



Extinction in relation to demographic and environmental stochasticity in age-structured models

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Abstract

The demographic variance of an age-structured population is defined. This parameter is further split into components generated by demographic stochasticity in each vital rate. The applicability of these parameters are investigated by checking how an age-structured population process can be approximated by a diffusion with only three parameters. These are the deterministic growth rate computed from the expected projection matrix and the environmental and demographic variances. We also consider age-structured populations where the fecundity at any stage is either zero or one, and there is neither environmental stochasticity nor dependence between individual fecundity and survival. In this case the demographic variance is uniquely determined by the vital rates defining the projection matrix. The demographic variance for a long-lived bird species, the wandering albatross in the southwestern part of the Indian Ocean, is estimated. We also compute estimates of the age-specific contributions to the total demographic variance from survival, fecundity and the covariance between survival and fecundity.

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1. Introduction

Leslie [1] introduced matrix algebra in the analysis of the dynamics of age-structured populations. The expected values of population size and age distribution in subsequent generations were found by multiplying the population age structure vector by the Leslie matrix, with elements that are the age-specific vital rates describing survival and reproduction of individuals in each age-class. Hence, the original Leslie model concerns expectations only, and does not include the effects of stochasticity.

Two different ways of introducing stochasticity in age-structured population models have been dealt with in the literature. Pollard [2] and Goodman [3] analyzed demographic stochasticity in the vital rates using models where each individual's contribution to the next generation are independent random variables with identical distributions each year for every age class. Pollard [2] calculated the mean and variance of population size and age-structure, whereas Goodman [3] dealt particularly with probabilities of extinction. A different class of stochastic models describes environmental stochasticity in the vital rates based on the theory of products of stochastic matrices, assuming that the projection matrices operating in subsequent years are some sequence of random matrices with distributions not depending on the population vector [4–9].

A major problem has been to quantify how stochasticity reduces the long-term growth rate defined as the slope of the logarithm of the population size versus time as time approaches infinity. A simple first order approximation for this effect was given by Tuljapurkar [7]. Lande and Orzack [9] pointed out that these models could be approximated by a univariate diffusion process with two parameters, the long-run growth rate and the environmental variance, provided that fluctuations in the vital rates are not too large. The time to extinction or quasi-extinction then approximately follows the inverse Gaussian distribution [9,10].

Engen et al. [11] gave precise definitions of demographic and environmental variances in stochastic population models without age-structure. Demographic variance is generated by independent stochastic contributions from each individual to the next generation conditioned on the state of the environment. Environmental variance is the covariance between individual contributions in a given year, typically generated by a fluctuating environment simultaneously affecting all individuals in the population. Hence, the stochasticity in the models of Pollard [2] and Goodman [3] is purely demographic, whereas models with stochastic projection matrices (e.g. [4,7,9]), include environmental stochasticity but ignore demographic stochasticity.

A typical age-structured model with demographic and environmental stochasticity has a large number of parameters. Even in cases where there are only a few age classes, say 3–4, as many as 20–30 parameters may be required. The main goal of this paper is to generalize the approach of Lande and Orzack [9] who characterized the stochastic projection matrix model with two parameters, which were used in the diffusion approximation when the stochastic fluctuations were small. Here we show that when demographic stochasticity is included, three parameters are required for an accurate characterization. Sæther et al. [12] defined the demographic variance for an age-structured model and developed a method for calculating it, based on extensive stochastic simulations of the age-structured model. In the present paper we present a much simpler method making it possible to calculate the demographic stochasticity directly from the projection matrix, combined with some knowledge of the between-individual variation in survival and reproduction. This method also enables us to split the demographic variance into separate

components generated by demographic stochasticity in each vital rate. We also show the applicability of this approach by estimating those demographic components in a population of the wandering albatross *Diomedea exulans* breeding in the southwestern Indian Ocean.

There are three main reasons for defining this characterization of age-structured population processes. (a) Reducing the number of parameters reduces the complexity and simplifies comparisons of different populations or species, and facilitates interpretations of changes in the dynamics over time [13]. (b) Such characterizations can be used to analyze the evolutionary and ecological consequences of variations in specific components of complex life history models (e.g. [14–17]). (c) If fluctuations in the vital rates are not too large, the diffusion approximation may also be used to calculate probabilities of extinction or probabilities of reaching certain barriers, which are important for population viability analysis in conservation biology.

2. Environmental and demographic components of stochasticity in age-structured models

Throughout this paper we deal only with the female part of the population assuming that males are not limiting in reproduction, i.e. that all females have access to mates. For definition and computation of demographic variance relevant for the total population size see [19,20]. We now consider an age-structured model where $n_{i,t}$ is the number of individuals in the i th age-class at time t and write $N_t = \sum_i n_{i,t}$ for the total population size. Reproduction is assumed to start just after the population is censused. Let L be a stochastic age or stage projection matrix with elements L_{ij} for population classes $0, 1, \dots, k$, and write $C_{ij,kl} = \text{cov}(L_{ij}, L_{kl})$. The practical interpretation of this stochasticity is that the L_{ij} fluctuate between years with values determined by fluctuating physical or biological factors like temperature or the abundance of competing species. We write Z for the vector of all such factors affecting L so that $L = L(Z)$. We assume that the variables Z are independent and identically distributed between years. The realized value at time t is denoted z_t . The dynamics of this population model are then determined by the basic recurrence formula

$$n_{i,t+1} = \sum_j L_{ij}(z_t) n_{j,t}. \quad (1)$$

In the case of no stochasticity (constant Z), under some mild conditions on L [13], the population will soon reach a stable age distribution, and the population growth rate will be $r = \ln(\lambda)$, where λ is the dominant eigenvalue of the projection matrix L .

Under the assumption that the distribution of L between years does not depend on the population vector, Tuljapurkar and Orzack [6] and Tuljapurkar [7,8] derived the first-order approximation for the stochastic growth rate

$$s = \text{E} \ln A_t \approx r - \frac{1}{2} \sum \frac{\partial r}{\partial l_{ij}} \frac{\partial r}{\partial l_{kl}} C_{ij,kl}. \quad (2)$$

Here $l_{ij} = \text{E} L_{ij}(Z)$ is the mean through time of L_{ij} , $\exp(r) = \lambda$ is the dominant eigenvalue of this matrix and $A_t = N_{t+1}/N_t$. The derivatives $\frac{\partial r}{\partial l_{ij}}$ are equivalent to $\frac{1}{\lambda} \frac{\partial \lambda}{\partial l_{ij}}$, where $\frac{\partial \lambda}{\partial l_{ij}}$ are the sensitivity coefficients. These can easily be calculated from the matrix L (see [9] or [13]) as shown towards the end of this section.

The simplest way of checking the accuracy of Eq. (2) is to perform stochastic simulations of the age-structured model repeatedly using the basic equation (1). The value of $\ln A_t$ can then be recorded each year and the mean values of these will approximate the stochastic growth rate, with accuracy increasing with the length and/or number of simulations. In order to avoid extremely large or small population sizes it is preferable to scale the population vector each year to obtain a constant population size (see [20]).

