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Estimating the effect of temporally autocorrelated environments on the demography of density-independent age-structured populations

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Summary

1. In age-structured populations, environmental autocorrelations influence the long-run population growth rate as well as the variance in future population size. We used the concept of individual reproductive value to examine how autocorrelated environments affect the dynamics of age-structured populations, leading to transparent interpretations and estimation of these effects.

2. Environmental autocorrelation is expressed by the covariances between mean individual reproductive values for each age class and size of the same age class with stochastic components depending only on noise matrices from previous years. Thus, if an age class that is large in a given year also tends to perform better than the temporal average of that class in the contribution per individual to future population sizes, then the environmental autocorrelation will be positive.

3. We use a simple model with temporal autocorrelation in recruitment rate to illustrate the theory through analytical results as well as stochastic simulations. We show how the effect of environmental autocorrelation, the term included in the long-run growth rate, as well as influencing the variance of future population size, can be estimated using a combination of individual-based demographic data and time series of fluctuations in age composition without estimating autocorrelations and cross-correlations of large numbers of age-specific vital rates.

4. The method was applied to data from four mammal species. These analyses revealed that the influence of autocorrelations in the environmental noise on the dynamics of these species was small and in two populations almost negligible.

5. The theoretical explorations as well as the empirical estimates indicate that the temporal scaling of the environmental autocorrelation must be long to substantially affect the long-term population growth rate. The white noise approximation is therefore often very accurate.

Key-words: age structure, autocorrelated noise, environmental stochasticity, individual reproductive value, life history, stochastic population growth rate

Introduction

All natural populations are influenced by stochastic variation in the environment. In the ecological literature, this stochasticity is commonly assumed to be white noise, meaning that there is no temporal correlation, so that values at two different time steps are completely independent of each other (Chatfield 2003). Recent evidence does indicate that there may be various degrees of correlations in time in the environmental fluctuations (Halley 1996). Steele (1985) suggested that the structure of these autocorrelations provides an important property of

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*Correspondence author. E-mail: steinaen@math.ntnu.no environmental variables affecting ecological processes. For instance, the pattern of environmental fluctuations is fundamentally different in marine and terrestrial environments. On land, the variance of most abiotic factors remains uniform over longer time periods and has approximately white noise, whereas in the oceans, many environmental variables are often positively autocorrelated (Halley 1996, 2005) and thus seem more 'reddened' than in terrestrial environments (Cyr & Cyr 2003; Vasseur & Yodzis 2004).

The pattern of autocorrelation in the environmental noise can be used not only to characterize differences among habitats, but is also important when making inferences about temporal changes in environmental conditions. For instance, the IPCC Fourth Assessment Report (IPCC 2007) indicates that the Earth's climate is likely to change dramatically over the coming decades, which may alter the autocorrelation structure in several climate variables (Halley 2009). Recent evidence indicates that the pattern of temporal variation in sea surface temperature has changed during the last century (Swanson, Sugihara & Tsonis 2009). Human impact can also influence the pattern of the environmental autocorrelations substantially (Ruokolainen *et al.* 2009).

However, how variation in environmental covariates affects population dynamics is complicated because the variance in population size is determined by the combined effect of environmental stochasticity and strength of density-dependent population regulation, and produce autocorrelations in the population fluctuations (Royama 1992; Ranta, Lundberg & Kaitala 2006). Such temporal (or spatial) autocorrelation is in general the correlation between two variables measured at different times (or locations). This article deals with temporal autocorrelation in the environmental noise, which in a structured population is a noise matrix. Autocorrelation in the noise must not be confused with autocorrelation in population size. If there are no autocorrelations in the noise (white noise), then there may still be large autocorrelations between sizes $n_{i,t}$ and $n_{j,t+h}$ of age classes i and j at times t and $t+h$.

Such environmental autocorrelation may influence the mean and variance of population size (Roughgarden 1975; Heino, Ripa & Kaitala 2000; Tuljapurkar, Horvitz & Pascarella 2003; Wichmann *et al.* 2005; Tuljapurkar, Gaillard & Coulson 2009; Morris *et al.* 2011). In density-independent populations with no age structure, environmental autocorrelation has no impact on the long-run growth rate of the population. Writing N_t for the population size at time t, the long-run growth rate is the limit of $(\ln N_t - \ln N_0)/t$ as t approaches infinity (Dennis, Munholland & Scott 1991). From the relation $\ln N_t - \ln N_0 = \sum_{u=1}^{t}(\ln N_u - \ln N_{u-1})$, it can be seen that the long-run growth rate is the expected value of $\ln N_u - \ln N_{u-1}$ for a stationary noise process even if there are autocorrelations because expectations in general are additive. Thus, only the environmental variance, here defined on absolute scale as $\sigma_e^2 = \mathrm{var}(N_{t+1}|N_t)/N_t^2$ (Lande, Engen & Sæther 2003), influences the long-run growth rate, which can be approximated by $\ln \lambda - \sigma_e^2/(2\lambda^2)$, where $r = \ln \lambda$ is the deterministic growth rate defined by $\lambda = E(N_t/N_{t-1})$. However, in age-structured models, environmental autocorrelation also affects the long-run growth rate (Tuljapurkar 1982; Caswell 2001; Doak *et al.* 2005; Tuljapurkar & Haridas 2006). The impact of this on the expected log population size over a time interval t is proportional to t, whereas the standard deviation is proportional to the square root of t. Hence, for extremely long time intervals, the effect on the mean becomes more important than the variance term even if the former is relatively small. However, for intervals, say 20–200 years, the situation may be the opposite, depending on the magnitude of these terms.

Tuljapurkar & Haridas (2006) analysed the effects of environmental autocorrelation on the dynamics of age-structured populations including second-order terms in the long-run growth rate due to environmental autocorrelation. First, there is an effect of approximately $-\sigma_e^2/(2\lambda^2)$ of the environmental variance in the age-structured dynamics (σ_e^2 also here defined on the absolute scale not including the factor λ^{-2}) as in the case of no age structure. Typical values of σ_e^2 are on the order of 0·01 per year (Sæther & Engen 2002; Lande, Engen & Sæther 2003; Sæther *et al.* 2005). Second, there is also an effect due to temporal autocorrelations and cross-correlations among elements in the projection matrix (Doak *et al.* 2005; Engen *et al.* 2005, 2007; Haridas & Tuljapurkar 2005; Morris *et al.* 2011; Sæther & Engen 2010). This term is usually negative and may be smaller or larger in magnitude than σ_e^2 depending on the mean projection matrix and the strength of temporal autocorrelations. Tuljapurkar & Haridas (2006) found that for large environmental autocorrelation, it may even be substantially larger in magnitude than σ_e^2.

The effects of temporal autocorrelations on population dynamics will strongly influence the degree to which the population is buffered against changes in the environment, for example, due to expected changes in climate (IPCC 2007). In general, the effects of environmental stochasticity on population dynamics tend to depend on life history (Sæther *et al.* 2005; Morris *et al.* 2008). For instance, Morris *et al.* (2008) found using elasticity analysis of the stochastic growth rate that responsiveness in population dynamics to a change in the environment was higher among short-lived than among long-lived species, indicating the buffering capacity towards environmental variability increases with life expectancy. However, this effect will be influenced by the correlation structure of the environmental components of age-specific vital rates (Doak *et al.* 2005; Engen *et al.* 2005; Haridas & Tuljapurkar 2005; Sæther & Engen 2010).

