

Reproductive Value and the Stochastic Demography of Age-Structured Populations

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Submitted January 12, 2009; Accepted August 7, 2009; Electronically published October 20, 2009

ABSTRACT: The dynamics of an age-structured population in a fluctuating environment is determined by the stochastic individual contributions from annual survival and fecundity to the total reproductive value of the population the next year. All parameters required to describe the population dynamics are simple properties of the distribution of these individual demographic contributions, which we call individual reproductive value. The asymptotic population growth rate in the average environment and the demographic and environmental variances are respectively the mean individual reproductive value over individuals through time and the variance within and between years. Our approach leads to an intuitive understanding of demographic and environmental variances in age-structured populations and their decomposition into additive age-specific components due to survival and reproduction. We show how to apply this approach to estimate the demographic and environmental variances and their components. The estimates are based on yearly random samples of individual vital rates and require no information about the total population size.

Keywords: individual reproductive value, age structure, demographic stochasticity, environmental stochasticity, reproductive value, age-dependent stochastic demography.

Introduction

Classical demographic models assuming no density regulation and a constant environment (Lotka 1924; Leslie 1945, 1948) revealed that age dependence in life histories causes multiple time delays in the population dynamics and transient fluctuations in age structure (Caswell 2001). To overcome this problem, Fisher (1930) introduced the concept of reproductive value, describing the extent to which individuals of different age contribute to future pop-

ulation growth. Fisher showed that for a large population in a constant environment, the total reproductive value, defined as the sum of the reproductive value of all individuals in the population, increases at a rate equal to the population's asymptotic growth rate, regardless of whether the population is in stable age distribution. By considering the change in total reproductive value one can obtain estimates of the population growth rate that are not biased by transient fluctuations in age structure (Crow and Kimura 1970, pp. 20–22; Charlesworth 1994, pp. 39–40).

Two sources of stochasticity, not included in Fisher's (1930) deterministic model, create continual fluctuations in population size and age structure. In a finite population, demographic stochasticity arises from random variation in individual vital rates, operating independently among individuals (Lande et al. 2003). Demographic stochasticity was included in age-dependent projection models by Pollard (1966, 1973) and Goodman (1967), who computed moments of future population sizes and probability of extinction using a projection matrix for expected population size as well as covariances. Environmental stochasticity affects the whole population or age class in the same or similar fashion (Lande et al. 2003). Expressions for the long-run growth rate and environmental variance σ_e^2 in large age-structured populations were first derived by Cohen (1977, 1979), Tuljapurkar and Orzack (1980), and Tuljapurkar (1982, 1989), who assumed that the projection matrices do not depend on population size and that the population is large enough to neglect demographic stochasticity. Lande and Orzack (1988) showed that an accurate diffusion approximation for the total size of a large age-structured population could be obtained by using the long-run growth rate and the environmental variance, and this was extended to include demographic stochasticity in a small population by Engen et al. (2005).

Stochasticity in age-structured populations may affect

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the vital rates of age-specific survival and reproduction of all age classes (Gaillard and Yoccoz 2003). Nevertheless, Engen et al. (2005) showed that the stochasticity can be decomposed into environmental and demographic components, as in the case of no age structure. Assuming density-independent population dynamics and no temporal autocorrelation in vital rates, the stochastic dynamics of total population size or total reproductive value can be accurately described using only three parameters, the long-run growth rate and the environmental and demographic variances. The environmental and demographic variances are additive components of the variance in annual change in the total reproductive value of the population (Engen et al. 2007). Time lags due to age structure create autocorrelation in population size and age structure, even when the environment has no autocorrelation. In contrast, the noise in the total reproductive value is white, with no temporal autocorrelations to the first order, explaining the success of the diffusion approximation (Engen et al. 2005) in describing the dynamics of age-structured populations. If the population attains the stable age distribution given by the mean projection matrix, then the total reproductive value equals exactly the total population size. Engen et al. (2007) showed that the difference between the population size and the total reproductive value is a process fluctuating around zero with short memory and a return time to equilibrium on the order of one generation. Consequently, information about future population sizes is contained solely in the properties of the stochastic process describing the total reproductive value. Therefore, the three parameters expressing this process contain all information about future population size and time to extinction that can possibly be obtained at a given time. Decompositions of the variances will further give information about the importance of different stochastic components of vital rates in determining future population sizes.

The purpose of this article is to develop a general theory for age-structured populations in a fluctuating environment by analyzing the contribution from each individual to the total reproductive value in the population the next year, which we henceforth call individual reproductive value. We deal only with the use of reproductive value to analyze the demography of an age-structured population, not its genetic variation or evolution (Taylor 1990; Grafen 2006; Engen et al. 2009). We show how the environmental and demographic variances can be partitioned into additive components due to survival and fecundity in each age class, giving a simple intuitive representation of variance components in age-structured populations. This enables construction of new estimators of demographic and environmental variances and their components from individual-based demographic data obtained from samples of known-aged individuals with observed survival and re-

production. Previously, no theory has been able to estimate the environmental variance in age-structured populations without having a time series of the total population size as well as the size of each age class (Engen et al. 2005, 2007). Hence, our theory, combined with well-known diffusion approximation (Lande et al. 2003), provides a new method for analyzing extinction and predicting future sizes of age-structured populations.