If the distribution of the matrix $L(Z)$ does not depend on the population size or the age distribution, the stochasticity generated is purely environmental, and the first-order approximation for the environmental variance is twice the reduction in stochastic growth rate due to environmental stochasticity

$$\sigma_e^2 \approx \sum_{i,j,k,l} \frac{\partial r}{\partial l_{ij}} \frac{\partial r}{\partial l_{kl}} C_{ij,kl}, \tag{3}$$

so that $s \approx r - \frac{1}{2}\sigma_e^2$. Provided that there is no density regulation affecting the distribution of L , the process $\ln N_t$ can, under moderate population fluctuations, be approximated by a diffusion process with infinitesimal mean s and variance σ_e^2 . For details on this approximation, see [9]. We may write this model as $L_{ij}(Z) = l_{ij} + e_{ij}(Z)$ where the e_{ij} represent environmental fluctuations with zero mean and $\text{cov}(e_{ij}, e_{kl}) = \text{cov}(L_{ij}, L_{kl}) = C_{ij,kl}$.

The diffusion approximation to an age structured process is a scaled approximation, that is, taking long time intervals and small rates of changes and combine them to get a continuous representation of a discrete process. It seems likely that this approach is applicable for small and moderate fluctuations also when the elements of the projection matrix has a demographic as well as an environmental stochastic component. In the following we propose a method for incorporating demographic stochasticity and investigate its performance by a number of stochastic simulations.

Even with no density regulation, the projection matrix operating in different years will generally have a distribution that depends on the population size due to random variation among individuals in survival and reproduction. Such demographic effects can be included in the model by replacing L_{ij} by

$$M_{ij} = L_{ij} + d_{ij} = l_{ij} + e_{ij} + d_{ij}, \tag{4}$$

where the demographic components d_{ij} , that will be defined precisely below, have a distribution depending on the population size with zero expectation when conditioned on the L_{ij} . The covariances $C_{ij,kl}$ in Eq. (3) must then be replaced by $\text{cov}(L_{ij}, L_{kl}) + \text{cov}(d_{ij}, d_{kl})$ since the demographic deviations by definition have zero means for a given L . We shall see below that for large population sizes the quantities of $D_{ij,kl} = N \text{cov}(d_{ij}, d_{kl})$ will be approximately constant. Therefore, $C_{ij,kl}$ is actually replaced by $C_{ij,kl} + D_{ij,kl}/N$, where the last term is generated by demographic stochasticity. The demographic variance associated with the model should accordingly be defined as

$$\sigma_d^2 = \sum_{i,j,k,l} \frac{\partial r}{\partial l_{ij}} \frac{\partial r}{\partial l_{kl}} D_{ij,kl}, \tag{5}$$

and the stochastic growth rate takes the form

$$s(N) = r - \frac{1}{2}\sigma_e^2 - \frac{1}{2N}\sigma_d^2, \tag{6}$$

which is equivalent to the formula for the stochastic growth rate in models with non-overlapping generations [18]. The corresponding variance is

$$\text{var}(N_{t+1}|N_t = N) = \sigma_e^2 N^2 + \sigma_d^2 N. \tag{7}$$

In order to define precisely and compute the $D_{ij,kl}$ we first write the projection matrix without demographic stochasticity in the form

$$L = \begin{bmatrix} F_0 & F_1 & \cdots & F_k \\ P_0 & 0 & \cdots & \\ 0 & P_1 & 0 & \cdots \\ \cdots & & & \\ \cdots & & P_{k-1} & P_k \end{bmatrix},$$

and write correspondingly $f_i = E F_i(Z)$ and $p_i = E P_i(Z)$ for the non-zero elements l_{ij} , where the expectations refer to the distribution of the environmental vector Z . From the definition of demographic stochasticity, assuming no demographic covariances between individuals [11,21,22], each individual in a given age class gives independent identically distributed contributions to the next generation for a given environment Z . Let the contributions to the next generation from individuals in stage i be independent observations of the bivariate stochastic variable (B_i, J_i) , where B_i is the number of offspring produced and $J_i = 1$ if the individual survives and otherwise zero. Then, by definition, conditioning on the environment Z , we have $E(B_i|F_i) = F_i$ and $E(J_i|P_i) = P_i$, while the unconditional expectations corresponding to the mean value over individuals through time are $E B_i = E E(B_i|Z) = E F_i(Z) = f_i$ and correspondingly $E J_i = p_i$. For a detailed discussion on these conditional and unconditional distributions of contributions to the next generation in a simple model without age-structure, see [11].

Now, including the between-individual variation in fecundity and survival within years, the matrix applicable in a given year is exactly

$$M = \begin{bmatrix} \bar{B}_0 & \bar{B}_1 & \cdots & \bar{B}_k \\ \bar{J}_0 & 0 & \cdots & \\ 0 & \bar{J}_1 & 0 & \cdots \\ \cdots & & & \\ \cdots & & \bar{J}_{k-1} & \bar{J}_k \end{bmatrix},$$

where all elements are mean values over all individuals within each age class. Then the projection equation $n_{i,t+1} = \sum_j M_{ij} n_{j,t}$, corresponding to (1) in the case of no demographic stochasticity, is exact by definition. In this way, remembering that $M_{0i} = \bar{B}_i$ and $L_{0i} = F_i$, we have for example the trivial identity $M_{0i} = L_{0i} + (\bar{B}_i - F_i)$. Then it follows from Eq. (4) that $d_{0i} = \bar{B}_i - F_i$. Correspondingly, all d_{ij} represent deviations of individual contributions in a particular year from the mean values given the environment in that year. The corresponding variance term conditioned on the environment is

$$E(d_{0i}^2|F_i) = \text{var}(\bar{B}_i|F_i) = \frac{1}{n_i} \text{var}(B_i|F_i),$$

since \bar{B}_i is the mean of n_i fecundities. Writing $a_i = n_i/N$ for the realized age distribution (proportion of individuals in different age classes), it follows by taking expectations with respect to Z that

$$D_{0i,0i} = N E E(d_{0i}^2 | F_i) = E \left[\frac{1}{a_i} \text{var}(B_i | F_i) \right]. \tag{8}$$

By the same kind of argument we also find

$$D_{(i+1)i,(i+1)i} = E \left[\frac{1}{a_i} \text{var}(J_i | P_i) \right] \tag{9}$$

and

$$D_{0i,(i+1)i} = D_{(i+1)i,0i} = E \left[\frac{1}{a_i} \text{cov}(B_i, J_i | F_i, P_i) \right]. \tag{10}$$

Here the distribution of (B_i, J_i) is independent of N but the distribution of $a_i = n_i/N$ is not. Hence, the quantities defined by Eqs. (8)–(10) will depend slightly on N for small population sizes.