In this article, we base our analysis on the result of Cohen (1977, 1979) that any linear combination of age classes asymptotically grows exponentially with the same long-run growth rate as for the total population size. Our approach employs the total reproductive value of the population. The concept of reproductive value was originated by Fisher (1930) and has proved useful in deterministic (Crow & Kimura 1970; Charlesworth 1994) as well as in stochastic (Caswell 1978; Tuljapurkar 1982; Lande, Engen & Sæther 2003; Engen *et al.* 2007, 2009) age-structured population modelling.

Engen *et al.* (2007) derived an estimation method for the long-run growth rate based on yearly total reproductive values of the population, assuming temporally uncorrelated environments. The method was applied by Sæther *et al.* (2007) to analyse the stochastic dynamics of an age-structured Moose (*Alces alces*) population. Here we show that this estimation method for the long-run growth rate is valid also when the environmental noise is temporally correlated, because the mean of differences in log reproductive values includes the term due to temporal autocorrelation. This enables us using the concept of individual reproductive value defined by Engen *et al.* (2009) to drive a simple transparent interpretation of the effect of environmental autocorrelations on the long-run growth rate. We then show how this effect, which is included in the estimates previously obtained by the methods of Engen *et al.* (2007) and Sæther *et al.* (2007), can be isolated and estimated by a simple statistical method that only requires computation of the dominant left and right eigenvectors of the estimated mean projection matrix. This use of reproductive value makes the results more easily interpreted than by the previous approaches of Tuljapurkar (1982). We also estimate the variance of future population sizes and show how the influence of environmental autocorrelation can be estimated from data and how to test its statistical significance. Our derivation leads to a univariate diffusion approximation for the population size with two parameters, the long-run growth rate of the population and the environmental variance. Finally, we demonstrate the application of this method by analysing data on four mammal species, Bighorn sheep (*Ovis canadensis*), Columbian ground squirrel (*Urocitellus columbianus*), Red deer (*Cervus elaphus*) and Yellow-bellied marmot (*Marmota flaviventris*). We show that the small effect of environmental autocorrelations on primate population dynamics (Morris *et al.* 2011) also applies to the species included in the present analyses. This provides a general approach to estimate how environmental autocorrelations affect the autocorrelation structure (e.g. noise colour) of fluctuations in size of age-structured populations.

Stochastic age-structured model

Let the changes in the population vector $\mathbf{n} = (n_1, n_2, \ldots, n_k)$ be given by the matrix multiplication $\mathbf{Ln}$ expressing the population vector next year. In age-structured models, the projection matrix $\boldsymbol{L}$ is a k by k matrix with mean annual fecundities (female offspring per adult female of a given age) in the first row and mean annual survival (fraction of individuals that survive) on the subdiagonal (Engen *et al.* 2005). Let $\boldsymbol{L}$ have expectation $\bar{\boldsymbol{L}}$ and write $\boldsymbol{L} = \bar{\boldsymbol{L}} + \boldsymbol{\varepsilon}$, where $\boldsymbol{\varepsilon}$ is a noise matrix with zero expectation generated by a fluctuating environment as well as demographic stochasticity defined by within-year differences in individual vital rates (Engen *et al.* 2009). We assume that the population is substantially smaller than the carrying capacity so that density dependence in vital rates can be ignored. In addition, the population is assumed to be large enough to ignore the demographic components, so that fluctuations in $\boldsymbol{L}$ and $\boldsymbol{\varepsilon}$ are independent of the population vector. This is usually correct for populations larger than a few hundred individuals (Lande, Engen & Sæther 2003). The mean matrix $\bar{\boldsymbol{L}}$ has a real dominant eigenvalue λ and associated right and left eigenvectors $\mathbf{u}$ (column vector) and $\mathbf{v}$ (row vector) defined by $\bar{\boldsymbol{L}}\mathbf{u} = \lambda\mathbf{u}$ and $\mathbf{v}\boldsymbol{L} = \lambda\mathbf{v}$. If $\mathbf{u}$ is scaled by $\sum u_i = 1$ and $\mathbf{v}$ by $\sum u_i v_i = 1$, then $\mathbf{u}$ is the stable age distribution and $\mathbf{v}$ is the vector of reproductive values for the different age classes (Caswell 2001). The total reproductive value of the population is the sum of reproductive values of all individuals, $V = \mathbf{vn}$. The total reproductive value at time $t + 1$ can then be written as

$$V_{t+1} = \mathbf{vn}_{t+1} = \mathbf{v}(\bar{\boldsymbol{L}} + \boldsymbol{\varepsilon}_t)\mathbf{n}_t = \lambda\mathbf{vn}_t + \mathbf{v}\boldsymbol{\varepsilon}_t\mathbf{n}_t, \qquad \text{eqn 1}$$

where subscript t denotes time measured in units of years. If the population is at its deterministic stable age distribution for the average environment, $\mathbf{n}_t = N_t\mathbf{u}$, then $V_t = \mathbf{vn}_t = \mathbf{v}N_t\mathbf{u} = N_t$. The vector $\mathbf{x}_t = \mathbf{n}_t/V_t - \mathbf{u}$ is therefore zero if the population is at the deterministic stable age distribution and more generally measures the deviation from the stable age distribution (Engen *et al.* 2007). Notice that, by this definition of $\mathbf{x}_t$ as deviation from the stable age distribution, we obtain $\mathbf{vx}_t = \sum_i v_i x_{it} = 0$. Inserting $\mathbf{n}_t = V_t(\mathbf{u} + \mathbf{x}_t)$ in the above dynamic equation for the reproductive value then gives

$$V_{t+1} = \lambda V_t[1 + \lambda^{-1}\mathbf{v}\boldsymbol{\varepsilon}_t(\mathbf{u} + \mathbf{x}_t)], \qquad \text{eqn 2}$$

and on the log scale, $\ln V_{t+1} = \ln V_t + r + \ln\,[1 + \lambda^{-1}\mathbf{v}\boldsymbol{\varepsilon}_t(\mathbf{u} + \mathbf{x}_t)]$, where $r = \ln\lambda$.

The concept of reproductive value was introduced in deterministic modelling of age-structured populations by Fisher (1930), showing essentially (he used continuous age) that the linear combination $V_t = \mathbf{vn}_t$ of age classes has exactly exponential growth, $V_{t+1} = \lambda V_t$, in agreement with eqn. 2 with $\boldsymbol{\varepsilon}_t = 0$. He suggested that reproductive weighting of individuals, rather than just counting them, is a simple method for overcoming the problems of fluctuating allele frequencies due solely to transient fluctuations or changes in age distribution, which should be separated from those due to selection. The above theory, based on results in Engen *et al.* (2009), is a stochastic generalization of this idea of Fisher.