Preliminary Population Model without Age Structure

If all females become adults after 1 year, with subsequent annual survival and reproduction independent of age, then in the next year the total number of females in the population is simply the sum of all individual contributions, W (Engen et al. 1998). The individual contribution of each female is the number of her female offspring that survive to age 1, plus 1 if she survives to the next year (Sæther et al. 1998b). The annual change in population size is consequently $\Delta N = \sum W - N$. In this preliminary model the environmental and demographic variances are defined by conditioning on the environment, Z :

$$\begin{aligned}\text{Var}(W) &= E \text{Var}(W|Z) + \text{Var} E(W|Z) \\ &= \sigma_d^2 + \sigma_e^2\end{aligned}$$

(Engen et al. 1998). The demographic variance $\sigma_d^2 = E \text{Var}(W|Z)$ is the mean through time of the variance of individual contributions within years, while the environmental variance $\sigma_e^2 = \text{Var} E(W|Z)$ is the variance through time of the mean individual contribution within years. Hence, the total variance in individual contribution is partitioned into two additive components, the demographic and environmental variances. Adding all individual contributions together and subtracting the previous population size gives the total yearly change in population size with expectation $E(\Delta N|N) = NEW - N = (\lambda - 1)N$, where $\lambda = EW$ is the mean individual contribution in a particular year, and variance $\text{Var}(\Delta N|N) = \sigma_d^2 N + \sigma_e^2 N^2$ (see Engen et al. 1998 for details).

Age-Structured Model

Consider an age-structured model with stochastic projection matrix L so that the population vector the next year is $n + \Delta n = Ln$. Using superscript T for the transpose of a vector, $n = (n_1, n_2, \dots, n_k)^T$ is a column vector of number of individuals in the different age classes. We assume prebreeding census so that the first row of L shows the fecundities including first-year survival, while the subdiagonal defines the survivals of age classes 1 to $k - 1$. Let the projection matrix have expectation $l = EL$ and define

λ as the real dominant eigenvalue of l , with right and left eigenvectors u (column vector) and v (row vector) defined by $lu = \lambda u$ and $vl = \lambda v$. If these eigenvectors are scaled using $\sum u_i = 1$ and $vu = \sum u_i v_i = 1$, then u is the stable age distribution for the deterministic model defined by l , while the components of v are the reproductive values for the different age classes (Caswell 1978). The total reproductive value of the population is the sum of reproductive values of all individuals, that is, $V = vn = \sum n_i v_i$. In a constant environment with a population large enough to ignore demographic stochasticity, the total reproductive value grows at a constant geometric rate λ , regardless of whether the population deviates from the stable age distribution, because $V + \Delta V = v(n + \Delta n) = vln = \lambda vn = \lambda V$ (Fisher 1930; Crow and Kimura 1970; Charlesworth 1994). The reproductive value of any subpopulation then also grows at the same geometric rate in a constant environment.

Engen et al. (2007) showed that in a fluctuating environment, the stochastic process V fluctuates around the total population size $N = \sum n_i$ and to first order (for small noise) has no temporal autocorrelation. If at some moment the population has exactly the same age distribution as the deterministic model, that is, $n_i = Nu_i$, then the reproductive value $V = \sum n_i v_i = \sum Nu_i v_i$ equals the population size N because $\sum u_i v_i = 1$. The variance in the reproductive value process can be split into environmental and demographic components as in the case of no age structure:

$$\begin{aligned} \text{Var}(\Delta V|V) &\approx \sigma_c^2 N^2 + \sigma_d^2 N \\ &\approx \sigma_c^2 V^2 + \sigma_d^2 V. \end{aligned} \quad (1)$$

The environmental and demographic variances σ_c^2 and σ_d^2 are given by the distribution of vital rates within and between years for the different age classes and by the dominant eigenvectors of the mean matrix (Engen et al. 2007). For statistical analysis of population dynamics it is usually preferable to work on the log scale (Cohen 1977, 1979; Tuljapurkar 1982; Lande et al. 2003). Then, writing $V + \Delta V = \lambda V + \varepsilon$, we find that $\Delta \ln(V) = \ln \lambda + \ln[1 + \varepsilon/(\lambda V)] \approx \ln \lambda + \varepsilon/(\lambda V)$, giving the first-order approximation

$$\text{Var}(\Delta \ln V|V) \approx \frac{\sigma_c^2}{\lambda^2} + \frac{\sigma_d^2}{\lambda^2} V^{-1}.$$

Here, to make the notation as simple as possible, we choose to derive the results on the absolute scale and to define the variances on this scale. However, it follows from the above derivation that all variances should be divided by λ^2 when applied on the log scale (Lande et al. 2003).

The general derivation of the above results was given

by Engen et al. (2005, 2007). Our first goal is now to demonstrate that the decomposition given by equation (1) can be simplified using statistics of individual reproductive value. We first consider separately models with only demographic or only environmental noise before we treat the general model in which both sources of stochasticity act together.

