

Estimating Density Dependence from Time Series of Population Age Structure

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ABSTRACT: Population fluctuations are caused by demographic and environmental stochasticity, time lags due to life history, and density dependence. We model a general life history allowing density dependence within and among age or stage classes in a population undergoing small or moderate fluctuations around a stable equilibrium. We develop a method for estimating the overall strength of density dependence measured by the rate of return toward equilibrium, and we also consider a simplified population description and forecasting using the density-dependent reproductive value. This generality comes at the cost of requiring a time series of the population age or stage structure instead of a univariate time series of adult or total population size. The method is illustrated by analyzing the dynamics of a fully censused population of red deer (*Cervus elaphus*) based on annual fluctuations of age structure through 21 years.

Keywords: rate of return to equilibrium, demographic stochasticity, environmental stochasticity, reproductive value, red deer.

Demographic and environmental stochasticity in age-specific vital rates, acting through time lags in the life

history and density dependence, create continual fluctuations in population size and age structure (Coulson et al. 2001; Clutton-Brock and Coulson 2002). Comparative studies attempting to analyze the influence of life history on population dynamics have been impeded by lack of a general theory to account for these factors (Pimm 1991; Ariño and Pimm 1995; Inchausti and Halley 2001, 2002).

Demographic stochasticity is caused by variation in fitness among individuals within years, usually attributed to independent chance events of individual survival and reproduction, producing random changes in population growth rate, with a variance inversely proportional to population size, σ_d^2/N . In contrast, environmental stochasticity affects the age-specific vital rates of all individuals in a population in the same or similar way, producing a constant variance among years in population growth rate, σ_e^2 , independent of population size. Thus, environmental stochasticity affects populations of all sizes, whereas demographic stochasticity most strongly affects small populations. Environmental stochasticity dominates for population sizes greater than the ratio of the demographic and environmental variances, $N > \sigma_d^2/\sigma_e^2$, usually on the order of a few hundred individuals (Lande et al. 2003).

Turchin (1990) analyzed population time series to detect delayed density dependence in a variety of species, caused in part by environmental autocorrelation and interspecific interactions (e.g., see also Turchin and Taylor 1992; Forchhammer 1998; Solberg et al. 1999; Fromentin et al. 2001). One problem with this method is that time lags inherent in individual development and life history can also give the appearance of delayed density dependence.

Lande et al. (2002a, 2002b) addressed this problem using a simple life history with age at maturity α and environmental stochasticity in the age-specific vital rates and assuming all density dependence to be exerted by the adult stage class. For age-structured populations reproducing at discrete annual intervals, Lande et al. (2002a, 2002b) analyzed small or moderate fluctuations in population size around a stable equilibrium, which is applicable to many vertebrate populations with coefficients of variation of population size less than about 30% (Lande et al. 2003).

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They derived an autoregressive equation for the adult population size, N , with time lags from 1 to α years. For such populations, the autoregression coefficients corresponding to different time lags are not simply measures of delayed density dependence; they also depend on life-history parameters. The theory indicates that the total density dependence in a life history, D , should be defined as the negative elasticity of population growth rate per generation, λ^T , with respect to change in the adult population size at equilibrium (where $N = K$ and $\lambda = 1$), where λ is the asymptotic multiplicative growth rate per year and T is the generation time. This gives the total density dependence per generation in the life history as $D = -(T\partial \ln \lambda / \partial \ln N)_K$, which can be estimated using the sum of the autoregression coefficients. The strength of density dependence per year, $\gamma = D/T$, gives the rate of return to equilibrium.

Lande et al. (2002a, 2002b) and Sæther et al. (2005) estimated D in populations of several vertebrate species for which life-history studies and long time series of adult numbers were available based on complete population censuses. In most cases, estimates of D were statistically significant and large, on the order of 1 or higher, indicating strong and statistically significant density dependence. Lande et al. (2002a) also showed that in an environment with no temporal autocorrelation, a density-dependent life history produces a red-shifted power spectrum typically observed for population fluctuations (Ariño and Pimm 1995).