Notice that $\text{cov}(B_i, J_i | F_i, P_i)$ is the covariance between reproduction and survival for an individual. It should not be confused with the concept of demographic covariance [11] which is a possible covariance between two individual’s contributions to the next generation. Here we assume that demographic covariances are zero. Inserting Eqs. (8)–(10) in the general expression for the demographic variance (Eq. (5)) we find

$$\sigma_d^2 = \sum_{i=0}^k \left[\left(\frac{\partial r}{\partial f_i} \right)^2 D_{0i,0i} + \left(\frac{\partial r}{\partial p_i} \right)^2 D_{(i+1)i,(i+1)i} + 2 \left(\frac{\partial r}{\partial f_i} \right) \left(\frac{\partial r}{\partial p_i} \right) D_{0i,(i+1)i} \right]. \tag{11}$$

As mentioned above, the proportions a_i fluctuate between years so that the values of the components of the above expression depend to some extent on stochastic fluctuations in the age-structure. However, we shall see below that we obtain an expression that is accurate enough to compute approximations for probabilities of extinction if we replace the stochastic a_i by the stable age distribution derived from the deterministic projection matrix l_{ij} , say $u_i = E(n_i/N)$. For a given model we can then compute $\sigma_{B_i}^2 = E \text{var}(B_i | F_i)$, $\sigma_{J_i}^2 = E \text{var}(J_i | P_i) = p_i(1 - p_i) - \text{var}(P_i)$, and $\tau_i = E \text{cov}(B_i, J_i | F_i, P_i)$, giving a demographic variance not depending on N ,

$$\sigma_d^2 = \sum_{i=0}^k u_i^{-1} \left[\left(\frac{\partial r}{\partial f_i} \right)^2 \sigma_{B_i}^2 + \left(\frac{\partial r}{\partial p_i} \right)^2 \sigma_{J_i}^2 + 2 \left(\frac{\partial r}{\partial f_i} \right) \left(\frac{\partial r}{\partial p_i} \right) \tau_i \right].$$

This expression can be further simplified by using the right and left eigenvectors u and v of the projection matrix l associated with the dominant eigenvalue λ , that is $lu = \lambda u$ and $vl = \lambda v$. Scaling u so that the sum of the components are 1, and v so that the ‘inner product’ $vu = 1$, then $\partial \lambda / \partial l_{ij} = v_i u_j$ [13,20] and u is the stable age distribution. Inserting this in the above expression for the demographic variance gives the simplified expression

$$\sigma_d^2 = \lambda^{-2} \sum_{i=0}^k u_i (v_0^2 \sigma_{B_i}^2 + v_{i+1}^2 \sigma_{J_i}^2 + 2v_0 v_{i+1} \tau_i). \tag{12}$$

As a numerical example we consider first a 4-stage model, that is, $k = 3$, and assume that all elements of L except P_0 are constant. The environmental variance is then

$$\sigma_e^2 = \left(\frac{\partial r}{\partial P_0} \right)^2 \text{var}(P_0).$$

Assuming that B_i and J_i are independent when conditioned on L , and that $\text{var}(B_i|F_i) = \theta F_i$, we find $\sigma_{B_i}^2 = \theta f_i$, $\sigma_{J_i}^2 = p_i(1 - p_i)$ for $i = 1, 2, 3$, $\sigma_{J_0}^2 = p_0(1 - p_0) - \text{var}(P_0)$, and $\tau_i = 0$. Notice that $\text{var}(P_0)$, which is a factor in the expression for the environmental variance, also has an effect on the demographic variance. For example, in the most extreme case that either all juveniles survive (good environment) or die (bad environment), so that P_0 only take values zero or one, we have $\text{var}(P_0) = p_0(1 - p_0)$, giving $\sigma_{J_0}^2 = 0$. This is easily understood intuitively, since, if the environmental conditions make individuals of age zero either all die or all survive, then there cannot be any demographic differences between the survival of these individuals in a given year. In Table 1, we show numerical examples of the decomposition of the overall stochasticity in this population with 4 age classes.

Although the above theory is general, it is interesting to observe that all components of the demographic variance in some cases can be derived from the Leslie matrix alone. Many long-lived vertebrate species never produce more than a single offspring during one season [16,23,24]. If there is no relationship between individual survival and reproduction, and no environmental stochasticity, all variances between individuals used to compute the demographic stochasticity are then variances in simple independent Bernoulli trials as all B_i and J_i then are independent and take values zero or one. The variance contributions then all have the form $l_{ij}(1 - l_{ij})$, and the demographic variance of the process can be computed just from knowing the projection matrix L , which is a constant matrix ($L_{ij} = l_{ij}$) when there is no environmental stochasticity. Eq. (12) then simplifies to

$$\sigma_d^2 = \lambda^{-2} \sum_{i=0}^k u_i [v_0^2 f_i(1 - f_i) + v_{i+1}^2 p_i(1 - p_i)] \tag{13}$$

so that the demographic variance is completely determined by the elements of the Leslie matrix.

Table 1a

Decomposition of stochasticity showing the contributions from each of four age class

Age-class i	p_i	f_i	q_i	$q_i^{-1} \sigma_J^2$	$q_i^{-1} \sigma_B^2$ (for $\theta = 1$)	$q_i^{-1} \sigma_B^2$ (for $\theta = 9$)
0	0.4	0	0.404	0.132	0	0
1	0.6	0.5	0.165	0.107	0.023	0.203
2	0.9	0.8	0.102	0.016	0.022	0.199
3	0.7	0.7	0.330	0.120	0.063	0.567

The parameter θ is the over-dispersion in the fecundity defined as $\text{var}(B_i|F_i)/F_i$.

Table 1b

Some parameter estimates for the model in Table 1a

Environmental noise, $\text{var}(P_0)$	0.040
Environmental variance, σ_e^2	0.011
Deterministic growth rate, $\lambda = e^r$	0.977
Demographic variance σ_d^2 for $\theta = 1$	0.483
Demographic variance σ_d^2 for $\theta = 9$	1.344

3. Extinction

If the parameters of the diffusion approximation for the log of total population size ($r, \sigma_e^2, \sigma_d^2$) are to be applied as simple characteristics of the dynamics, for example in comparative studies (e.g. [25]), it is important that these parameters express most of the information contained in the full age-structured model with respect to the probability of extinction. Lande and Orzack [9] discussed this for small fluctuations in age-structured populations without demographic stochasticity using the diffusion with infinitesimal mean and variance $r - \frac{1}{2}\sigma_e^2$ and σ_e^2 on the log-scale, which is a Wiener process for which the time to extinction or quasi-extinction has an inverse Gaussian distribution [10]. To check if a diffusion approximation for the process also can be applied for an age-structured model including demographic stochasticity, we have simulated both the age-structured model and the diffusion approximation for a number of population models with different parameters, different number of age classes, and different initial populations sizes and age structure.

To perform stochastic simulations of full age-structured models the distribution of the B_i , the number of offspring, must be specified. We choose this to be the Poisson-lognormal distribution [26,27]. This is the distribution obtained by assuming that each individual produces a Poisson distributed number of offspring, the mean values of these distributions being lognormally distributed among individuals within years. Using the numerical example in Table 1 we show in Fig. 1 (left panel) the quantiles of the distribution of population sizes, with over-dispersion parameter $\theta = 1$