We show in the Appendix S1 that, consistent with Tuljapurkar (1982), the second-order approximation to the long-run growth rate is

$$s = r - \frac{1}{2}\lambda^{-2}\sigma_e^2 + \lambda^{-1}\tau, \qquad \text{eqn 3}$$

where $\sigma_e^2 = \mathrm{E}(\mathbf{v}\boldsymbol{\varepsilon}_t\mathbf{u})^2 = \sum v_i u_j v_k u_m \mathrm{cov}[L_{t,ij}, L_{t,km}]$ is the environmental variance (on the absolute scale) and $\tau = \mathbf{v}E(\boldsymbol{\varepsilon}_t\mathbf{x}_t)$. If the projection matrices $\boldsymbol{L}_t = \bar{\boldsymbol{L}} + \boldsymbol{\varepsilon}_t$ are temporally uncorrelated, then $\mathbf{x}_t$ depends only on noise matrices $\boldsymbol{\varepsilon}_s$ at earlier times $s < t$ so that $\mathbf{x}_t$ and $\boldsymbol{\varepsilon}_t$ are uncorrelated and $\mathrm{E}(\boldsymbol{\varepsilon}_t\mathbf{x}_t) = \mathbf{0}$, giving $\tau = 0$. For temporally autocorrelated environments, however, $\mathbf{x}_t$ and $\boldsymbol{\varepsilon}_t$ are no longer uncorrelated, and the last term may then be of the same magnitude as the environmental variance. More precisely, this occurs because $\mathbf{x}_t$ is a linear function of $\boldsymbol{\varepsilon}_{t-1}, \boldsymbol{\varepsilon}_{t-2}, \ldots$ and $\mathrm{E}(\boldsymbol{\varepsilon}_t\boldsymbol{\varepsilon}_{t-h})$ are generally different from zero for temporally correlated matrices. Appendix S1 shows how τ can be calculated from the temporal autocorrelations within and between the different vital rates and how the autocorrelated process V_t can be approximated by a diffusion process with white noise. Below, we present two much simpler expressions for τ that are useful for biological interpretations as well as statistical analysis.

Interpretations of τ

The elements in the projection matrix $\boldsymbol{L}_t$ are the realized vital rates in year t. For an age-structured (Leslie) projection matrix, $L_{1j} = \bar{B}_j$ is the mean number of offspring of individuals in age class j, while $L_{j+1,j} = \bar{I}_j$ is the fraction of individuals in that age class that survive to the next census, which is the mean value of the indicators I_j of survival for each individual (Engen *et al.* 2005) taking the value one if the individual survives and otherwise zero. Engen *et al.* (2009) defined the concept of individual reproductive value as an individual's contribution to the total reproductive value of the population the next year. Accordingly, an individual of age j with survival I_j producing B_j offspring surviving to the next census has individual reproductive value $W_j = v_1 B_j + v_{j+1} I_j$, where $v_{k+1} = 0$ for a Leslie matrix. We see that the mean individual reproductive value for individuals of age j at time t , $\bar{W}_j = v_1 \bar{B}_j + v_{j+1} \bar{I}_j$, is determined by the elements $\bar{B}_j$ and $\bar{I}_j$ of the Leslie matrix $\bar{\boldsymbol{L}}_t$. Because the L_{ij} are the mean vital rates of individuals a given year (exemplified by $\bar{B}_j$ and $\bar{I}_j$ above), it follows that $\sum_i v_i L_{ij}$ for a Lefkovitch model (Caswell 2001) with a terminal age class, or a general stage-structured model is the average individual reproductive value $\bar{W}_j$ of individuals in class j. The expectation of the individual reproductive values is $\mathrm{E} W_j = \sum_j v_i \bar{L}_{ij} = \lambda v_j$. In a given year with population vector $\mathbf{n}$, the total reproductive value of the population is $V = \sum n_j v_j$, while the value the next year is the stochastic quantity $V + \Delta V = \sum n_j \bar{W}_j$ determined by the environment in the current year. Accordingly, the distribution of the individual reproductive values determines the stochastic properties of age-structured populations. For a more detailed discussion of individual reproductive values and their role in dynamics of stochastic age-structured models, see Engen *et al.* (2009).

For an age-structured population in which the fluctuations in age structure have achieved stationarity, the stochastic multiplicative growth rate Λ_t for the reproductive value process defined by $V_{t+1} = \Lambda_t V_t$ is also a stationary process with some mean $\mathrm{E}\Lambda_t$ and variance var (Λ_t). To the second order of approximation, the long-run growth rate is accordingly $s = \mathrm{E} \ln \Lambda \approx \ln \mathrm{E}\Lambda_t - \frac{1}{2}\mathrm{var}(\Lambda_t)$. For age-structured populations, the effect of environmental autocorrelation on the long-run growth acts through the mean of the multiplicative growth rate $\mathrm{E}\Lambda_t$ and not the variance, which is affected only by the stationary distribution of $\boldsymbol{L}$ regardless of environmental autocorrelation.

To see this, we write (ignoring time subscripts)

$$\mathrm{E}\Lambda = \frac{\mathrm{E}(V + \Delta V)}{V} = \frac{\sum_j n_j \mathrm{E} \bar{W}_j}{\sum_j n_j v_j}.$$

Inserting $\bar{W}_j = \sum_i \mathrm{v}_i L_{ij} = \lambda v_i + \sum_i v_i \varepsilon_{ij}$ and $n_i = u_i V + x_i V$, and using $E x_j = E \varepsilon_{ij} = 0$, yields

$$\mathrm{E}\Lambda = \lambda + \mathrm{E}\left(\sum_{ij} v_i \varepsilon_{ij} x_j \right) = \lambda + \tau. \qquad \text{eqn 4}$$

This equation is fundamental for understanding the role of autocorrelated noise in age-structured dynamics. In models with no age structure as well as when using total reproductive values in age-structured models with no temporal autocorrelations in the environment, the expected value of the multiplicative factor Λ is always equal to the deterministic multiplicative growth λ. However, for age- or stage-structured models in temporally autocorrelated environments, these two quantities differ exactly by $\tau = \boldsymbol{v}\mathrm{E}(\boldsymbol{\varepsilon}_t \mathbf{x}_t) = \mathrm{E}\Lambda - \lambda$, where Λ is the stochastic multiplicative growth rate for the total reproductive value and λ is the multiplicative growth rate for the corresponding deterministic model with projection matrix $\bar{\boldsymbol{L}} = \mathrm{E}\boldsymbol{L}$. The variance of Λ is the conditional variance of $(V{+}\Delta V)/V$ given V. It follows from our previous results and those of Engen *et al.* (2009) that this variance is $\lambda^{-2}\mathrm{E}(v \varepsilon u) = \lambda^{-2}\sigma_e^2$, giving again $s = \mathrm{E}\ \ln\Lambda \approx \ln(\lambda + \tau) - \frac{1}{2}\lambda^{-2}\sigma_e^2 \approx r + \lambda^{-1}\tau - \frac{1}{2}\lambda^{-2}\sigma_e^2$. Notice that σ_e^2 and τ are defined at the absolute scale. On the log scale, however, on which s is defined, these additive components yield $\lambda^{-2}\sigma_e^2$ and $\lambda^{-1}\tau$, respectively.

