimates, in contrast to the method proposed by Kendall (1998). The precision of the estimated environmental variance was a function of the length of the time series (error bars in

Table 1. Estimated environmental variance (average, and 25th and 75th percentiles) in survival rate, from time series created by simulations with means ranging from 0.2 to 0.8, and standard deviations ranging from 0.05 to 0.15. Input distribution variance is the realized variance of the sampled survival rates. Estimated variance is the environmental variance calculated as the difference of total and demographic variance.

Input distribution				Estimated variance		
Type*	Mean	SD	Variance	Average	25th percentile	75th percentile
L	0.2	0.050	0.0025	0.0025	0.0018	0.0031
L	0.2	0.101	0.0102	0.0102	0.0067	0.0125
L	0.2	0.150	0.0224	0.0225	0.0136	0.0296
N	0.5	0.050	0.0025	0.0025	0.0018	0.0031
N	0.5	0.100	0.0100	0.0100	0.0078	0.0118
N	0.5	0.150	0.0225	0.0224	0.0181	0.0262
ML	0.8	0.050	0.0025	0.0025	0.0018	0.0031
ML	0.8	0.101	0.0101	0.0101	0.0067	0.0123
ML	0.8	0.150	0.0224	0.0224	0.0135	0.0293

* L: lognormal, N: normal; ML: mirrored lognormal (i.e. lognormally distributed mortality).

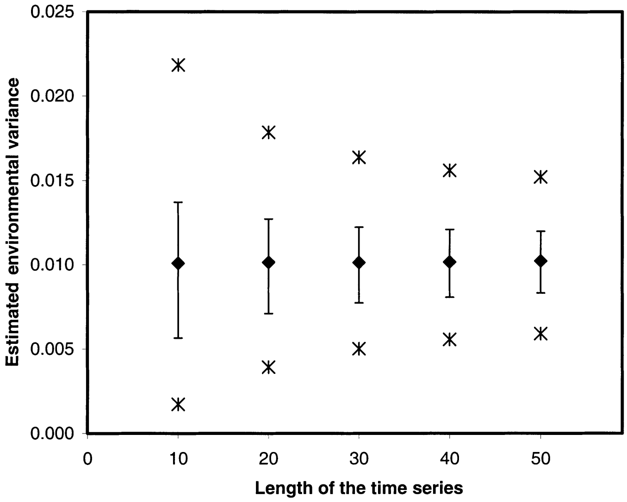

Fig. 1. Estimated environmental variance of survival rate (diamonds), with quartiles (error bars) and 90% confidence interval (stars) for 10,000 time series of lengths from 10 to 50. True environmental variance was 0.01.

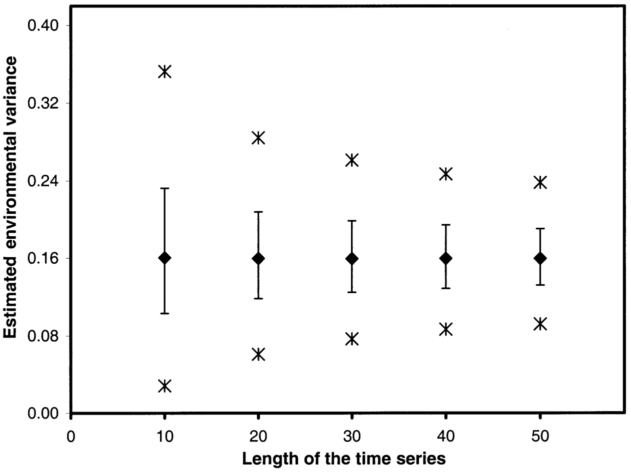

Fig. 2. Estimated environmental variance of fecundity (diamonds), with quartiles (error bars) and 90% confidence interval (stars) for 10,000 time series of lengths from 10 to 50. True environmental variance was 0.16.

Fig. 1). There was a similar pattern for fecundities (Fig. 2). The survival distributions were truncated to be between 0 and 1, and fecundity distributions were truncated at 0. Less than 0.4% of any distribution was truncated, and the truncations did not affect the results, because the true variances given in Table 1 are the realized variances of the (truncated) distributions.

The proposed method is demonstrated by applying it to the data on juvenile and adult acorn woodpeckers from Stacey & Taper (1992). The weighted average of survival rates for juvenile acorn woodpeckers is 0.4007 (115/287; see Table 2). Using the method described above (equation 3), the demographic variance of juvenile survival is estimated as 0.00608 (1.7453/287). This estimate is subtracted from total (weighted) variance of 0.01897 (the method for calculating a weighted total variance is given by Kendall (1998, eq. 1)). The difference, 0.01289, is an estimate of the environmental variance (Table 3).