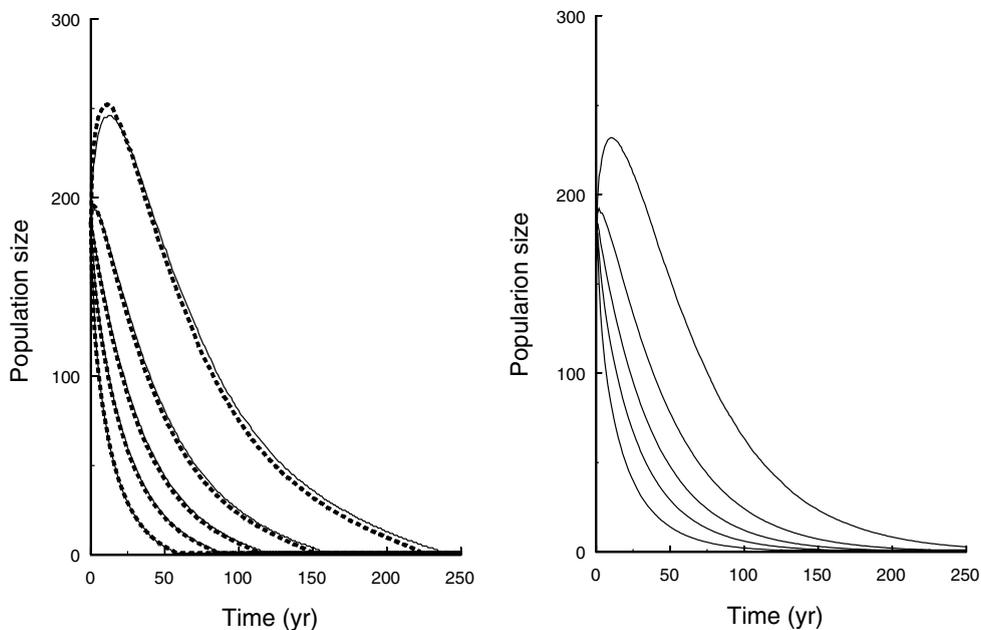


Fig. 1. Stochastic simulations of the model given in Table 1 with $\theta = 1$, that is, Poisson distributed number of offspring. The solid lines from bottom to top in the left panel are the 0.05, 0.25, 0.50, 0.75 and 0.95 quantiles computed from 100 000 simulations of the full age-structured model while the dotted lines are from the corresponding simulations of the diffusion approximation. The right panel shows the same simulations of the full model ignoring demographic stochasticity, that is, using the matrix L instead of M .

corresponding to Poisson distributed number of offspring, initial population size of 200, and an equal number of individuals in each age class at time zero. This initial age distribution is far from the stable age distribution determined by the l_{ij} . The quantiles are based on 100 000 simulations of the full age-structured model and the diffusion approximation using infinitesimal mean $r - \frac{1}{2}\sigma_e^2 - \frac{1}{2N}\sigma_d^2$ and infinitesimal variance $\sigma_e^2 + \sigma_d^2/N$ on the log scale, where all three parameters are those computed by the prescribed method. The initial value used in the diffusions is not 200, but the value based on the total reproductive value of the initial population as described by Lande and coworkers [9,20]. Scaling the eigenvectors of the expected projection matrix as before, the adjusted initial total population size for the diffusion approximation is the initial total reproductive value $N_0 = vn_{(0)}$, where $n_{(0)}$ here is the initial population column vector. The right panel of Fig. 1 shows the same quantiles for the full age-structured model ignoring demographic stochasticity, that is, using the matrix L rather than M . We see that when demographic stochasticity is included there is a probability of 0.05 of extinction within about 55 years since 5% of the simulated population trajectories reach the extinction barrier within this time. When demographic stochasticity is ignored this occurs after about 140 years demonstrating the importance of taking the demographic stochasticity into account even if the over-dispersion parameter in the fecundity is small. A similar example with 10 age classes and $\lambda > 1$ is shown in Fig. 2, and yet another example with 15 age classes and λ slightly less than one in Fig. 3. In this last example we clearly see some initial regular fluctuations in the populations size which are generated by starting rather far from the stable age distribution. Nevertheless, the diffusion approximation still gives a remarkably accurate approximation to the distribution of population size after this initial period.

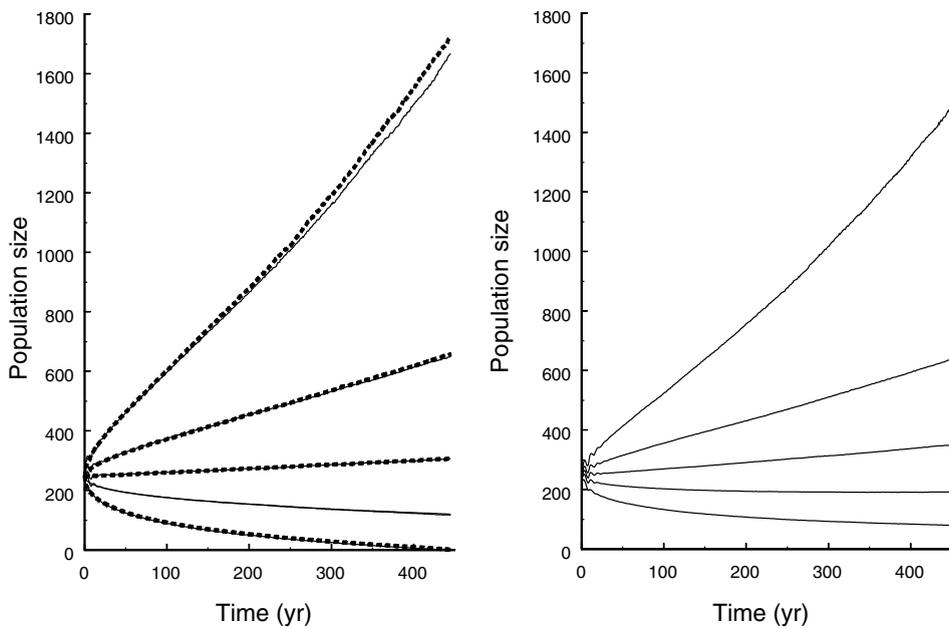


Fig. 2. The same simulations as shown in Fig. 1 but for a model with 10 age classes. The parameters are $\theta = 3$, $\text{var}(P_0) = 0.04$, $(f_0, f_1, \dots, f_9) = (0, 0, 0, 0, 0, 0.6, 0.8, 1.2, 1.0, 0.5)$, $(p_0, p_1, \dots, p_9) = (0.5, 0.7, 0.8, 0.9, 0.9, 0.9, 0.9, 0.8, 0.8)$, and the initial populations size is 20 for all 10 age classes. This gives $\lambda = 1.0018$, $\sigma_e^2 = 0.0018$ and $\sigma_d^2 = 0.3186$.