Demographic Stochasticity Only

Consider an individual in age class i with reproductive value v_i and let W_i be its contribution to the total reproductive value of the population the next year, which we call individual reproductive value. Then $EW_i = \lambda v_i$ because, as mentioned above, any subpopulation has geometric growth in reproductive value with multiplicative rate λ in the deterministic model. The mean over all individuals in the population is, however, $E\bar{W} = \lambda \bar{v} = \lambda \sum u_i v_i = \lambda$. Notice that individual reproductive value is a stochastic variable defined for each individual at each stage. The distribution of W_i may differ between stages i but is assumed to be the same for individuals in the same stage.

We let J_i be the indicator of survival for this individual in age class i so that $J_i = 1$ if the individual survives and $J_i = 0$ if it dies. Writing B_i for the number of offspring it produces, the annual contribution from a single individual to the total reproductive value the next year is

$$W_i = J_i v_{i+1} + B_i v_1. \quad (2)$$

Equation (2) defines a decomposition of individual reproductive value into additive components $J_i v_{i+1}$ due to individual survival and $B_i v_1$ due to individual fecundity and offspring survival to age 1. If estimates of the mean vital rates defining the expected projection matrix l are available, then the vector v of reproductive values can be computed, and the annual reproductive values can be computed for individuals of age i from their vital rates J_i and B_i . We can also consider a simple stage-structured model in which individuals below age k are classified by their age and all individuals of age $\geq k$ are included in a terminal stage k . Individuals in stage k thus remain in this stage if they survive, so the above equation is also valid for $i = k$ provided that we define $v_{k+1} = v_k$. Writing p_i and $s_{di} = p_i(1 - p_i)$ for the mean and variance of J_i and f_{di} for the variance of B_i , we see that the variance of reproductive value next year produced by an individual of age i in the case of no environmental stochasticity is $\sigma_{di}^2 = \text{Var}(W_i) = s_{di} v_{i+1}^2 + f_{di} v_1^2 + 2c_{di} v_{i+1} v_1$, where $c_{di} = \text{Cov}(J_i, B_i)$. Since there are n_i individuals in class i and assuming that all contributions are independent among individuals when there is no environmental stochasticity,

the variance of the total reproductive value the next year is $\sum n_i \text{Var}(W_i)$. Finally, approximating n_i using the stable age distribution, we have $n_i \approx Nu_i$, and the variance in the reproductive value the next year, assuming that contributions from different individuals are uncorrelated, is

$$\begin{aligned} \text{Var}(V + \Delta V|V) &\approx N \sum_{i=1}^k u_i (s_{di} v_{i+1}^2 + f_{di} v_1^2 + 2c_{di} v_{i+1} v_1) \\ &= N \sum u_i \sigma_{di}^2. \end{aligned} \tag{3}$$

This variance is approximately proportional to the population size $N \approx V$, and the total demographic variance is accordingly (cf. eq. [1])

$$\sigma_d^2 = \sum_{i=1}^k u_i (s_{di} v_{i+1}^2 + f_{di} v_1^2 + 2c_{di} v_{i+1} v_1) = \sum u_i \sigma_{di}^2, \tag{4}$$

where $\sigma_{di}^2 = \text{Var}(W_i)$ is the within-year variance of individual reproductive value among individuals of age i .

This is the expression for the demographic variance given by Engen et al. (2005). Notice that equation (4) defines a simple decomposition of σ_d^2 into additive components from the stochasticity in survival and reproduction, as well as the covariation between them, for each age class.

Environmental Stochasticity Only

Now consider a population sufficiently large that demographic stochasticity can be ignored, that is, N (or V) $\gg \sigma_d^2/\sigma_e^2$ so that the demographic term in equation (1) can be ignored compared to the environmental term (Lande et al. 2003). The model is then $n + \Delta n = Ln$, where L is a function of the environment Z , so that its stochasticity is determined primarily by temporal environmental fluctuations. The total reproductive value the next year is then $(n + \Delta n)v = Lw = \sum_{ij} L_{ij} n_j v_i$. Again approximating n_j by Nu_j , we find that the variance in total reproductive value the next year is

$$\begin{aligned} \text{Var}(V + \Delta V|V) &\approx N^2 \sum_{ijkl} v_i v_k u_j u_l \text{Cov}(L_{ij}, L_{kl}) \\ &= N^2 \sigma_e^2 \end{aligned} \tag{5}$$

so that the environmental variance is

$$\sigma_e^2 = \sum_{ijkl} v_i v_k u_j u_l \text{Cov}(L_{ij}, L_{kl}). \tag{6}$$

Here, $v_i u_j = \partial \lambda / \partial l_{ij}$, and $v_k u_l = \partial \lambda / \partial l_{(kl)}$ (Caswell 1978). Thus, σ_e^2 is the environmental variance given by Tuljapurkar (1982, 1989) except for the factor λ^{-2} . As already pointed out, this factor is just determined by choice of

scale for measuring population size (N vs. $\ln N$). The environmental variance for $\ln N$ to the first order is the above expression divided by λ^2 and hence agrees with the result of Tuljapurkar (1982).