The primary purpose of this article is to develop a method for analyzing density dependence in populations with a general life history allowing density dependence within and among age classes. For example, many reptiles and fish grow continually so that female fecundity increases with age, and in large birds and mammals, midlife survival may be sufficiently high that senescent declines in adult survival and fecundity become demographically important (Fisher 1958; Roff 1992; Stearns 1992; Charnov 1993; Charlesworth 1994). This increased generality comes at the cost of requiring substantially more data than the previous method. Instead of a univariate time series of adult population numbers, the current method requires a multivariate time series of the age or stage structure. A limitation of this approach is that the number of age or stage classes must be restricted to a small proportion of the length of the population time series to obtain statistically accurate estimates of the density dependence among classes; this will often necessitate lumping older age groups into a few classes or otherwise describing the life history with a moderate number of parameters.

Tuljapurkar and Lee (1997) and S. Engen, R. Lande, and B.-E. Sæther (unpublished manuscript) showed that age-structured populations undergoing density-independent

fluctuations can be described using Fisher's (1958) reproductive value. The current practice of estimating environmental variance directly from observed fluctuations in total population size (e.g., Holmes 2001; Morris and Doak 2002) fails to account for fluctuations in age structure, which can greatly inflate estimates of environmental variance. S. Engen, R. Lande, and B.-E. Sæther (unpublished manuscript) demonstrate by simulation that the use of reproductive value can eliminate this source of bias in estimates of environmental variance, if there is no environmental autocorrelation.

Here we extend the approach of S. Engen, R. Lande, and B.-E. Sæther (unpublished manuscript) to density-dependent populations by defining a density-dependent reproductive value. For a population undergoing small or moderate fluctuations around a stable equilibrium, we develop a general method for estimating the overall strength of density dependence in the life history, measured by the rate of return to equilibrium, as well as a description of environmental stochasticity. If density dependence is not very strong, we also show that the density-dependent reproductive value can provide a simplified univariate description that is nearly as accurate as using the full projection matrix to predict fluctuations in population size around the equilibrium. For simplicity, the model is developed for a stochastic environment, assuming that the population size remains sufficiently large to neglect demographic stochasticity. However, we show that the effective total stochasticity near equilibrium, and the contribution of demographic stochasticity to it, can also be estimated. The method is illustrated by analyzing the age-structure dynamics of a fully censused population of red deer (*Cervus elaphus*) through 21 years.

Density-Dependent Model

Denoting the transpose of a matrix by a prime, we write $\mathbf{n} = (n_1, n_2, n_3, \dots)'$ for the column vector describing a population with age or stage classes censused just before reproduction, and $N = \sum n_i$ for the total population size. In a density-regulated population, the elements of the projection matrix are functions of the population vector, $L_{ij} = L_{ij}(\mathbf{n})$. We assume that there is a stable equilibrium at $\hat{\mathbf{n}} = K\mathbf{u}$, where \mathbf{u} is the stable age distribution normalized so that its elements sum to unity and K is the equilibrium population size or carrying capacity. The leading (or dominant) left and right eigenvectors of $\hat{\mathbf{L}} = \mathbf{L}(\hat{\mathbf{n}})$ associated with the leading eigenvalue $\lambda = 1$ are the reproductive value vector \mathbf{v} (a row vector) and the stable age distribution \mathbf{u} (a column vector), respectively, satisfying $\mathbf{v}\hat{\mathbf{L}} = \mathbf{v}$ and $\hat{\mathbf{L}}\mathbf{u} = \mathbf{u}$ (Fisher 1958; Caswell 1989, 2001). The reproductive value vector is normalized so that $\mathbf{v}\mathbf{u} = \sum v_j u_j = 1$. Thus, at equilibrium, the total repro-

ductive value in the population equals the carrying capacity $\mathbf{v}\hat{\mathbf{n}} = K$.

Assuming that the population is sufficiently large to neglect demographic stochasticity, the dynamics are governed by the stochastic projection matrix $\mathbf{M}_t = \mathbf{L}(\mathbf{n}_t) + \boldsymbol{\varepsilon}_t$, where $\boldsymbol{\varepsilon}_t$ is a matrix of environmental noise, with mean 0, appearing in the general density-dependent model,

$$\mathbf{n}_{t+1} = \mathbf{M}_t \mathbf{n}_t.$$

The equilibrium total population size, K , given by the sum of elements of the equilibrium population vector, $\hat{\mathbf{n}}$, is completely determined by the density dependence of age- or stage-specific birth and death rates and is not an independent parameter. Thus, there is no need for special consideration of fluctuations in carrying capacity.