DISCUSSION

The method gives results similar to those of Kendall (1998; see Table 3); however, there was no bias in the estimated standard deviations or variances (Table 1; Figs 1 & 2). The method appears to be an unbiased estimator of environmental variance for a large range of distributions (with CVs ranging from 6% to 75%), with demographic variance accounting for 3% to 33% of the total variance (at the initial time step), and with abundances ranging from one to several thousands. When abundance is very high, demographic stochasticity becomes less important relative to environmental stochasticity. However, in the simulations, the median abundance was only slightly over 100.

Table 2. Number of individuals (*N*), and number surviving to the following spring (*m*) of juvenile and adult acorn woodpeckers, as used by Kendall (1998), based on Stacey & Taper (1992). Survival rate ($p = m/N$) is used to calculate the sum of $p(1-p)$, which is used to estimate variance due to environmental stochasticity (see text).

	Juveniles				Adults			
Year	*N*	*m*	*p*	*p(1 – p)*	*N*	*m*	*p*	*p(1 – p)*
1975	59	33	0.559	0.2465	46	24	0.522	0.2495
1976	22	14	0.636	0.2314	46	31	0.674	0.2198
1977	43	13	0.302	0.2109	40	28	0.700	0.2100
1978	42	7	0.405	0.2409	51	19	0.373	0.2338
1979	1	0	0.000	0.0000	52	28	0.538	0.2485
1980	48	18	0.375	0.2344	32	22	0.688	0.2148
1981	39	7	0.179	0.1473	46	30	0.652	0.2268
1982	8	2	0.250	0.1875	49	24	0.490	0.2499
1983	25	11	0.440	0.2464	35	21	0.600	0.2400
Total	287	115		1.7453	397	227		2.0931

Table 3. Calculation of the variance due to environmental stochasticity, based on data in Table 1.

	Juveniles	Adults
Average survival (weighted)	0.40070	0.57180
Total variance of survival (weighted)	0.01897	0.01113
Demographic variance (weighted)	0.00608	0.00527
Environmental variance	0.01289	0.00586
Environmental variance (Kendall, 1998)	0.01210	0.00560

The reason this method works is that demographic and environmental stochasticity are, by definition, statistically independent, although the magnitude of demographic stochasticity depends on abundance (*N*), which is affected by both demographic and environmental stochasticity. The fact that they are independent is demonstrated by the lack of bias. If demographic and environmental stochasticity were dependent, the estimated variance would have a strong positive or negative bias, depending on whether the correlation is negative or positive, respectively.

The confidence intervals of the estimated environmental variance (Figs 1 & 2) are wider than (but generally comparable to) the confidence interval for a sample variance (Sokal & Rohlf 1981: 155), because the estimated variance is not a sample variance, but the difference between a sample variance and a theoretical (calculated) variance. The confidence intervals of the estimated environmental variance can be either calculated based on the assumption of the independence of environmental and demographic variances, or estimated by a resampling method (such as jack-knife or bootstrap).

Both the total variance and the demographic variance can be calculated using abundance (sample size) as weights (equations 3 and 5), or without weights (equations 2 and 4). As Kendall (1998) points out, different ways of calculating variance reflect different assumptions about the reliability of individual estimates. In the simulations, it seems reasonable to assume that all estimates are equally reliable, because there is no variation of sampling effort or observer quality. Thus, in analyzing simulation results, I used non-weighted methods (equations 2 and 4). In demonstrating the method using the acorn woodpecker data from Stacey & Taper (1992), I used weighted methods (equations 3 and 5), mainly because these methods are comparable to Kendall's. In general, weighted methods should be used when the variation in sample size results from variation in sampling effort.

The main advantage of this method is its simplicity. The calculations can be easily made with a calculator or spreadsheet software. Other advantages are that the equations are the same regardless of the underlying distribution of environmentally induced fluctuations, and that the same approach can be used to estimate environmental variance of fecundity.

It is not easy to make generalizations about when it is important to remove demographic or sampling variance from observed variance, because this depends on many factors, including the proportion of demographic variance and various aspects of the life history. The proportion of demographic variance increases with decreasing abundances and decreasing environmental variability. Demographic variance can be crudely estimated based on average abundance and average survival rate (equation 1), and compared to the observed variance of survival rates. If this crude estimate is a substantial proportion of total variance, then failure to remove demographic variance may lead to overestimation of variability.

What proportion of variance can be considered "substantial" depends on various other aspects of the model in which the variance estimate is to be used. In general, even a small decrease in variance may make a substantial difference in the risk estimates in models with no or weak density dependence, especially if the effects of habitat loss or catastrophes are limited. Once the demographic variance is removed, the environmental variance will accurately reflect the fluctuations in vital rates. However, in this case it is important that the model incorporates demographic stochasticity; otherwise extinction or decline risks can be underestimated (Burgman *et al.*, 1993; McCarthy *et al.*, 1994).

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