In the previous model with demographic stochasticity only, all individuals had independent annual reproductive values generating the stochasticity. In contrast, when there is environmental stochasticity only, the variation in individual reproductive value between individuals in the same age class is negligible by the law of large numbers. The variance in total reproductive value the next year, $\sigma_e^2 V^2 \approx \sigma_e^2 N^2$, is now generated by change in mean individual reproductive value among years and still equals the variance through time of the sum of individual reproductive values over all individuals in the population.

For a Leslie matrix with nonzero components representing survival and reproduction, including the extended case with possible survival of individuals in the last stage class, equation (6) also defines a decomposition into additive components from survival, reproduction, and their covariation, now for each pair of age classes. Defining the survival contributions $s_{eij} = \text{Cov}(L_{i+1,i}, L_{j+1,j})$ with $L_{k+1,k} = L_{k,k}$, the fecundity contributions $f_{eij} = \text{Cov}(L_{1i}, L_{1j})$, and the covariation $c_{eij} = \text{Cov}(L_{i+1,i}, L_{1j})$, the expression for the environmental variance by analogy with equation (4) takes the form

$$\begin{aligned} \sigma_e^2 &= \sum_{ij} u_i u_j (s_{eij} v_{i+1} v_{j+1} + f_{eij} v_1^2 + c_{eij} v_{i+1} v_1) \\ &= \sum_{ij} u_i u_j \tau_{eij}. \end{aligned} \tag{7}$$

General Model with Demographic and Environmental Stochasticity

As with no age structure, the variance in the individual demographic contributions to the next year can generally be partitioned into environmental and demographic components:

$$\begin{aligned} \sigma_i^2 &= \text{Var}(W_i) \\ &= \text{E Var}(W_i|Z) + \text{Var E}(W_i|Z) \\ &= \sigma_{di}^2 + \tau_{eii}, \end{aligned} \tag{8}$$

where we define $\tau_{eij} = \text{Cov}[E(W_i|Z), E(W_j|Z)]$ so that τ_{eii} is the between-year variance in the expected individual reproductive values of individuals of age i generated by temporal fluctuations in the environment Z . The demographic component σ_{di}^2 is the temporal mean of the variance within year in individual reproductive value of individuals of age i .

These variance components are the age-specific contributions to the total demographic and environmental variances that are found by considering the sum of individual reproductive values over all individuals:

$$\text{Var}(V + \Delta V) = E \text{Var}(V + \Delta V|Z) + \text{Var} E(V + \Delta V|Z). \quad (9)$$

For a given constant environment Z , $\text{Var}(V + \Delta V|Z)$ is exactly the demographic variance for the environment Z multiplied by N , as in equation (4), which we now denote $N\sigma_d^2(Z)$. Consequently, the demographic variance is $\sigma_d^2 = E\sigma_d^2(Z)$, where the expectation refers to the distribution of the environment Z through time. Similarly, all variance components of equation (4) are functions of Z . Hence, the demographic variance is the sum in equation (4), with the modification that variances and covariances are replaced by their mean values through time. For example, if the survival of age class i in environment Z is $p_i(Z)$, then $s_{di} = p_i(1 - p_i)$ must be replaced by

$$\begin{aligned} E s_{di}(Z) &= E p_i(Z)[1 - p_i(Z)] \\ &= E p_i(Z)[1 - E p_i(Z)] - \text{Var}[p_i(Z)]. \end{aligned}$$

Similarly, f_{di} and c_{di} are replaced by $E f_{di}(Z)$ and $E c_{di}(Z)$. With these definitions the complete decomposition of the demographic variance in equation (4) is valid in a fluctuating environment.

Considering the second term in equation (9), $\text{Var} E(V + \Delta V|Z)$, we write $L(Z)$ for the expected projection matrix in a particular environment Z ; that is, its components are the probabilities of survival and expected number of offspring for a given Z . Then, in environment Z , $E(V + \Delta V|Z) = \sum_{ij} L_{ij}(Z) n_j v_i$ by the definition of the age-structured model defining n_i the next year as $\sum_j L_{ij}(Z) n_j$. Consequently, the variance in equation (6) now has L_{ij} replaced by $L_{ij}(Z)$. Finally, this produces an environmental variance equivalent to equation (7) with the modification that $\text{Cov}(L_{ij}, L_{kl})$ is replaced by $\text{Cov}[L_{ij}(Z), L_{kl}(Z)]$. Applying the same definitions to the components s_{eij} , f_{eij} , and c_{eij} , equation (7) is also valid for a finite population with demographic stochasticity.

Using the relation $E(V + \Delta V|Z) = \sum N_i E(W_i|Z)$ and again inserting $N_i \approx N u_i$, we reestablish the decomposition in equation (7) with τ_{eij} defined as following equation (8).