A different interpretation turns out to be the most useful for estimating and testing the impact of environmental autocorrelation on the long-run growth rate. Inserting $\boldsymbol{\varepsilon} = \boldsymbol{L} - \bar{\boldsymbol{L}}$ and $x_i = n_i/V - u_i$ in terms of $\tau = \mathbf{v}\mathrm{E}(\boldsymbol{\varepsilon}\mathbf{x})$, we find the alternative expression $\tau = \sum_j \mathrm{cov}\left(\sum_i v_i L_{ij}, n_j/V\right)$. Here the covariance as well as expectations refers to the temporal distribution of $\boldsymbol{\varepsilon}$ generated by temporal variation in the environment. It appears that the component τ in the long-run growth rate generated by temporal autocorrelation in the projection matrices $\boldsymbol{L}$ can simply be written as

$$\tau = \sum_j \mathrm{cov}(\bar{W}_j, n_j/V). \qquad \text{eqn 5}$$

The parameter τ depends in a complex way on the sequence of noise matrices $\boldsymbol{\varepsilon}_t$, and it is possible to express it in different forms. Here, we have given two simple expressions in addition to the complex mathematical formula (eqn. 11 in Appendix S1). For a conceptual insight, we believe that eqn. 4 is most useful, expressing τ as the difference between the expected multiplicative growth rate and the multiplicative growth rate λ for the corresponding model in the average environment, which is the dominant eigenvalue of $\bar{\boldsymbol{L}}$. Equation 5 expresses τ as a sum of age-specific covariances that can be estimated from data. It also gives some conceptual insight as it is expressed by the covariances between mean individual reproductive values for each age class with stochastic component depending solely on the noise matrix the actual year, and the size of the same age class that has a stochastic component depending only on noise matrices from previous years. So, if the noise through some time has contributed to build a strong age class n_j and this age class also contributes strongly to future population sizes relative to its own size by a large $\bar{W}_j$, then $\mathrm{cov}(\bar{W}_j, n_j)$ is a positive contribution to τ. In other words, if an age class that is strong a given year also tends to perform better that year than the temporal average of that class in contribution per individual to future population sizes, then it contributes positively to τ. Contrarily, if it tends to give smaller than average contributions when the age class is strong, then this age-specific contribution to τ is negative.

Estimation and testing

Previously, we have shown how to estimate the stochastic growth rate in a density-independent age-structured population subject to demographic and environmental stochasticity in the absence of autocorrelation (Engen *et al.* 2007). The method is similar to the one proposed by Dennis, Munholland & Scott (1991), but is based on using the annual observed differences in log of total reproductive value, $\ln V_{t+1} - \ln V_t$, rather than log population sizes, as input observations in a likelihood function, assuming that these differences are approximately normal. The method requires that the demographic variance and reproductive values are first estimated from individual measurements of survival and reproduction (Engen *et al.* 2005) and then considered as known in a pseudolikelihood function (Cox & Reid 2004). The mean of the above difference is approximately $\ln\lambda - \lambda^{-2}\sigma_e^2/2 - \lambda^{-2}\sigma_d^2/(2V_t)$ assuming no environmental autocorrelation, where σ_d^2 is the demographic variance for the age-structured process defined by Engen *et al.* (2005). With environmental autocorrelation $\ln\lambda$ should be replaced by, or reinterpreted as, $\ln\lambda + \tau/\lambda$. The previous estimate of the long-run growth rate $\ln\lambda - \lambda^{-2}\sigma_e^2/2$ will now also serve as an estimate of the long-run growth rate with the term τ/λ included. So, the method for estimating the long-run growth rate by this approach remains exactly the same in the case of autocorrelated environments, and no separate estimate of τ is required for estimating s. Demographic noise terms are by definition serially independent (Engen, Bakke & Islam 1998) and therefore have no influence on τ.

However, it may still be of interest to explore how much environmental autocorrelation influences the long-run growth rate. This can be made by computing each term in eqn. 5 from time-series observations of $\bar{W}_j$ and n_j/V. This approach does not require that the whole population is observed as long as approximately unbiased estimators of the n_j/V are available from random samples or from some other sampling technique correcting for possible unequal sampling intensities of the different age classes, because covariances in eqn. 5 are unaffected by stochastic errors in the n_j/V with zero expectations, although the precision in the covariance estimates is decreased.

To estimate the autocorrelation ρ_h for the environmental noise in the differences of log reproductive values, we compute the variables $\xi_t = [\ln V_{t+1} - \ln V_t - (\ln\lambda + \tau/\lambda - \lambda^{-2}\sigma_e^2/2 - \lambda^{-2}\sigma_d^2/(2N_t)]/\sigma_e$ with estimated values inserted for the parameters. These variables can be written as $\xi_t = \mathrm{U}_{et} + \mathrm{U}_{dt}\sqrt{\sigma_d^2/(\sigma_e^2 N_t)}$, where all U_{et} and U_{dt} are independent standardized variables. Then $\mathrm{E}(\xi_t\xi_{t+h}) = \mathrm{corr}(\mathrm{U}_{et}, \mathrm{U}_{e,t+h}) = \rho_h$. Testing is most conveniently performed by parametric bootstrapping, assuming that the noise components on the log scale, U_{et} and U_{dt}, are normally distributed. Then ξ_t can be simulated under the null hypothesis of no environmental autocorrelation in U_{et}, and the simulated replicates can be compared with the observations.

A simple illustrative model

To facilitate the interpretation of the general results, we consider a simplified model with a terminal stage for individuals of age a and older and constant annual survival probabilities, that is, $L_{i+1,i} = p_i$ for $i = 1,2\ldots a{-}1$, and $L_{aa} = p_a$. Individuals do not reproduce until the terminal class is reached, that is, $L_{1,i} = 0$ for $i = 1,2,\ldots,a{-}1$. Assuming a post-breeding annual census of the population, the final element in the top row of the projection matrix is the recruitment rate, that is, the adult annual fecundity multiplied by the survival from birth to age 1, so that $L_{t,1a} = F_t$, which is stochastic with mean $\bar{L}_{1a} = f$. The other elements of L_t are zero. We shall assume that annual fecundity times first year survival F_t can be described by a first-order autoregressive model

$$F_{t+1} = f + \beta(F_t - f) + \sigma U_t,$$

where U_t is a sequence of independent standardized variables with zero mean and unit variance. The stationary variance of F_t is $\sigma_f^2 = \mathrm{var}(\varepsilon_{1a}) = \sigma^2/(1-\beta^2)$, and the autocovariance function is $\mathrm{cov}(F_t, F_{t-h}) = \sigma_f^2\beta^{|h|}$. We define the mean return time to equilibrium T_f as the time it takes for the temporal autocorrelation to decrease to e^{-1}, that is $T_f = -1/\ln\beta$. In this model, there is only a single term in the summation for the environmental variance, $\sigma_e^2 = \lambda^{-2}v_1^2u_a^2\sigma_f^2$. For further details, see Appendix S2.

We use this model to provide three examples illustrating the importance of the term $\lambda^{-1}\tau$ compared with the term $\lambda^{-2}\sigma_e^2/2$. In these examples, the term due to environmental autocorrelation exceeds that due to the environmental variance when T_f is larger than about 2 (Fig. 1) and is more than twice as large when T_f is large.

Figure 2 depicts sample trajectories of this model with four age classes for four different time-scales of environmental autocorrelation in fecundity, β = 0·5,0·75 and 0·9 (corresponding to T_f = 1·44, 3·48 and 9·49), as well as β = 0 (T_f = 0) corresponding to white noise. As T_f increases, the population size displays increased autocorrelation, resulting in a smoother graph. Consequently, the diffusion approximation, which has white noise, cannot be expected to perform well for short time intervals. The diffusion approximation, however, is based on calculating the variance over moderately long time intervals, which are also usually most interesting in relation to conservation and population viability analysis (see Appendix S2). Figure 3 illustrates this in a model with three age classes, showing quantiles of the actual population size, with its rather complex dynamics, compared with those found from the univariate diffusion approximation with only two parameters (Turelli 1977). It appears that the diffusion is quite accurate for small as well as large time steps when β = 0·5. For β = 0·9, on the other hand, the diffusion does not perform well for time intervals smaller than about $2T_f \approx 20$, but still performs remarkably well for longer intervals. Notice also that the lower graph (Fig. 3b)