The deviation from the equilibrium or stable age distribution is defined by the relation $\mathbf{y}_t = \mathbf{n}_t/K - \mathbf{u}$. For small or moderate fluctuations around the equilibrium, the linearized dynamics are derived in the appendix in the online edition of the *American Naturalist*:

$$\mathbf{y}_{t+1} = (\hat{\mathbf{L}} - \mathbf{D})\mathbf{y}_t + \boldsymbol{\varepsilon}_t \mathbf{u}. \quad (1)$$

The stability matrix $\hat{\mathbf{L}} - \mathbf{D}$ differs from the equilibrium projection matrix for the population structure $\hat{\mathbf{L}}$ by the matrix \mathbf{D} containing all of the density dependence expressed as derivatives of the vital rates with respect to densities of the age or stage classes, evaluated at equilibrium. The element $D_{ij} = -K \sum_k (\partial L_{ik} / \partial n_j) u_k$ is the net effect of a small change in n_j on the vital rates of all age classes k contributing to age class i , weighted by the frequency of age class k .

Transforming back to the population vector \mathbf{n}_t by substituting the definition of \mathbf{y} on both sides, and writing the stability matrix as $\tilde{\mathbf{L}} = \hat{\mathbf{L}} - \mathbf{D}$, equation (1) can be expressed as

$$\mathbf{n}_{t+1} = K\mathbf{u} + \tilde{\mathbf{L}}(\mathbf{n}_t - K\mathbf{u}) + K\boldsymbol{\varepsilon}_t \mathbf{u}. \quad (2)$$

The expected age structure approaches the equilibrium $K\mathbf{u}$ according to a power of the stability matrix,

$$E[\mathbf{n}_t | \mathbf{n}_0] = K\mathbf{u} + \tilde{\mathbf{L}}^t(\mathbf{n}_0 - K\mathbf{u}).$$

Denote the dominant left and right eigenvectors of $\tilde{\mathbf{L}}$ as \mathbf{z} and \mathbf{w} , respectively, normalized so that the elements of \mathbf{w} sum to 1 and $\mathbf{z}\mathbf{w} = 1$. The dominant eigenvalue of the stability matrix $\tilde{\mathbf{L}}$ is written as $\tilde{\lambda} = 1 - \gamma$. Because a matrix power is dominated asymptotically by the root of maximum modulus, $\tilde{\mathbf{L}}^t \approx (1 - \gamma)^t \mathbf{w}\mathbf{z}$, where $\mathbf{w}\mathbf{z}$ is an outer product matrix with elements $w_i z_j$ (Gantmacher 1959; Cas-

well 1989, 2001), this shows that γ gives the asymptotic rate of return toward the expected equilibrium age structure, which is also the asymptotic rate of return of the total population size N toward carrying capacity K . We can therefore interpret γ as a measure of the strength of density regulation per year in an age-structured population.

Density-Dependent Reproductive Value

Consider the scalar quantity $Z_t = \mathbf{z}\mathbf{n}_t$ analogous to the total reproductive value in the density-independent model. Premultiplying equation (2) by \mathbf{z} , the dynamics take the form

$$Z_{t+1} = (1 - \gamma)Z_t + \gamma K\mathbf{z}\mathbf{u} + K\mathbf{z}\boldsymbol{\varepsilon}_t \mathbf{u}. \quad (3)$$

In contrast to the dynamics of population size, which generally have multiple time lags, if $\tilde{\lambda}$ is real, the density-dependent reproductive value obeys a first-order autoregressive process, which is Markovian (with changes depending only on the current value), assuming no environmental autocorrelation.

Under weak density dependence, the elements of \mathbf{D} will be small, and $\tilde{\mathbf{L}} = \hat{\mathbf{L}} - \mathbf{D}$ will have elements that are nearly nonnegative; hence, by the Perron-Frobenius theorem (Gantmacher 1959; Caswell 1989, 2001), the largest eigenvalue $\tilde{\lambda} = 1 - \gamma$ is real and positive or nearly so, with corresponding left and right eigenvectors \mathbf{z} and \mathbf{w} having all elements real and nonnegative or nearly so. If $\tilde{\lambda}$ is real, then the environmental variance in the direction of \mathbf{z} can be written as $K^2\sigma_e^2$, where

$$\sigma_e^2 = \text{Var}[\mathbf{z}\boldsymbol{\varepsilon}_t \mathbf{u}] = \mathbf{z}\mathbf{S}\mathbf{z}', \quad (4)$$