Stochasticity of the Projection Matrix

To establish the relations between the above variance components and the variances and covariances of elements of the projection matrix, we first observe that the matrix elements are yearly mean values \bar{J} and \bar{B} of survival and

fecundity (Engen et al. 2005). Since the demographic stochastic components are independent between individuals, the demographic contribution to $\text{Cov}(L_{ij}, L_{kl})$ is different from zero only for different columns, that is, for $j \neq l$. Hence, for $i \neq j$ we get only the environmental contributions $\text{Cov}(L_{i+1,i}, L_{j+1,j}) = s_{eij}$, $\text{Cov}(L_{1,i}, L_{1,j}) = f_{eij}$ and $\text{Cov}(L_{i+1,i}, L_{1,j}) = c_{eij}$. For $i = j$ the demographic components s_{di}/N_i , f_{di}/N_i , and c_{di}/N_i must be added to produce, for example, $\text{Cov}(L_{i+1,i}, L_{i+1,i}) = s_{eii} + s_{di}/N_i$. Since the number of individuals in age class i the next year is given by $\sum L_{ij} n_j$, these relations determine the covariance matrix for the population vector conditioned on the population vector the previous year, the covariance between n_i and n_j next year being $\sum_{km} n_k n_m \text{Cov}(L_{ik}, L_{jm})$.

Estimation

Although estimation of environmental stochasticity from individual data in general may be rather uncertain (Lande et al. 2003; Sæther et al. 2005), such data, if collected over a number of years, contain information about environmental as well as demographic stochasticity. We have used a single subscript i to indicate that the variables J_i , B_i , and W_i are the stochastic variables describing age-specific variation in survival and reproduction and to indicate their combined effect in the individual reproductive value of individuals in age class i . When variables referring to two different age classes are considered jointly, we use subscripts i and j to indicate age classes such as in $\text{Cov}(W_i, W_j)$. To describe the data to be used for estimation we need two additional subscripts m and t , writing, for example, B_{imt} for the observed number of offspring produced by individual number m among those of age i recorded at time t . The complete data set is accordingly records of survival and reproduction, (J_{im}, B_{im}) , for ages $i = 1, 2, \dots, k$ in years $t = 1, 2, \dots, T$; and individuals $m = 1, 2, \dots, n_{it}$ where n_{it} is the number of individuals in age class i recorded at year t . When a distinction between two different individual recordings is required, we use subscripts q as well as m for numbering individuals. Similarly we use y as well as t to denote time when required.

Expected Projection Matrix

The mean values of all records of (J_{im}, B_{im}) then lead to an estimate of the mean projection matrix $l = EL$, from which estimates of the long-run growth rate λ , the stable age distribution u , and reproductive values v can be computed. Uncertainties can be found by simulating bootstrap replicates of the data. Since yearly variation in the environments is not important for these estimates, the best bootstrap replicates are simply resampling of the recordings of (J_{im}, B_{im}) with replacement within each year.

Demographic Stochasticity

Using the estimate of the expected projection matrix, we can then calculate the individual reproductive values defined by equation (2) for each individual recorded; that is, $W_{imt} = J_{imt}v_{i+1} + B_{imt}v_1$. Estimation of all variance components can now be performed using these observed values of individual reproductive value, the definitions $\sigma_{di}^2 = E \text{Var}(W_i|Z)$ and $\tau_{eij} = \text{Cov}[E(W_i|Z), E(W_j|Z)]$, and the relations $\sigma_e^2 = \sum_{ij} u_i u_j \tau_{eij}$ and $\sigma_d^2 = \sum_i u_i \sigma_{di}^2$. For a particular year t with environment Z (which is unknown), an unbiased estimator for the demographic variance component $\sigma_{di}^2(Z) = \text{Var}(W_i|Z)$ is the simple sum of squares:

$$\hat{\sigma}_{di}^2(Z) = \frac{1}{n_{it} - 1} \sum_{m=1}^{n_{it}} (W_{imt} - \bar{W}_{it})^2, \tag{10}$$

where $\bar{W}_{it} = n_{it}^{-1} \sum_{m=1}^{n_{it}} W_{imt}$. The estimate $\hat{\sigma}_{di}^2$ of σ_{di}^2 is the weighted mean of the above estimates over years with at least two records from individuals in the age class with weights $n_{it} - 1$, and the estimate of the total demographic variance is $\hat{\sigma}_d^2 = \sum u_i \hat{\sigma}_{di}^2$. Bootstrap replicates can simply be performed as for the estimation of the expected projection matrix because the variation between years is not important for the demographic stochasticity. However, the expected value (with respect to the bootstrap sampling) of the sum of squares for year t and age class i divided by $n_{it} - 1$ is an unbiased estimate for the corresponding empirical variance $n_{it}^{-1} \sum_{m=1}^{n_{it}} (W_{imt} - \bar{W}_{it})^2$. Therefore each of these sums of squares should be multiplied by $n_{it}/(n_{it} - 1)$ to make the bootstrap replicates unbiased for the estimator in equation (10).

The age-specific components generated by survival and fecundity, s_{di} and f_{di} , can similarly be estimated by replacing W_{imt} by J_{imt} and B_{imt} , respectively, while the estimate for the covariance c_{dij} is the corresponding sum of cross products.