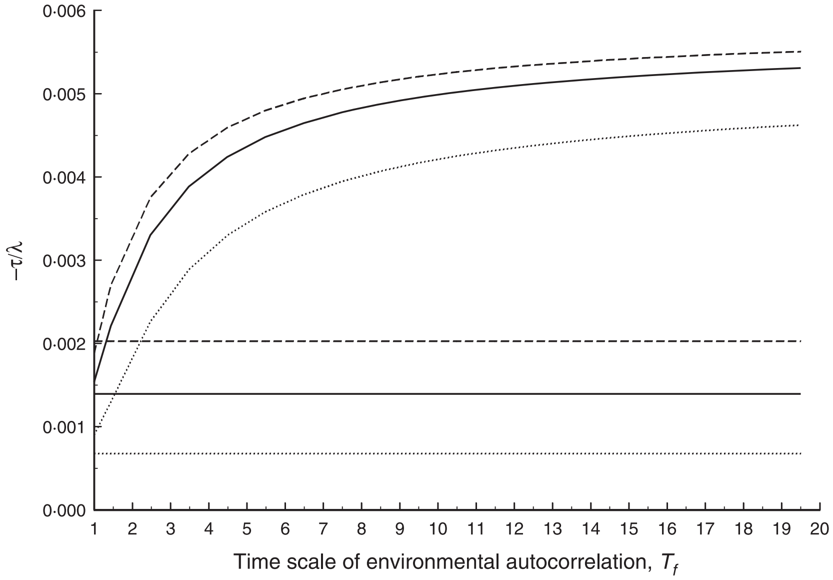

Fig. 1. The term $-\tau/\lambda$ in the second-order approximation to the long-run growth rate (eqn 3) as a function of T_f for three different models, together with the constant term $\lambda^{-2}\sigma_e^2/2$. No temporal autocorrelation corresponds to $T_f = 0$. The solid and dashed lines are for the same model as in Figs 2 and 3, respectively. The dotted line represents a model of the same type with seven age classes. Annual survival probabilities for the first six age classes are 0·8, 0·95, 0·95, 0·95, 0·9, 0·9, while the terminal age class has annual survival 0·7. Fecundity times first year survival is nonzero only for the seventh (terminal) class, with mean 0·5 and variance 0·03.

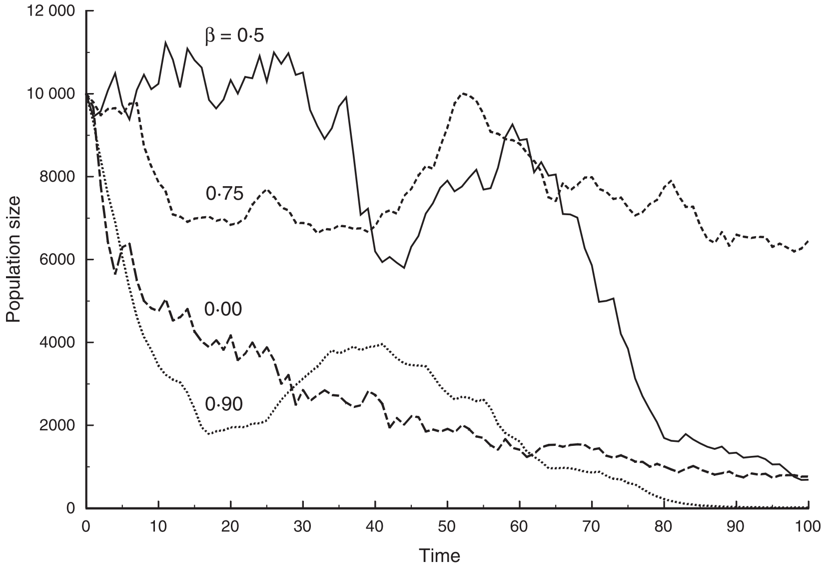

Fig. 2. Trajectories for populations described by a projection matrix with four age classes, where the 4th (terminal) class has survival 0·7. The survival for the first three classes are 0·7, 0·9 and 0·8. The fecundities are zero except for the terminal class, which has mean fecundity 0·5. The only stochastic element in the matrix is the recruitment rate or adult fecundity times first year survival. The variance in recruitment rate is 0·03. The recruitment rate is temporally autocorrelated, following the first-order autoregressive model in the text. Trajectories are shown for four different time-scales of environmental autocorrelation, $\beta = 0{,}0{\cdot}5$, 0·75 and 0·90. The temporal autocorrelation function for recruitment is $\rho(h) = \beta^{|h|}$, giving $T_f = -1/\ln\beta$, so the mean return times to equilibrium are 0, 1·44, 3·48, and 9·49 years.

with $\beta = 0{\cdot}9$ has slightly smaller growth in population size due to the effect of parameter τ.

Our results are all based on the second-order approximation to the long-run growth rate. One can show that if all environmental stochastic deviations in vital rates are normally distributed, then the third-order term is exactly zero, indicating that the second-order approximation in general is very accurate. Figure 4 depicts simulations of the long-run growth rate, each based on 10^6 simulations of yearly change in log population size, for the model in Fig. 1 with a multivariate normal distribution for the fecundity through time. The second-order approximation turns out to be very accurate for $T_f < 2{\cdot}5$

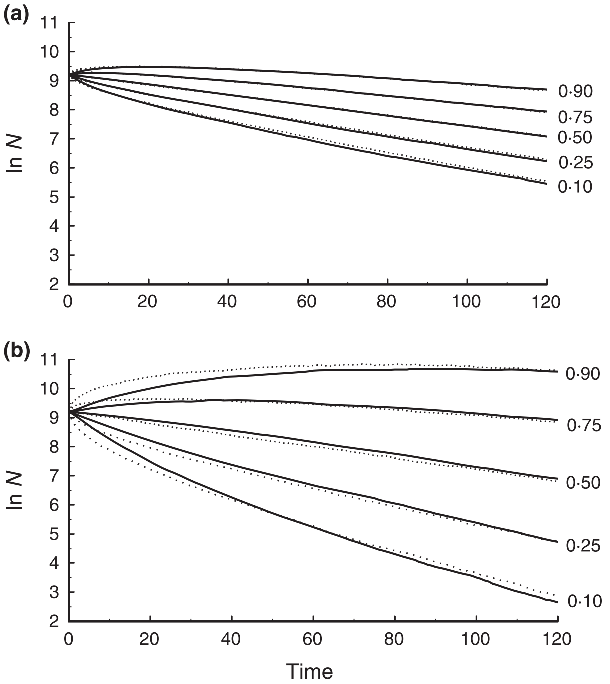

Fig. 3. Quantiles for the population size based on 10 000 simulations. The projection matrix has three stages with a terminal age class with survival 0·7. The first two age classes have survival 0·7 and 0·8. Reproduction only occurs in the terminal class with mean 0·5 and variance 0·03. Recruitment follows the first-order autoregressive model in the text. In the upper panel (a), the time-scale of environmental autocorrelation for recruitment is $T_f = 1{\cdot}44$ ($\beta = 0{\cdot}5$). With these assumptions, we find $r = \ln\lambda = -0{\cdot}0128$, $\sigma_e^2 = 0{\cdot}0040$, and $\tau = -0{\cdot}0027$. The infinitesimal mean and variance of the diffusion approximation are $\mu = -0{\cdot}0175$ and $\nu = 0{\cdot}0122$. In the lower panel (b), the time-scale of environmental autocorrelation in recruitment is $T_f = 9{\cdot}49$ ($\beta = 0{\cdot}9$), giving the same r and σ_e^2, but different $\tau = -0{\cdot}0051$, $\mu = -0{\cdot}0200$ and $\nu = 0{\cdot}0771$.

corresponding to a temporal correlation of fecundity at time lag one being smaller than 0·67. The diffusion approximation is also quite accurate for the whole range of values shown with autocorrelations at time lag one year up to 0·95 ($T_f = 20$), which is much larger than realistic values under environmental stochasticity in recruitment rate.