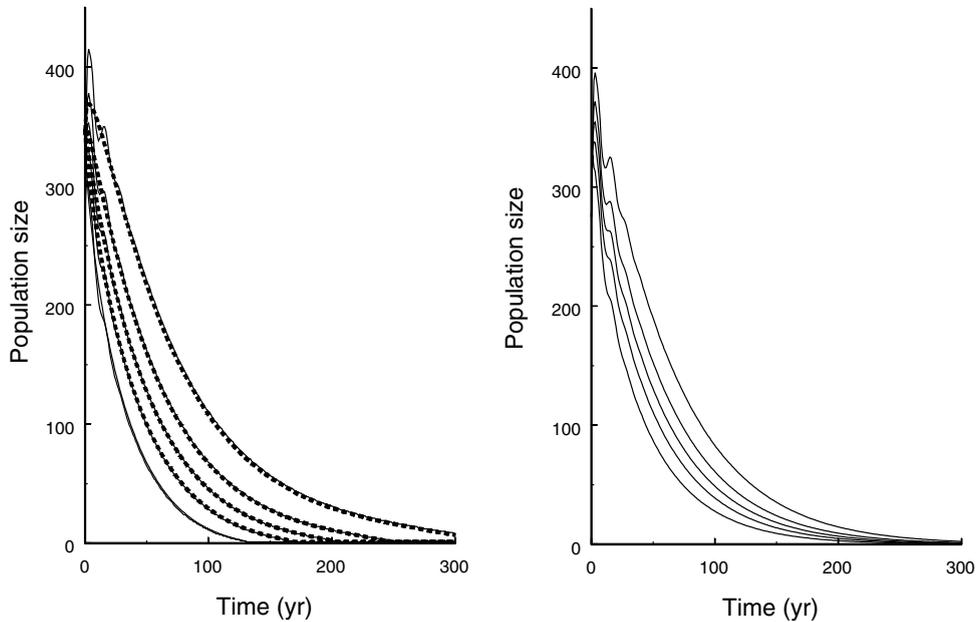


Fig. 3. The same as Fig. 2 but with 15 age classes and the following parameters: $\theta = 3$, $\text{var}(P_0) = 0.04$, $(f_0, f_1, \dots, f_{14}) = (0, 0, 0, 0, 0, 0, 0, 0.5, 0.6, 0.7, 0.9, 1.0, 1.0, 1.0, 1.0)$, and $(p_0, p_1, \dots, p_{14}) = (0.5, 0.6, 0.7, 0.9, 0.95, 0.95, 0.95, 0.95, 0.9, 0.9, 0.85, 0.85, 0.8, 0.8, 0.6)$, and initial population size 20 for classes 0–9 and 15 for classes 10–14. This gives $\lambda = 0.9813$, $\sigma_e^2 = 0.0011$, and $\sigma_d^2 = 0.2615$.

Using the approximations for environmental and demographic variance and the initial value based on the total reproductive value of the population [9,20] the diffusion approximation turns out to be surprisingly accurate all the way down to extinction even if the initial age population vector is far from the stable age distribution. This is quite remarkable remembering that we have calculated the demographic stochasticity by studying the fluctuations in large populations, and have not taken into account the large fluctuations one will have in the age-structure when the population approaches extinction.

Although no simple expression for the time to extinction is available when demographic variance is included in the diffusion approximation, a number of simulation studies [20,28,29] have shown that the demographic stochasticity has a large effect on probabilities of extinction since it reduces the infinitesimal mean as well as strongly increases the infinitesimal variance when the population reaches small values. For population sizes $N < \sigma_d^2/\sigma_e^2$ the demographic variance is more important than the environmental variance (see Eq. (7)). This effect can also be seen from the expression for the probability of ultimate extinction in this diffusion, which can be derived from general formulas for diffusions given by Karlin and Taylor [10]. A population that is not density regulated will either go extinct or approach infinity which in practice is interpreted as reaching its carrying capacity starting from a much smaller population size. If $s = r - \frac{1}{2}\sigma_e^2 \leq 0$ the probability of ultimate extinction at $N = 1$ is 1, and for $s > 0$ it turns out to be

$$P(N_0) = \left(\frac{\sigma_d^2 + \sigma_e^2}{\sigma_d^2 + \sigma_e^2 N_0} \right)^{2s/\sigma_e^2} \tag{14}$$

As σ_e^2 tends to zero this approaches $\exp[-2s(N_0 - 1)/\sigma_d^2]$, while for $\sigma_d^2 = 0$ it gives the well known result $\exp[-2 \ln(N_0)/\sigma_e^2]$ for a Wiener process [10]. Since the diffusion approximation turns out to be very accurate also when the demographic variance is included, these formulas also give approximations for the probability of ultimate extinction for stochastic age-structured models.

When there is no environmental stochasticity the appropriate diffusion approximation for the process N_t has infinitesimal mean rN and variance $\sigma_d^2 N$. The cumulative distribution of the time to extinction (T_{ext}) at $N = 0$ for this model was derived by Cox and Miller [30]. It takes the simple form

$$P(T_{\text{ext}} \leq t) = \exp \left[-\frac{2N_0 r}{\sigma_d^2 (1 - e^{-rt})} \right], \quad (15)$$

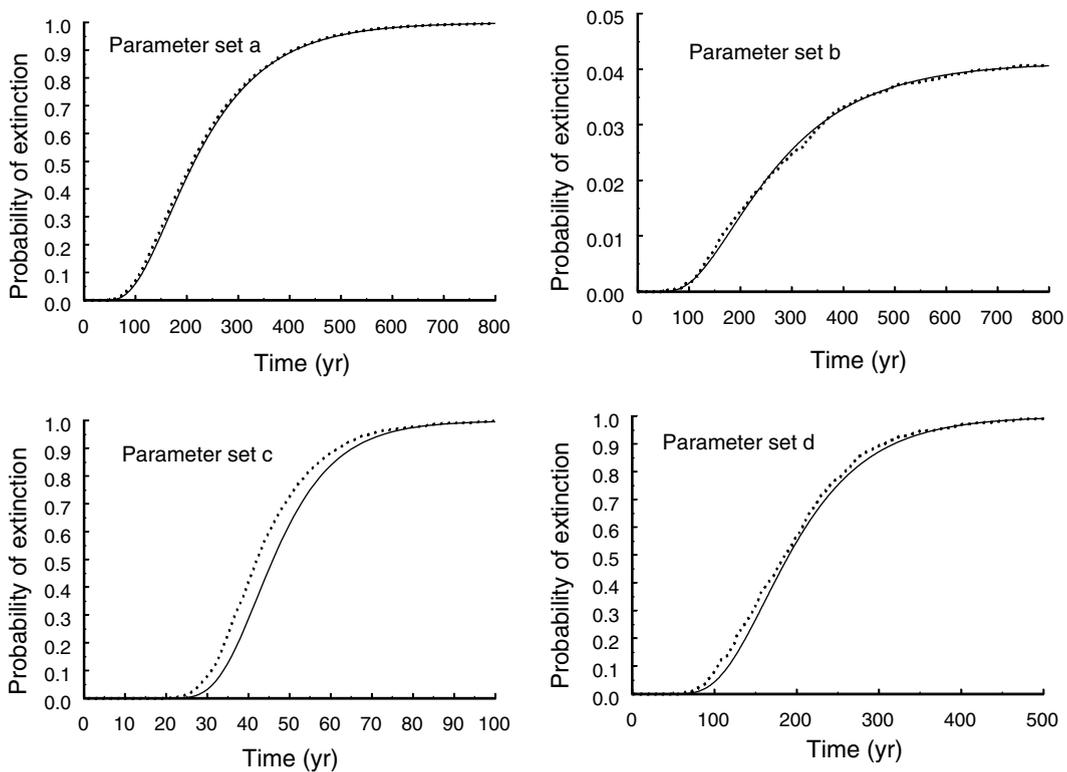


Fig. 4. Cumulative distributions of time to extinction for processes without environmental stochasticity. Solid lines are the cumulative distribution for the diffusion approximations given by Eq. (15), while the dotted lines are based on stochastic simulations of the age-structured process. The individual yearly fecundity is restricted to take values 0 or 1. Demographic stochasticity is then uniquely determined by the elements of the projection matrix. The initial population size is 100. Parameter sets *a* and *b* are for populations with 4 age classes. For set *a* the survivals are (0.4, 0.6, 0.9, 0.7), the fecundities (0, 0.6, 0.9, 0.7). For set *b* the growth rate is slightly positive so that the probability of ultimate extinction is smaller than one. The survival rates in set *b* are the same as in set *a* while the fecundities are (0, 0.6, 0.9, 0.8). Parameter sets *c* and *d* are populations with 9 age-classes. The survivals in set *c* are (0.6, 0.7, 0.7, 0.8, 0.9, 0.9, 0.9, 0.7, 0.5), and the fecundities (0, 0, 0, 0.4, 0.5, 0.8, 0.8, 0.9, 0.8). The survivals in set *d* are (0.5, 0.7, 0.7, 0.8, 0.8, 0.9, 0.9, 0.7, 0.5) and the fecundities are (0, 0, 0, 0, 0.2, 0.5, 0.6, 0.9, 0.8).

as pointed out by Engen and Sæther [31]. For $r \leq 0$ the probability of ultimate extinction is 1, while for $r > 0$ this probability is $\exp(-2N_0r/\sigma_d^2)$ which is approximately the same as the above formula for extinction at $N = 1$ with $N_0 - 1$ replaced by N_0 . In Fig. 4 we show the cumulative distribution for some simplified models with $\sigma_e^2 = 0$ and $B_i \leq 1$ based on simulations of the full model for 4 different projection matrices together with the cumulative distribution for the appropriate diffusion given by Eq. (15).