and $\mathbf{S} = E[\boldsymbol{\varepsilon}_t \mathbf{u}\mathbf{u}'\boldsymbol{\varepsilon}_t']$ is the covariance matrix of environmental stochasticity in equation (1) with elements $S_{ij} = \sum_k \sum_l u_k u_l \text{Cov}[\boldsymbol{\varepsilon}_{ik}, \boldsymbol{\varepsilon}_{jl}]$. Note that \mathbf{S} does not include density-dependent fluctuations; thus, in contrast to the density-independent case (Tuljapurkar 1982; Tuljapurkar and Lee 1997; S. Engen, R. Lande, and B.-E. Sæther, unpublished manuscript), it cannot be estimated directly from the observed covariance matrix of temporal fluctuations in the vital rates. We show how to estimate \mathbf{S} and components of the environmental variance in the direction of left eigenvectors of the stability matrix, particularly the density-dependent reproductive value.

The variance of the stationary distribution of Z_t is the equilibrium solution of the recursion obtained from equation (3), $\sigma_z^2(t+1) = (1 - \gamma)^2 \sigma_z^2(t) + K^2 \sigma_e^2$, denoted as $\sigma_z^2 = \sigma_z^2(\infty)$,

$$\sigma_z^2 = \frac{K^2 \sigma_e^2}{2\gamma - \gamma^2}. \quad (5)$$

Stationary Variance of Population Size

The variance of the stationary distribution of the total population size N can be expressed in terms of variances and covariances of the scalar factors $Z_t^{(j)} = \mathbf{z}^{(j)} \mathbf{n}_t$, associated with the j th left eigenvector (a row vector) $\mathbf{z}^{(j)}$ of the stability matrix, and the corresponding eigenvalue $\tilde{\lambda}_j$, satisfying $\mathbf{z}^{(j)} \tilde{\mathbf{L}} = \tilde{\lambda}_j \mathbf{z}^{(j)}$. The total population size at any given time can be expressed as the carrying capacity K plus the sum of deviations of $Z_t^{(j)}$ from their expected values, $K\mathbf{z}^{(j)} \mathbf{u}$ (see appendix),

$$N_t = K + \sum_j [Z_t^{(j)} - K\mathbf{z}^{(j)} \mathbf{u}]. \quad (6)$$

This implies that the stationary variance of N equals the sum of the variances and covariances of the $Z^{(j)}$ in the stationary distribution of age structure, defined as $\phi_{ij} = \text{Cov}[Z_t^{(i)}, Z_t^{(j)}]$. The appendix shows that

$$\sigma_N^2 = K^2 \sum_i \sum_j \frac{S^{(ij)}}{1 - \tilde{\lambda}_i \tilde{\lambda}_j}, \quad (7)$$

where $S^{(ij)} = \mathbf{z}^{(i)} \mathbf{S} \mathbf{z}^{(j) \prime}$ is the environmental covariance between the i th and j th left eigenvectors. The first term in equation (7) is $\phi_{11} = \sigma_Z^2$ (eqq. [4], [5]), the component of σ_N^2 created by environmental stochasticity in the density-dependent reproductive value $Z = Z^{(1)}$ (eq. [3]), not including its covariance with the other left eigenvectors.

Because any complex eigenvalues and corresponding eigenvectors of the stability matrix $\tilde{\mathbf{L}}$ occur as complex conjugate pairs (in which the sum of the imaginary parts cancel), equation (6) reveals that the population size at any time can be expressed in terms of the real parts of the left eigenvectors. For empirical analysis of components of variance in N , we therefore define the real variances and covariances $\Phi_{ij} = \text{Cov}(\text{Re}[Z_i], \text{Re}[Z_j])$ and note that $\sigma_N^2 = \sum_i \sum_j \Phi_{ij}$, similar to equation (7). (For complex eigenvalues, ϕ_{ij} is complex whereas Φ_{ij} is real, so these individual terms generally are not equal, although their sums over i and j both give σ_N^2 .)