Environmental Stochasticity

To estimate the components of the environmental variance, we first consider the decomposition of the covariance between recordings of individual reproductive values the same year. The recordings for any two individuals in a particular year are assumed to be independent when conditioned on the environment Z . This assumption of no demographic covariance, as defined by Engen et al. (1998), was also made in the derivation of equation (4) and the yearly demographic variance $\sigma_d^2(Z)$ for a given environment Z . Applying the formula for the total covariance

$$\begin{aligned} \text{Cov}(W_{imt}, W_{jqt}) &= E \text{Cov}[W_{imt}, W_{jqt}|Z] \\ &+ \text{Cov}[E(W_{imt}|Z), E(W_{jqt}|Z)], \end{aligned}$$

we then see that

$$\begin{aligned} \text{Cov}(W_{imt}, W_{jqt}) &= \text{Cov}[E(W_{imt}|Z), E(W_{jqt}|Z)] \\ &= \tau_{eij}, \end{aligned}$$

where $m \neq q$ when i and j refer to the same age class ($i = j$). To estimate this covariance we consider the two bivariate observations (W_{imt}, W_{jqt}) and $(W_{im'y}, W_{jqt'y})$ at times $t \neq y$, where i and j may refer to any age classes. If $i = j$ we must require that $q \neq m$ and $q' \neq m'$, while the last subscript otherwise may refer to any observed individual in the class. Then, from the assumption of stochastic independence of vital rates between years, we find

$$\begin{aligned} &\text{Cov}(W_{imt} - W_{im'y})(W_{jqt} - W_{jqt'y}) \\ &= \text{Cov}(W_{imt}, W_{jqt}) + \text{Cov}(W_{im'y}, W_{jqt'y}) \\ &= 2\tau_{eij}. \end{aligned}$$

Because the factors like $(W_{imt} - W_{im'y})$ have zero expectation each product of the type $(1/2)(W_{imt} - W_{im'y})(W_{jqt} - W_{jqt'y})$ has expectation τ_{eij} . We thus obtain an efficient unbiased estimator for τ_{eij} as the mean value of these products over all combinations of $t \neq y$, and all appropriate combinations of the second subscript, which is straightforward to compute even if the number of terms is large.

Since environmental stochasticity is generated by among-year variation in the environments, bootstrapping for uncertainties in components of the environmental variance must be performed in a way that reflects the variation among years in the data (the variation among individuals within years is accounted for by estimation of demographic variance). This can be done by choosing T years at random with replacement and using the data from these years to calculate one bootstrap estimate. Because the same year tends to appear more than once, the bootstrap variances tend to be a little too small. It is therefore recommended to multiply all estimates of environmental variance with the appropriate factor making the mean of the bootstrap estimates equal to the estimate obtained from data.

Estimation of the age-specific variance components s_{eij} and f_{eij} due to survival and fecundity can be done in the same way, replacing the W_{imt} by the recordings of J_{imt} and B_{imt} , respectively. To estimate the covariance terms c_{eij} we consider the cross product $(1/2)(J_{imt} - J_{im'y})(B_{jqt} - B_{jqt'y})$ with expectation c_{eij} and again compute the mean over all combinations. Bootstrap replicates are produced by the same resampling scheme as that used for τ_{eij} .

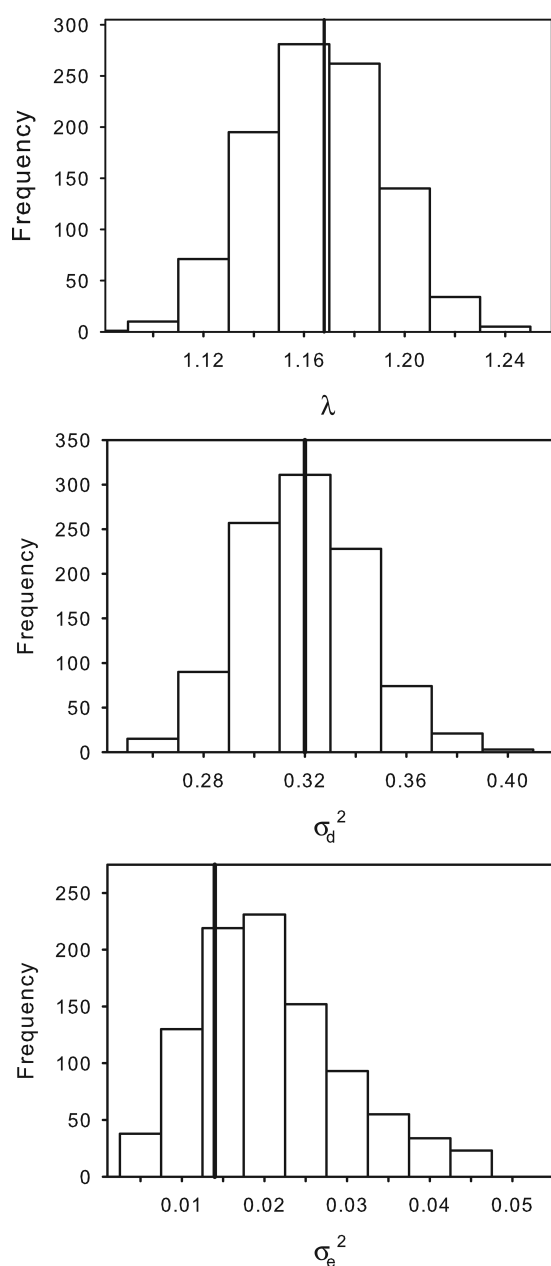


Figure 1: The distribution of the bootstrap replicates ($n = 1,000$) of the population growth rate, the demographic variance, and the environmental variance, for the population of Columbian ground squirrel. The thick black lines denote the estimated values, and the 95% confidence intervals are 1.12–1.22, 0.28–0.37, and 0.004–0.045 for λ , σ_d^2 , and σ_e^2 , respectively.