Impact of environmental autocorrelation on the dynamics of four mammal populations

We applied our method by estimating the impact of environmental autocorrelation on the population dynamics of two ungulate and two rodent species during periods of relatively continuous density-independent growth. We used data on the Bighorn sheep population at Ram Mountain (52°N, 115°W) in Alberta, Canada, during a period of exponential growth from 1981 to 1992 after removal of individuals for translocation to other areas was stopped (Festa-Bianchet 1998; Engen *et al.* 2007). Later, the population stabilized and then declined, partly because of intense Cougar (*Puma concolor*) predation (Festa-Bianchet *et al.* 2006). The demographic data of the Columbian ground squirrel was obtained at 1500 m elevation at the Sheep River Wildlife Sanctuary in the Rocky Mountains of south-western Alberta, Canada (50°N, 110°W). All adults older than 1 year of age were removed in 1990, ensuring that when the study started in 1992, the population was likely to be far below the carrying capacity (Engen *et al.* 2009). Red deer has been studied at the Island of Rum, Scotland (57°01′N, 6°17′W), for several decades (Clutton-Brock & Coulson 2002). In the present analyses, we include data only from the period 1974–1988. During most of this period, the population recovered from the termination of harvesting in 1972 (Coulson *et al.* 2004). Yellow-bellied marmots are a large diurnal burrow-dwelling rodent, living in mountain regions of western North

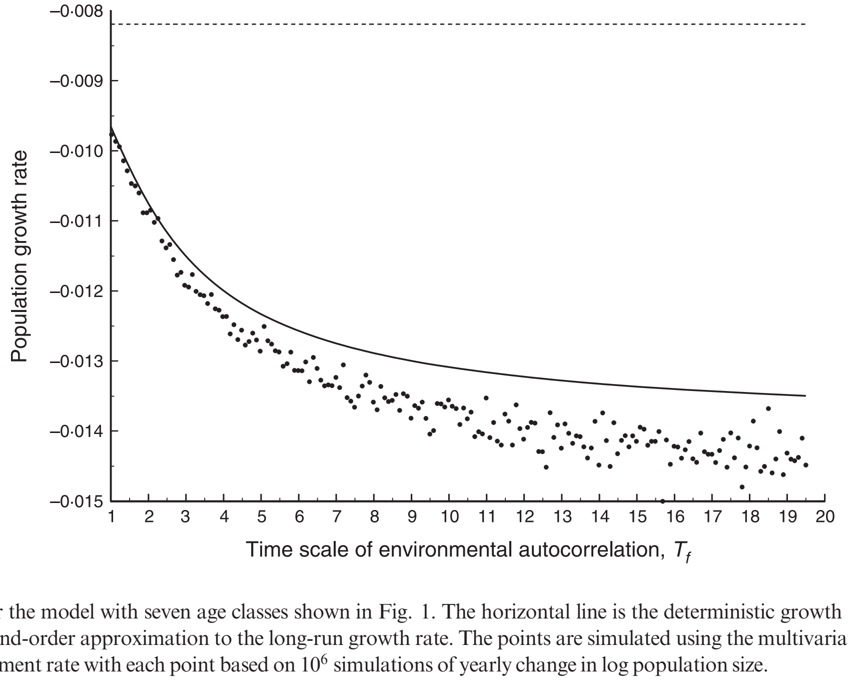

Fig. 4. Growth rates for the model with seven age classes shown in Fig. 1. The horizontal line is the deterministic growth rate $r = \ln\lambda$, while the solid line shows the second-order approximation to the long-run growth rate. The points are simulated using the multivariate Gaussian distribution for the stochastic recruitment rate with each point based on 10^6 simulations of yearly change in log population size.

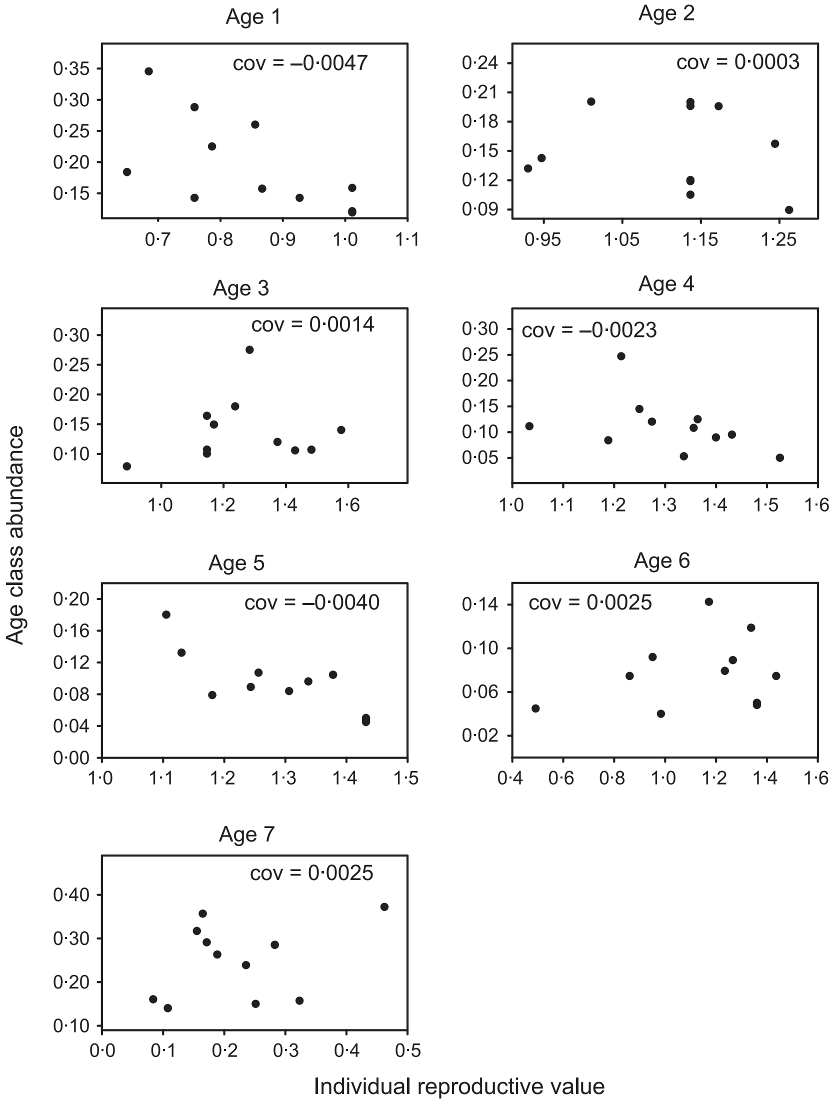

Fig. 5. Relative abundance of age classes n_j/V versus mean individual reproductive value $\bar{W}_j$ for age classes 1– 7 for the Bighorn sheep. The 7th (terminal) class contains all individuals of age 7 and older.