4. Estimation

It is known from analysis of simple models without age structure that estimation of demographic variances requires individual data on reproduction and survival [32]. Here we give the procedure for estimating the three components $\sigma_{B_i}^2$, $\sigma_{J_i}^2$ and τ_i for a given age class. Let (U_{jt}, V_{jt}) , where $V_{jt} = 0$ or 1, denote c_t individual observations of the number of female offspring and mother’s survival in year t for age class i , with $j = 1, 2, \dots, c_t$. Then $(c_t - 1)^{-1} \sum_{j=1}^{c_t} (U_{jt} - \bar{U}_t)^2$ is an unbiased estimator for the conditional variance $\text{var}_t(B_i|F_i)$ for this age class at time t . Correspondingly, $(c_t - 1)^{-1} \sum_{j=1}^{c_t} (V_{jt} - \bar{V}_t)^2$ and $(c_t - 1)^{-1} \sum_{j=1}^{c_t} (U_{jt} - \bar{U}_t)(V_{jt} - \bar{V}_t)$ are unbiased for $\text{var}(J_i|P_i)$ and $\text{cov}(B_i, J_i|F_i, P_i)$. Consequently, any weighted mean of these estimators over T years will be unbiased for the temporal mean values. In analogy with analysis of variance we use the weights $c_t - 1$ (degrees of freedom) giving the unbiased estimator

$$\hat{\sigma}_{B_i}^2 = (C - T)^{-1} \sum_{t=1}^T \sum_{j=1}^{c_t} (U_{jt} - \bar{U}_t)^2 \tag{16}$$

for $\sigma_{B_i}^2$, where $C = \sum_{t=1}^T c_t$ is the total number of observed individuals in age class i . By the same method we find for the other two parameters

$$\hat{\sigma}_{J_i}^2 = (C - T)^{-1} \sum_{t=1}^T \sum_{j=1}^{c_t} (V_{jt} - \bar{V}_t)^2, \tag{17}$$

$$\hat{\tau}_i = (C - T)^{-1} \sum_{t=1}^T \sum_{j=1}^{c_t} (U_{jt} - \bar{U}_t)(V_{jt} - \bar{V}_t). \tag{18}$$

The estimates given by Eqs. (16)–(18) must be computed separately for each age class. Estimates of the other parameters to be plugged into Eq. (12) to give an estimator for σ_d^2 are all derived from the estimated matrix l . Each estimated element \hat{l}_{ij} is just a simple mean value over individuals and time of the relevant observed reproductive rates.

5. An example: the wandering albatross

The population of the wandering albatross at Possession Island has been censused regularly since 1981 (Fig. 5) and also for some earlier years back to 1968 [37]. Based on the large number of color-ringed birds, these population estimates are likely to be quite accurate. The wandering

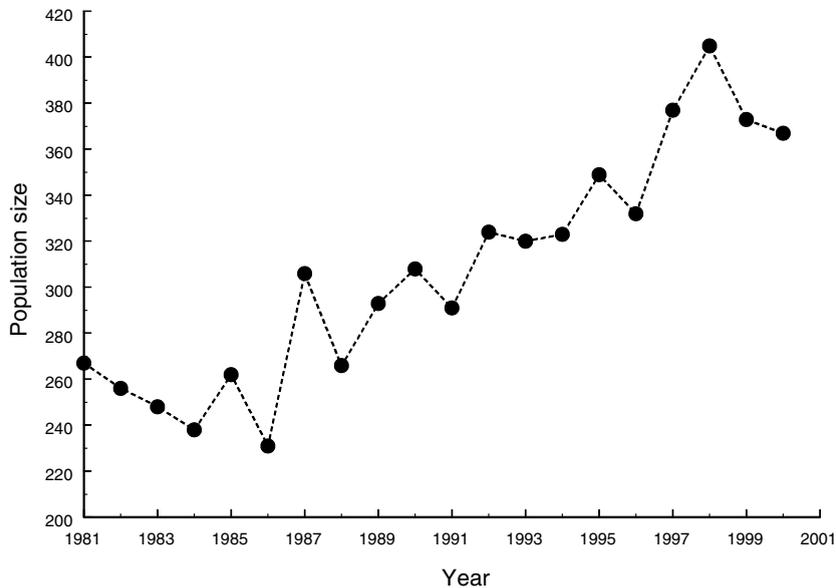


Fig. 5. Fluctuations in the size of the population of the wandering albatross at Possession Island in southwestern Indian Ocean.

albatross is a long-lived bird species, with an annual adult survival rate ranging from 0.909 to 0.968 [33–36]. It matures late, with an average age of first breeding around 10 years for the females [34]. The wandering albatross is a typical ‘survival species’ [38], situated at the slow end of the ‘slow-fast continuum’ of life history variation in birds [16]. The demography and the population dynamics of wandering albatross have been studied since 1960 on Possession Island, Crozet Archipelago (46°S, 52°E), in the southwestern part of the Indian Ocean. In the beginning of the study up to 500 pairs bred in the study area. Each year since 1966 chicks were ringed by monel rings. The study sites were visited each year and previously banded birds were identified. This study is based on data from 754 females of known age that later returned to the study sites as breeders. Hence, individuals not returning to the study site as breeders are defined not to be members of the population and are not included in the birth record. Each year we determined whether the female was able to successfully produce a chick. The sex of chicks were determined when they first returned to the colony using plumage characteristics and behavior, and later also by breeding behavior: in a few cases the sex was registered as unknown. Only years when the breeding success of a female was known for certain were included in the analyzes. To avoid incomplete cohorts, only data collected earlier than 1994 were included in the analysis. In total, data on 2687 bird-years were obtained.

The estimation procedure described above was performed for data sets where the offspring with unknown sex was chosen as male or female with probability 0.5. Only the female population was then included in the analysis. Estimates based on this random selection of sex were calculated 10000 times with different independent simulations of unknown sex, and the mean values of the estimates were finally used. Since there are little data within classes for ages larger than 17 years, and the rates seems to be approximately constant for ages larger than this, we collect all

individuals of age 17 or more in the final age class. The estimated vital rates for this population are shown in Fig. 6 (upper and middle panel) together with the corresponding age-specific sensitivity coefficients $d\lambda/dl_{ij} = \lambda dr/dl_{ij}$ (lower panel). The mean growth rate over this period, the largest eigenvalue of the projection matrix, was estimated to be $\lambda = 1.01384$.