An Example: Columbian Ground Squirrel

We illustrate the application of the estimation procedures by analyzing demographic data from a population of Columbian ground squirrel (*Spermophilus columbianus*) dur-

ing the period 1992–2002 at the Sheep River Wildlife Sanctuary in the Rocky Mountains of southwestern Alberta (50°N, 110°W; 1,500 m elevation). In 1990 all older adults older than 1 were removed, leaving only 1-year-olds, so when the study started in 1992, the population was likely to be far below the carrying capacity. Accordingly, the population grew continuously throughout the study period from 14 females at least 1 year old in 1992 to 77 females in 2002. Columbian ground squirrels emerge from their hibernation burrows in spring and mate within a few days. The active season is short because the families start to prepare for the 8–9-month period of hibernation soon after the young are weaned in early summer (Dobson et al. 1999). Life histories are extremely plastic and are strongly influenced by the body condition of the females (Dobson and Murie 1987; Dobson 1992; Broussard et al. 2005). Mean litter size increases from 2.6 among females breeding for the first time yearlings to 3.0 among experienced females (Broussard et al. 2008). Columbian ground squirrels are quite long lived for such a small mammal (to about 9 years; Dobson and Oli 2001). Here we have used a model with three stages where individuals of age ≥ 3 define the terminal stage. The growth of this Columbian ground squirrel population was rapid ($\hat{\lambda} = 1.17$). Both the demographic and environmental variances were significantly different from 0 (fig. 1; $\hat{\sigma}_d^2 = 0.32$ and $\hat{\sigma}_e^2 = 0.014$). The estimators appeared to be approximately unbiased with relatively small uncertainties in the population growth rate and demographic variance, with somewhat larger uncertainty in the environmental variance (fig. 1).

An important feature of our approach is that it can decompose the stochasticity in population dynamics into age-specific components. The overall contributions from fecundity and survival to the demographic variance were nearly equal, with a significant positive covariation between them (table 1). Contributions to the demographic variance differed by age class, with the largest contributions from both fecundity and survival coming from the oldest age class. Overall, the environmental stochasticity in fecundity ($\hat{f}_e = 0.005$) was larger than that from survival ($\hat{s}_e = 0.003$), and both were significant ($P \approx .01$)

Table 1: The age-specific contributions from fecundity and survival to the demographic variance of the Columbian ground squirrel

Age (years)	Component		
	Fecundity	Survival	Covariance between fecundity and survival
1	.0046	.0362	.0005
2	.0292	.0390	.0063
≥ 3	.1082	.0727	.0058
Total	.1420	.1478	.0126

larger than 0. However, the covariance between environmental components of fecundity and survival was not significant ($P \approx .08$). The (symmetric) matrix of the estimated environmental components $\hat{\tau}_{eij}$ was

$$\widehat{\mathbf{T}}_e = \begin{bmatrix} 0.0015 & 0.0002 & 0.0016 \\ 0.0002 & 0.0002 & 0.0015 \\ 0.0016 & 0.0015 & 0.0058 \end{bmatrix}.$$

This shows that the largest contribution to the environmental stochasticity arises from fluctuations in the oldest age classes operating through an influence on both fecundity ($\hat{f}_{e33} = 0.0030$) and survival ($\hat{s}_{e33}^2 = 0.0017$).

Discussion

Fisher (1930) originated the concept of reproductive value for a density-independent age-structured population in a constant environment in continuous time. In his model, the reproductive value v_x is defined for individuals of age x , such that all individuals of a given age have the same reproductive value. Regardless of the initial age distribution in the population at time 0, the total reproductive value at a later time t of the descendants of a group of individuals with reproductive value v_x is exactly $v_x e^{rt}$, where r is the asymptotic growth rate of the log population size (Charlesworth 1994; Caswell 2001). This result does not depend on the scaling of Fisher's reproductive value (e.g., Crow and Kimura 1970; Charlesworth 1994; Caswell 2001). Often v_0 is chosen equal to 1. However, it may be more appropriate, as we do here, to choose the scaling that makes the total reproductive value equal to the population size when the population reaches its stable age distribution.

We employ a discrete time model in which the reproductive values are the components of the left eigenvector associated with the dominant eigenvalue λ of the mean projection matrix. Using these reproductive values we define the individual reproductive value, W_i , as the stochastic contribution by individuals of age i to the total reproductive value in the population the next year as in equation (2). For a standard age-structured model, or a simple stage-structured model (Caswell 2001) in which the oldest individuals are combined into a terminal stage, the individual reproductive value is the sum of two components, due to stochastic survival and reproduction. Brommer et al. (2007) used a similar decomposition in their definition of individual reproductive value in a study of senescence, although they failed to include the weighting by reproductive values, which is required to find the correct expected contribution to future generations. Another attempt, which is related to the statistical technique of jackknifing and is termed the method of "de-lifing," was

proposed by Coulson et al. (2006). This method is also based on contributions from individuals of different ages, but it fails to filter out the stochastic fluctuations in contributions due to age structure fluctuations, which is one important goal of our method, which is based on Fisher's reproductive value.