Assuming that the joint distribution of the $\text{Re}[Z_j]$ is approximately multivariate normal, the proportion of variance in N explained by variation in $\text{Re}[Z_1]$, including its covariance with the other $\text{Re}[Z_j]$, can be approximated by the square of the correlation between $\text{Re}[Z_1]$ and N (Kendall and Stuart 1979),

$$\rho_{\text{Re}[Z_1], N}^2 \approx \frac{(\sum_j \Phi_{j1})^2}{\Phi_{11} \sum_i \sum_j \Phi_{ij}}. \quad (8)$$

Population Prediction

We now rescale the density-dependent reproductive value of the population, Z , so that at equilibrium Z is real and equal to K . Defining $Z_t^* = cZ_t = c\mathbf{z}\mathbf{n}_t$, we require that $c\mathbf{z}\hat{\mathbf{n}} = c\mathbf{z}K\mathbf{u} = K$, implying that $c = 1/(\mathbf{z}\mathbf{u})$, where the constant c is complex if the leading eigenvalue and eigenvector are complex. Then from equation (3) we obtain the dynamics $Z_{t+1}^* = \tilde{\lambda}Z_t^* + (1 - \tilde{\lambda})K + c\mathbf{z}\epsilon_t\mathbf{u}$ and hence the prediction equation for the scaled density-dependent reproductive value,

$$E[Z_{t+1}^* | Z_t^*] = K + \tilde{\lambda}(Z_t^* - K). \quad (9)$$

The (real part of the) scaled density-dependent reproductive value, and its predicted value next year (eq. [9]), can be used as a surrogate for describing and forecasting changes in population size.

For comparison, we can use the full stability matrix (eq. [2]) to forecast the expected population vector and hence the expected total population size next year, given the population vector in the current year. The projection formula for the total population size also can be expressed in terms of the full set of left eigenvectors of the stability matrix (see appendix),

$$E[N_{t+1} | \mathbf{n}_t] = K + \sum_j \tilde{\lambda}_j [Z_t^{(j)} - K\mathbf{z}^{(j)} \mathbf{u}],$$

which can be compared with equations (6) and especially equation (9) to view the simplification involved in prediction using the scaled density-dependent reproductive value. Although equation (9) incorporates only a single eigenvector of the stability matrix, it should give a fairly accurate approximation of the full dynamics based on all the eigenvectors, provided that the density-dependent reproductive value explains a large fraction of the variance in the stationary distribution of N (eq. [8]).

Strength of Density Dependence

With weak density regulation, the density-dependent reproductive value Z (eq. [5]) produces the main contribution to the total variance in the stationary distribution of N . There are two reasons for this.

Largest Environmental Stochasticity. Since $\hat{\mathbf{L}}$ is a Leslie matrix with nonnegative elements and \mathbf{D} has elements that tend to be negative but small (under weak density dependence), then the stability matrix $\hat{\mathbf{L}} - \mathbf{D}$ is “nearly” nonnegative, and by the Perron-Frobenius theorem, the eigenvalue of largest modulus is real and positive, with corresponding left and right eigenvectors having elements

that are “nearly” real and positive. The eigenvectors obey the orthogonality relationships $\mathbf{z}^{(i)}\mathbf{w}^{(j)} = 1$ if $i = j$; $\mathbf{z}^{(i)}\mathbf{w} = 0$ otherwise (Gantmacher 1959). If $\mathbf{w} = \mathbf{w}^{(1)}$ has all positive elements, then $\mathbf{z}^{(j)}$ for $j \geq 2$ must have both positive and negative elements since $\mathbf{z}^{(i)}\mathbf{w} = 0$ for $i \geq 2$. Because environmental covariance in the vital rates tends to be positive—with some exceptions due to, for example, trade-offs between reproduction and survival within a year (Lande 1982; van Tienderen 1995; Coulson et al. 1999, 2005; Albon et al. 2000; Sæther and Bakke 2000)—this suggests that the environmental stochasticity should tend to be largest for the dominant eigenvector, $S^{(11)} > S^{(ij)}$ for $j \geq 2$.

Weakest Restoring Force. The dominant factor has the eigenvalue of largest modulus, $\tilde{\lambda}_1 = \tilde{\lambda} = 1 - \gamma$. Under weak density dependence, when $\tilde{\lambda}$ is real and positive, this gives γ as the slowest rate of return toward equilibrium, with a timescale of $1/\gamma$. Thus, under weak density dependence, the density-dependent reproductive value is the component of total population size that produces changes of the largest magnitude with the most prolonged duration.