America, which hibernates from September or October to April or May. The critical factor determining winter survival and subsequent reproductive success is the amount of fat accumulated before hibernation (Melcher, Armitage & Porter 1989). Survival and reproduction are affected by the length of the active season, which shows substantial annual variation due to onset and termination of snow cover (Schwartz, Armitage & Van Vuren 1998; Ozgul *et al.* 2010). We included data collected during the period 1962–2007 from a population living in a subalpine habitat in the Upper East River Valley (38°57′N, 106°59′W), Colorado, USA. Parameter estimates are based on fluctuations in the size of the different age classes as well as on individual variation in reproductive success (see Engen *et al.* 2007 for further details).

If environmental autocorrelation influences population growth rate, there must be a temporal covariance between mean individual reproductive value $\bar{W}_j$ and n_j/V. In Fig. 5, we plot these covariances for Bighorn sheep through time. It is evident that for all age classes, these covariances are small and insignificant. A similar pattern also appeared for the other species. Accordingly, the estimates of the component τ/λ of the long-run growth rate due to possible temporal autocorrelations in vital rates were not significantly different from zero in any of the species (Table 1, Fig. 6). The distributions of the bootstrap replicates reveal that in all species, the uncertainties in the estimates of τ/λ are large (Fig. 6).

There were large interspecific differences in the estimates of the environmental variance, being smallest in the Bighorn sheep and largest in the Columbian ground squirrel (Table 1). The reduction in the long-term population growth rate due to fluctuations in the environment was negligible in the two ungulate species , whereas in the two smaller mammals, both the environmental variance and the autocorrelation in the environment showed a greater influence on the stochastic population growth rate (Table 1).

Table 1. Estimates of parameters characterizing the dynamics of 4 mammal species during periods of density-independent growth. $r = \ln \lambda$ is the long-term population growth rate, σ_e^2 is the environmental variance, τ/λ is the environmental autocorrelation, and s is the stochastic population growth rate. The terms $\frac{1}{2}\sigma_e^2\lambda^{-2} - \tau/\lambda$ denote the contribution from environmental stochasticity and temporal environmental autocorrelation to s

Species	Locality	Period	r	σ_e^2	τ/λ	$\frac{1}{2}\sigma_e^2\lambda^{-2} - \tau/\lambda$	s
Bighorn sheep	Ram Mountain	1981–1992	0·1054 ± 0·0195	0·0027 ± 0·0013	−0·0041 ± 0·0049	0·0053	0·1003 ± 0·0189
Columbian ground squirrel	Sheep River Wildlife Sanctuary	1992–2007	0·0783 ± 0·0967	0·1057 ± 0·0551	0·0172 ± 0·0250	0·0340	0·0443 ± 0·0895
Red deer	Island of Rum	1974–1988	0·0538 ± 0·0185	0·0038 ± 0·0015	0·0023 ± 0·0019	−0·0006	0·0543 ± 0·0184
Yellow-bellied marmot	Upper East River Valley	1992–2007	0·0856 ± 0·0524	0·0231 ± 0·0102	−0·0218 ± 0·0116	0·0341	0·0531 ± 0·0509

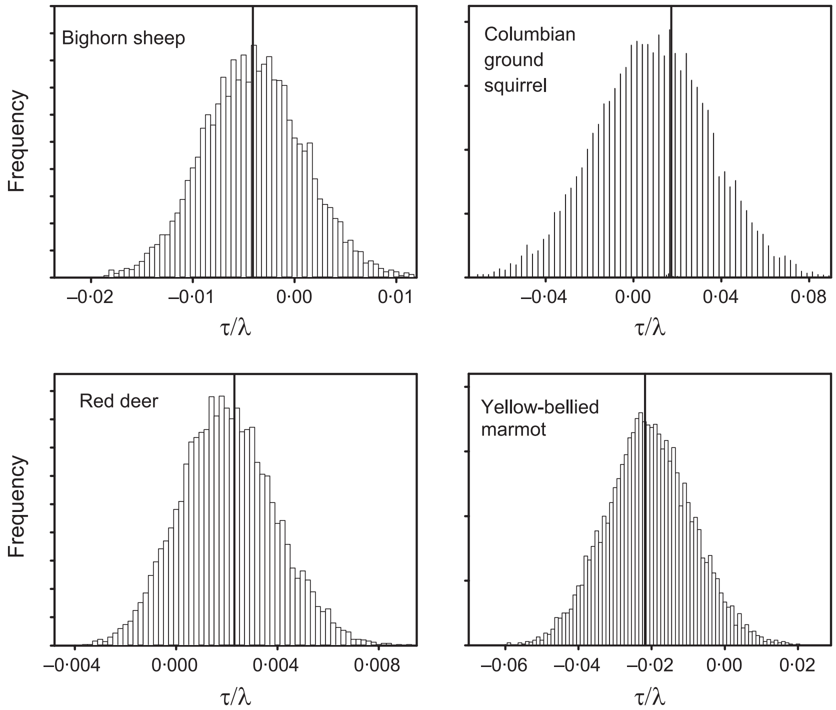

Fig. 6. Histogram of 10 000 bootstrap replicates of the environmental autocorrelation τ/λ for Bighorn sheep, Columbian ground squirrel, Red deer, and Yellow-bellied marmot. The vertical line shows the estimated value of τ/λ.

Discussion

The complexity of temporal autocorrelation makes it difficult to analyse, theoretically as well as empirically (Heino, Ripa & Kaitala 2000; Halley & Inchausti 2004; Staples *et al.* 2009). In age-structured populations, this becomes particularly difficult if one is interested in the dynamics of the total population size, because stochastic fluctuations in age structure by itself produce temporal autocorrelations (Holmes 2004). Fisher (1930) elegantly showed how to partly avoid this problem in deterministic theory by introducing the concept of total reproductive value of the population to eliminate transient fluctuations caused by age structure, assuming no density-dependent population regulation. Engen *et al.* (2007) showed how Fisher's concept can be extended to stochastic population fluctuations. If the population vector is subject to white environmental noise, then the total population size may be substantially autocorrelated, whereas the total reproductive value is not autocorrelated. Accordingly, the first step in analysing age-structured populations in a stochastic environment is to work with the total reproductive value rather than the total population size. If temporal autocorrelation in total reproductive value still exists, this then results only from environmental autocorrelation. In general, the fluctuations in the total reproductive value of the population provide an accurate description of the population dynamics if there is no or weak density regulation (Engen *et al.* 2007; Sæther *et al.* 2007). We then used this to estimate the long-run growth rate under temporally correlated environmental noise in four populations of mammals (Table 1) and the component due to this autocorrelation (Fig. 6, Table 1).

Environmental autocorrelation affects the long-run growth rate of the population through the extra term τ/λ (eqns 3–5). In the absence of age-structure, τ/λ is always zero. So, the effect of autocorrelations on τ/λ and the variance v used in the diffusion approximation must depend strongly on the life history of the species. This makes it difficult to make or draw any general conclusions about the influence of τ/λ on the population dynamics. Even in our simplified illustrative model (Appendix S2), in which stochasticity occurs only in recruitment, we can only conclude that increased time-scale of autocorrelation in recruitment increases τ/λ as well as the environmental variance (eqns 6 and 7). Each model must be investigated separately to assess the impacts of environmental autocorrelation.