The overall mean of our individual reproductive values W_i across individuals, age classes, and time is the asymptotic multiplicative growth rate of the population in the average environment $\lambda = e^r$. The sum of W_i over all age classes and individuals in a given year equals the total reproductive value V the next year. The variance of individual reproductive values defines in a simple way the demographic and environmental variances of an age-structured population that comprise additive components defined by conditioning on the environment (eq. [9]). The parameters required for an accurate diffusion approximation of the stochastic dynamics of a density-independent age-structured population, the deterministic multiplicative growth rate in the average environment, λ , and the demographic and environmental variances, σ_d^2 and σ_e^2 , are all deduced from the distribution of W_i among individuals and between years. The demographic variance reflects the stochastic variation in individual reproductive value among individuals within a year, while the environmental variance describes the temporal fluctuations in individual reproductive value, typically generated by a fluctuating environment.

A practical advantage of this approach is that estimates of environmental variance can be obtained, assuming no density dependence, from individual-based demographic data in population samples, even when time series of fluctuations in total population size are not available (table 1). This implies that the properties of the stochastic process describing the temporal changes in total reproductive value can be determined from such data. However, if the goal is to perform predictions of future population sizes or time to extinction, then an estimate of the last population size or total reproductive value must also be available.

Engen et al. (2007) showed that the total reproductive value obeys a process with no temporal autocorrelations to the first order, provided that there are no temporal autocorrelations in the stochastic projection matrices. The difference between the total population size N and the total reproductive value V is a process fluctuating around zero with a memory on the order of one generation, representing transient fluctuations in age structure. Thus, V serves as a filter, removing stochastic fluctuations in age structure, and all information about the total population size more than a few generations in the future is contained in V alone, in accordance with the initial interpretation of Fisher (1958).

The general concept of individual reproductive value can

be applied to any density-independent stage-structured model defined by a projection matrix. Even more generally, the population may be classified into any kind of categories with transitions among them, for example, with individual demographic effects that persist across ages (Vindenes et al. 2008) or geographic location of individuals. The variance of total reproductive value next year can then still be decomposed into components different from age-specific survival and fecundity, which may prove informative for the particular problems under study.

Individual reproductive value defined in this way also enables construction of simple estimation methods for the population parameters based on individual data on survival and reproduction over several or many years. In general for density-independent population dynamics, the observed values of W are data from a model with additive variance components. The age-specific components of demographic variance are estimated from variances in fitness within years, whereas the components of environmental variance are estimated from variances in fitness between years. The best weighting of observations when estimating variances between years depends on the unknown variances. For example, if there is no demographic variance so that W is identical for all individuals of the same age within a year, then there is no additional information gained from multiple individuals of the same age a particular year. However, the demographic variance of W within years, σ_d^2 , is often as much as 100 times larger than the environmental variance among years, σ_e^2 . This supports the method we have proposed, which employs all observed values of W with equal weights for all terms when calculating the mean of the cross-products used to estimate the components of σ_e^2 . Although the derivation of more efficient methods may be an interesting area for further research, their success will in general depend on the distribution of individual survival and fecundity within and between years, which typically is unknown.

This estimation method was applied to the Columbian ground squirrel population. We estimated σ_d^2 to be 0.32 (fig. 1), a demographic variance exceeding that for other mammalian species with litter size of 1–3 offspring (Sæther et al. 1998a, 2002, 2007a; Lande et al. 2003). The litter size of adult Columbian ground squirrel females usually varies from 2 to 6 young (Broussard et al. 2003). In birds, demographic stochasticity increases with clutch size (Sæther et al. 2004). Such a relationship may explain the relatively large demographic variance for the Columbian ground squirrel.

The estimate of the environmental variance for this population of the Columbian ground squirrel was significantly larger than 0, with great uncertainty (fig. 1), but within the range of estimates for other mammalian species (Sæther et al. 1998a, 1998b, 2002, 2005; Lande et al. 2003).

The great uncertainty occurred because the study period was only 11 years and reliable estimates of the environmental variance require long time series (Sæther et al. 2007b).

Our method allows stochastic influences on population dynamics to be partitioned into age-specific components. Application of this approach to the Columbian ground squirrel showed strong age-specific differences in contributions to both demographic and environmental stochasticity (table 1). In general, the stochastic effects were larger among the oldest females. This may be related to the life-history strategy of this species. Reproductive variance increases strongly with age (Broussard et al. 2003) depending on the body condition of the females (Dobson et al. 1999; Broussard et al. 2003, 2005), which in turn seems to be influenced by resource availability (Dobson and Oli 2001).

Acknowledgments

We are grateful for financial support from the Research Council of Norway (STORFORSK) and the Royal Society of London and strategic funding from the Norwegian University of Science and Technology. We thank J. O. Murie for generously providing data on the ground squirrels from 1992 to 1998 and J.-M. Gaillard for comments on a previous version of the manuscript. The field research was funded by a National Science Foundation grant to F.S.D. (DEB-0089473).

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Associate Editor: Andrew R. Solow
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