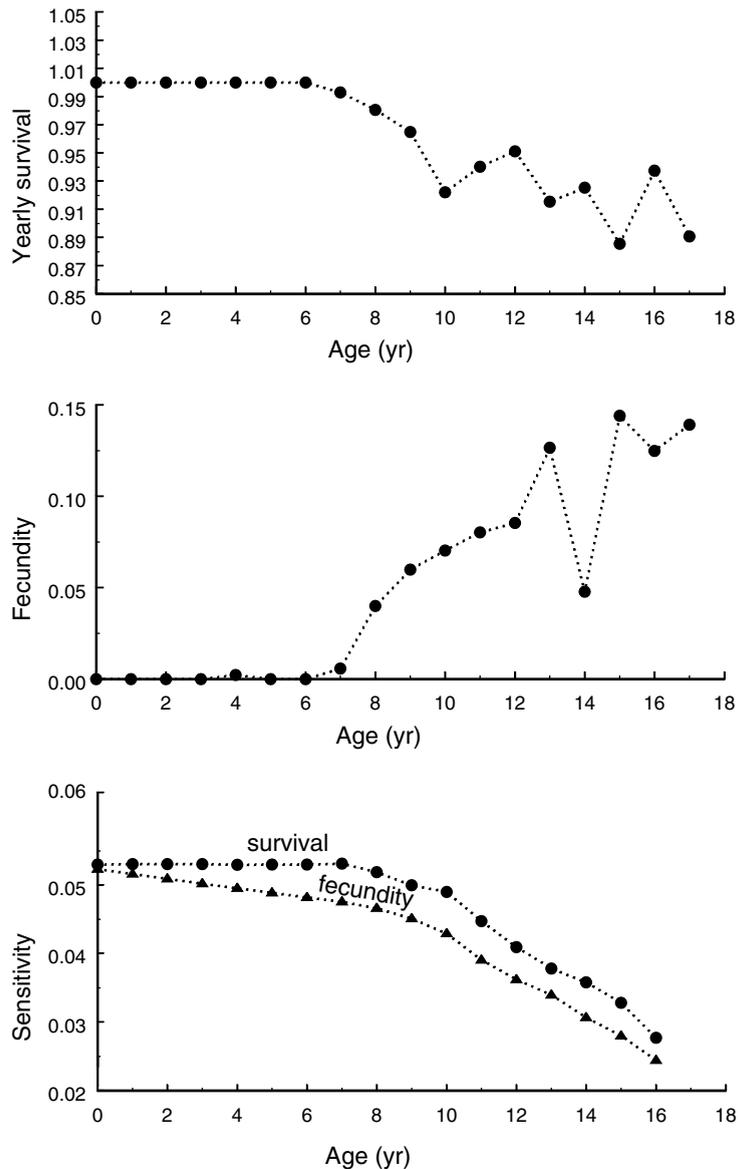


Fig. 6. Estimated yearly survival (upper panel) and fecundity (middle panel) for the wandering albatross. Age class 17 contains all individuals of age at least 17 years. The mean growth rate is estimated to be $\lambda = 1.0138$. The lower panel shows the corresponding age-specific sensitivity coefficients $\partial\lambda/\partial l_{ij}$. The values for the last class, not shown in the figure, are 0.212 for the survival and 0.186 for the fecundity.

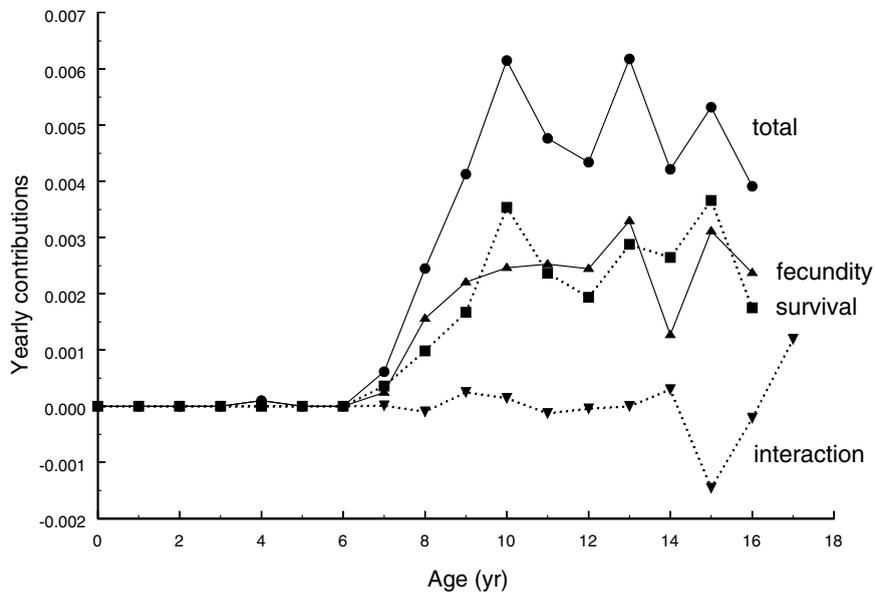


Fig. 7. Estimated contributions to the demographic variance of the wandering albatross from survival, fecundity, and covariance between survival and fecundity for each age class. The upper curve shows the total contribution for each age class.

An examination of the components showed that in all age-classes, individual variation in fecundity and survival contributed almost equally to the total demographic stochasticity, which was $\hat{\sigma}_d^2 = 0.084$ (Fig. 7). The final class (17+) gave a total contribution of 0.042 (not shown in Fig. 7) to the estimated demographic variance, with survival component 0.021, fecundity component 0.019 and covariance component 0.001. The vital rates as well as their contribution to the demographic variance varied a lot between age classes. For fecundity as well as survival there were large age-specific variation in the vital rates (Fig. 6) as well as in contributions to the demographic variance (Fig. 7). Finally, we note that the demographic covariance between fecundity and subsequent adult survival was close to zero (Fig. 7).

6. Discussion

We have shown how the demographic variance of an age-structured process can be computed and split up into components generated by age-specific random survival and stochastic fecundity. The components depend on the joint distribution of the age-specific individual contributions to the next generation as well as the population growth rate and sensitivity coefficients of the projection matrix for the population. Components with a large sensitivity coefficient and a large variance among individuals in the number of offspring, will generate large contributions to the total demographic variance.

A precise description of the dynamics of age-structured populations must necessarily include a large number of parameters [13]. If there are $k + 1$ age classes and no density regulation, just the

expected projection matrix will have up to $2(k + 1)$ parameters. If there is environmental variation in the elements, up to $(k + 1)(2k + 3)$ additional parameters are required just to give the variances and covariances. If there is demographic stochasticity as well, a large number of parameters is required also to describe the distribution of the individual reproduction and survival at each age, (B_i, J_i) , conditioned on their expectation for the prevailing environment in a given year (F_i, P_i) .

It is well known that with small environmental fluctuations and no demographic stochasticity, the dynamics of total population size can be accurately described by only two parameters, the population growth rate for the corresponding deterministic model, and the environmental variance, given by the last term in the expression for the stochastic growth rate in Eq. (2) [9]. For large populations, demographic stochasticity will only add very little to the fluctuations, and it is not surprising that it can be handled in the same way as the environmental stochasticity. Accordingly, the definition we have given for the demographic variance is based on the same formula, Eq. (2), and assumes large population size and hence small fluctuations in the age-structure. One therefore would not expect the dynamics to be given accurately by the three parameters r , σ_e^2 and σ_a^2 when the population size is small. However, we have demonstrated and confirmed by a large number of simulations, some of which are shown here, that the diffusion approximation for the distribution of the time to extinction is remarkably accurate. The discrepancies for the probabilities of extinction are very small compared to the uncertainty one will have in estimates of such probabilities. We can conclude that all three parameters are essential for the dynamics and quite suitable for comparisons between species.