The extra term τ/λ was derived by Tuljapurkar (1982) and further discussed by Tuljapurkar & Haridas (2006). It is a rather complicated term, depending on temporal autocorrelations between all vital rates, as expressed formally by Tuljapurkar (1982) using Kronecker products and all eigenvalues of the mean projection matrix $\bar{\boldsymbol{L}}$ (see Appendix S1, eqn 11). Here, we have given an expression for τ (eqn. 5) that facilitates a much simpler and transparent interpretation and that also leads to a simple estimation method. Both results are, however, derived from the same second-order terms and are therefore equivalent. We find that τ is a sum over all age classes of covariances between mean individual reproductive values $\bar{W}_j$ and size of the class relative to total reproductive value, n_j/V (Fig. 5). Provided that an estimate of the mean projection matrix is available, these quantities can be computed for each age class, giving correlation (covariance) plots illustrating the age-specific contributions (Fig. 5). The plots require that vital rates are measured for random samples of individuals from the population or from the total population. A biased sampling of age classes would lead to biased estimates of the variables n_j/V and would therefore also give biased estimates of the covariance terms. The variables $\bar{W}_j$, however, can be estimated without bias even if age classes are sampled in a nonproportional way. The advantage of this approach is that no estimation of the temporal autocorrelations and cross-correlations in the large number of age-specific vital rates is required. Instead, we use directly the fluctuations in the observed age distribution expressed by the quantities n_j/V, generated by all previous noise terms in vital rates. Although we have formally assumed that the demographic variance can be ignored for the populations we have analysed, this assumption is not critical for the results. This is because we estimate covariances from the data, and the demographic noise terms do not contribute to these covariances. However, it will decrease precision of the estimates.

The computation of $\bar{W}_j$ requires that the reproductive values $v_1, v_2, \ldots, v_k$ first are estimated using an estimate of $\boldsymbol{L}$ based on temporal means of vital rates. Although this leads to sampling errors in the $\bar{W}_j$, this uncertainty is not likely to give significant bias in the estimated covariances because the errors are practically independent of the values of n_j a single year. When analysing small sets of data, however, this uncertainty should be investigated by including it in the resampling method used to produce Fig. 6, that is, choosing a resampled $\mathbf{v}$ for each replicate of τ/λ.

We have also illustrated another interpretation of τ. In the absence of age structure, the expected multiplicative growth rate $\lambda = \mathrm{E}\Lambda$ expressing the growth of the expected population size is not affected by temporal environmental autocorrelation. With age structure, on the other hand, the expected value of $\Lambda = V_{t+1}/V_t$ is affected by environmental autocorrelation as in eqn. 4, $E\Lambda = \lambda + \tau$, where λ is the expectation in the absence of autocorrelations. This occurs even if we have used the total reproductive value rather than the total population size in the definition of Λ. So, it appears that environmental autocorrelation affects the multiplicative growth rate $\mathrm{E}\Lambda$, while the environmental variance $\sigma_e^2 = \mathrm{var}(\Lambda)$ affects what happens when transforming from absolute to log scale, contributing the term $-\lambda^{-2}\sigma_e^2/2$ to $\mathrm{E}\ln\Lambda$.

Our illustrations of τ in Figs 1 and 3 indicate that this term is likely to be rather small compared with the term $-\lambda^{-2}\sigma_e^2/2$, for realistic values of the environmental autocorrelation. Realistic time-scales of environmental autocorrelation are rarely longer than a few years. Only long time-scales of environmental autocorrelation will contribute substantially to the long-run growth rate (Fig. 3). Furthermore, the impact of environmental autocorrelation on the variance of the diffusion approximation is much more important than that on the long-run growth rate for time intervals as large as 120 years.

Because the time series with annual increments are rarely longer than a few decades, estimates of environmental variances are generally rather uncertain (Holmes 2004; Sæther *et al.* 2008; Staples *et al.* 2009). In small populations where the demographic variance also must be taken into account, this difficulty is magnified. The same argument applies to the estimation of the extra component τ/λ of the long-run growth rate due to environmental autocorrelation. Our estimates of this extra term are negative for the Bighorn sheep and Yellow-bellied marmots, but positive in two other species (Table 1). However, none of the estimates were significantly different from zero (Fig. 6). This suggests that the conclusions of Morris *et al.* (2011) of small impact of autcorrelations in the environment on the dynamics of primate populations may indicate a general pattern in mammals. Similar uncertainty also occurs in estimation of the environmental autocorrelations ρ_h. The variables ξ_t we used have substantial demographic components due to small population size making the variance in products like $\xi_{t+1}\xi_t$ large (although demographic stochasticity does not affect the expectation of these products), resulting in lower power of the test. The only way of improving these estimates is by collecting data over longer time periods (Dennis *et al.* 2006; Sæther *et al.* 2008) or having parallel sampling in space at distances large enough to give small spatial autocorrelations in environmental noise (Dennis, Kemp & Taper 1998).

The present model is based on the assumption of no density regulation. In general, density dependence in age-structured populations is complicated because all age classes may have different unknown effects on each other (Lande *et al.* 2006). On the other hand, if a population fluctuates around an equilibrium, the average growth rate is zero, so the effect of temporal autocorrelation is not that interesting, although it may affect the stationary distribution of population size. The present theory is more important when it comes to analysing populations that are far below the carrying capacity and may be threatened by extinction. We have shown how the temporal autocorrelation then affects the dynamics that can be approximated accurately by a diffusion even when temporal autocorrelation in vital rates is considerable. Well-known diffusion formulas for extinction or quasi-extinction (Lande, Engen & Sæther 2003) then apply and can be used to explore how autocorrelations affect the expected lifetime of populations (e.g. Petchey, Gonzalez & Wilson 1997; Ripa & Heino 1999; Heino, Ripa & Kaitala 2000).

An important question in population ecology is how the effects of changes in the environment on population dynamics are related to differences in life history. Some evidence indicates that the influence of environmental stochasticity in annual changes in population size decreases with life expectancy (Morris *et al.* 2008; Sæther *et al.* in preparation), indicating that long-lived species are more buffered against environmental fluctuations than short-lived species. Such a buffering effect may also be dependent of the autocorrelation in the environment (Cuddington & Yodzis 1999; Drake 2005; Wilmers, Post & Hastings 2007; van de Pol *et al.* 2011). Accordingly, the data for the two ungulate species were collected during a period of rapid population growth after a period of forced removal of individuals (Bighorn sheep) and cessation of hunting (Red deer). During this period, adult survival was high and the temporal variation in recruitment was small (Coulson *et al.* 2004; Jorgenson *et al.* 1997; Portier *et al.* 1998). Our results show that a negative extra component τ/λ of the long-run growth rate due to environmental autocorrelation will reduce the stochastic growth rate s. In fact, such a negative effect of autocorrelation (although not statistically significant) was estimated in the two smaller mammals included in the present study (Table 1). In Yellow-bellied marmots, this negative autocorrelation may be influenced by the social system. For instance, as matriline size increases, the net reproductive rate may first increase and then decline in the largest matrilines (Armitage 2012), which may produce autocorrelations in the population growth rates. The theoretical analysis suggests that the temporal scaling of this autocorrelation must be long to substantially affect the long-term population growth rate (Figs 1 and 2).

Empirical analyses of temporal variation in environmental variables have revealed several large-scale pattern of variation, indicating that, for example, in marine environments, the temporal scaling of changes in the environment often is long (Steele 1985; Vasseur & Yodzis 2004; Cyr & Cyr 2003; Halley 2009). Our method can be used to examine how such differences in environmental autocorrelations affect the long-term growth of populations. This will be important for fully exploring the effects on population viability of expected changes in climate that are likely to strongly affect the autocorrelation structure in many environmental variables (IPCC 2007).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Long-run growth rate and temporal autocorrelations.

Appendix S2. A simple illustrative model.