In particular we have shown that the demographic variance will be determined uniquely by the projection matrix if the fecundity at any age never exceeds one. This special result is only valid if there is no individual correlation between survival and fecundity at any age. Nevertheless, this is a realistic assumption for a large number of species producing a maximum of one offspring per year.

We have demonstrated how the components of the demographic variance appearing in Eq. (12) can be estimated from data (Fig. 6). However, in order to obtain reliable estimates, one will need rather large data sets with repeated observations of individuals through time, collectively spanning the entire life history.

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References

- [1] P.H. Leslie, Some further notes on the use of matrices in population mathematics, *Biometrika* 35 (1948) 213.
- [2] E.H. Pollard, On the use of the direct matrix product in analysing certain stochastic population models, *Biometrika* 53 (1966) 397.
- [3] L. Goodman, The probability of extinction for birth-and-death processes that are age-dependent or phase-dependent, *Biometrika* 54 (1967) 579.

- [4] J.E. Cohen, Ergodicity of age structure in populations with Markovian vital rates, III: Finite-state moments and growth rate; an illustration, *Adv. Appl. Prob.* 9 (1977) 462.
- [5] J.E. Cohen, Comparative statistics and stochastic dynamics of age-structured populations, *Theo. Populat. Biol.* 16 (1979) 159.
- [6] S.D. Tuljapurkar, S.H. Orzack, Population dynamics in variable environments. I: Long run growth rates and extinction, *Theo. Populat. Biol.* 18 (1980) 314.
- [7] S.D. Tuljapurkar, Population dynamics in variable environments. III: Evolutionary dynamics of r -selection, *Theo. Populat. Biol.* 21 (1982) 141.
- [8] S.D. Tuljapurkar, An uncertain life: demography in random environments, *Theo. Populat. Biol.* 35 (1989) 227.
- [9] R. Lande, S.H. Orzack, Extinction dynamics of age-structured populations in a fluctuating environment, *Proc. Natural Acad. Sci.* 85 (1988) 7418.
- [10] S. Karlin, H.M. Taylor, *A Second Course in Stochastic Processes*, Academic Press, New York, 1981.
- [11] S. Engen, Ø. Bakke, A. Islam, Demographic and environmental stochasticity – concepts and definitions, *Biometrics* 54 (1998) 840.
- [12] B.-E. Sæther, S. Engen, J. Swenson, Ø. Bakke, F. Sandegren, Viability of scandinavian brown bear *Ursus arctos* populations: the effect of uncertain parameter estimates, *Oikos* 83 (1998) 403.
- [13] H. Caswell, *Matrix Population Models*, 2nd ed., Sinauer Assoc., Sunderland, 2001.
- [14] T.G. Benton, A. Grant, How to keep fit in the real world: elasticity analysis and selection pressures on life histories in a variable environment, *Am. Natur.* 147 (1996) 115.
- [15] C.A. Pfister, Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications, *Proc. Natural Acad. Sci.* 95 (1998) 213.
- [16] B.-E. Sæther, Ø. Bakke, Avian life history variation and contribution of demographic traits to the population growth rate, *Ecology* 81 (2000) 642.
- [17] S. Tuljapurkar, S.H. Orzack, Reproductive effort in variable environments, or environmental variation is for the birds, *Ecology* 82 (2001) 2659.
- [18] R. Lande, Demographic stochasticity and Allee effect on a scale with isotropic noise, *Oikos* 83 (1998) 353.
- [19] S. Engen, R. Lande, B.-E. Sæther, Demographic stochasticity and Allee effects in populations with two sexes, *Ecology* (2003).
- [20] R. Lande, S. Engen, B.-E. Sæther, *Stochastic Population Dynamics in Ecology and Conservation*, Oxford University, Oxford, 2003.
- [21] B.E. Kendall, G.A. Fox, Variation among individuals and reduced demographic stochasticity, *Conservat. Biol.* 16 (2002) 109.
- [22] G.A. Fox, B.E. Kendall, Demographic stochasticity and the variance reduction effect, *Ecology* 83 (2002) 1928.
- [23] B.-E. Sæther, Patterns of covariation among life history traits of European birds, *Nature* 331 (1988) 616.
- [24] P.H. Harvey, A.F. Read, D.E.F. Promislow, *Life history variation in placental mammals: unifying the data with the theory*, *Oxford Surv. Evolut. Biol.* 6 (1989) 13.
- [25] B.-E. Sæther, S. Engen, E. Matthysen, Demographic characteristics and population dynamical patterns of solitary birds, *Science* 295 (2002) 2070.
- [26] M.G. Bulmer, On fitting the Poisson lognormal distribution to species abundance data, *Biometrics* 30 (1974) 651.
- [27] S. Engen, R. Lande, T. Walla, P.J. DeVries, Analyzing spatial structure of communities using the two-dimensional Poisson lognormal species abundance model, *Am. Natur.* 160 (2002) 60.
- [28] B.-E. Sæther, S. Engen, R. Lande, P. Arcese, J.N.M. Smith, Estimating time to extinction in an island population of song sparrows, *Proc. R Soc. B* 267 (2000) 621.
- [29] S. Engen, B.-E. Sæther, A.P. Møller, Stochastic population dynamics and time to extinction of a declining population of barn swallow, *J. Animal Ecol.* 70 (2001) 789.
- [30] D.R. Cox, H.D. Miller, *The Theory of Stochastic Processes*, Methuen & Co. Ltd., London, 1970.
- [31] S. Engen, B.-E. Sæther, Stochastic population models: some concepts, definitions and results, *Oikos* 83 (1998) 345.
- [32] B.-E. Sæther, S. Engen, A. Islam, R. McCleery, C. Perrins, Environmental stochasticity and extinction risk in a population of a small songbird, the great tit, *Am. Natur.* 151 (1998) 441.
- [33] H. Weimerskirch, P. Jouventin, Population dynamics of the wandering albatross, *Diomedea exulans*, of the Crozet Islands: causes and consequences of the population decline, *Oikos* 49 (1987) 315.

- [34] H. Weimerskirch, N. Brothers, P. Jouventin, Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam Albatross *D. amsterdamensis* in the Indian Ocean and their relationships with longline fisheries: conservation implications, *Biol. Conservat.* 79 (1997) 257.
- [35] J.C. Croxall, P. Rothery, S.P.C. Pickering, P. Prince, Reproductive performance, recruitment and survival of Wandering Albatrosses *Diomedea exulans* at Bird Island, South Georgia, *J. Animal Ecol.* 59 (1990) 773.
- [36] J.C. Croxall, P.A. Prince, P. Rothery, A.G. Wood, Population changes in albatrosses at South Georgia, in: G. Robertson, R. Gales (Eds.), *Albatross Biology and Conservation*, Surrey Beatty & Sons, Chipping, Norton, 1997, p. 69.
- [37] H. Weimerskirch, J. Clobert, P. Jouventin, Survival in five southern albatrosses and its relationship with their life history, *J. Animal Ecol.* 56 (1987) 1043.
- [38] B.-E. Sæther, T.H. Ringsby, E. Røskaft, Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms, *Oikos* 77 (1996) 217.