Although the equilibrium projection matrix $\hat{\mathbf{L}}$ has all elements nonnegative, density dependence generally causes some elements of the stability matrix to be negative, so the Perron-Frobenius theorem does not strictly apply. Therefore, as pointed out by Caswell (1989, p. 239; 2001, p. 521), the leading eigenvalue of the stability matrix need not be positive or real. The leading eigenvalue $\tilde{\lambda}$ may be real and negative, representing “overcompensation” (Begon et al. 1996). In this case, the rate of return to equilibrium is $\gamma = 1 - |\tilde{\lambda}|$ with timescale $1/\gamma$, where bars denote absolute value. Alternatively, the leading eigenvalue may be represented by a complex conjugate pair, $\tilde{\lambda}_1 = a + bi$ and $\tilde{\lambda}_2 = a - bi$ (where $i = (-1)^{1/2}$), with identical modulus $\|\tilde{\lambda}\| = (a^2 + b^2)^{1/2}$. Then the rate of return to equilibrium is $\gamma = 1 - \|\tilde{\lambda}\|$ with timescale $1/\gamma$, and the period of oscillation is approximately $2\pi/\arctan(b/a)$. When the leading eigenvalue is real and negative, the approach to equilibrium is a damped 2-year oscillation. In both cases, stability of the equilibrium requires that $\|\tilde{\lambda}\| < 1$, and in general, γ as defined above represents the strength of density dependence.

Under strong density dependence, the leading eigenvalue may have a modulus comparable to that of the subsequent eigenvalues associated with eigenvectors describing short-term fluctuations in age structure, which may also be damped by density regulation. Multiple eigenvectors may then contribute substantially to the total variance in the stationary distribution of N (eq. [7]) such that the leading eigenvector does not explain a very large fraction of the total variance in N . In this situation, a single scalar

quantity describing the environmental variance cannot be meaningfully defined.

A simple model with no age structure suggests that the strength of total density dependence in the life history is determined by the intrinsic rate of increase of the population at low density as well as nonlinearity in density dependence. Consider the stochastic theta-logistic model in discrete time (Lande et al. 2003), $\Delta N/N = \beta[1 - (N/K)^\theta] + \epsilon_t$, in which ΔN is the annual change in population size, β represents the intrinsic rate of increase at low population density, and θ describes the degree of nonlinearity in density dependence, with $\theta \rightarrow 0$ for the Gompertz model (linear on the log scale), $\theta = 1$ for the classical logistic model, and $\theta \rightarrow \infty$ for exponential growth up to a ceiling. In this model, the strength of density dependence, or the expected rate of return toward equilibrium following a small perturbation, is simply $\gamma = \theta\beta$ (Lande et al. 2003). For the logistic model with linear density dependence, this confirms the intuitive expectation that at equilibrium the strength of density dependence must balance the intrinsic rate of increase.

The theta-logistic model also helps to understand when a linearized model is adequate to describe stochastic dynamics of a population fluctuating around an equilibrium. Analysis of the stochastic logistic and Gompertz models using nonlinear diffusion theory (Lande et al. 2003) and comparison with the results of corresponding linear models suggest that a linear approximation accurately produces the mean and variance of the quasi-stationary distribution of population size (with <10% error) for coefficients of variation of population size, σ_N/\bar{N} , up to 30% (Lande et al. 1999). Large values of θ would require lower coefficients of variation in N for accuracy of a linear model. However, with small variation in N , it is not possible to accurately estimate both θ and β but only their product γ (Lande et al. 2003). Assessing nonlinearity of density dependence in an age-structured population would necessarily be more complicated. Nevertheless, in most cases, a linear model is likely to be accurate for a small values of σ_N/\bar{N} and to be reasonably reliable for moderate values, of which many examples exist (Pimm 1991; Lande et al. 2002a, 2002b).

Comparison to Previous Definitions of Density Dependence

Lande et al. (2002a, 2002b) also measured the strength of density dependence per year by the rate of return to the equilibrium age structure. They derived an autoregression model based on demographic theory for analysis of time series of adult numbers to estimate γ , assuming that all density dependence on the different age classes is exerted by the adult population N . They also examined a model in which all density dependence is exerted by a single linear combination of age classes, denoted as N (Charlesworth

1994; Caswell 1989, 2001; Lande et al. 2002a). In both cases, they showed that the overall strength of density dependence can be expressed as the negative elasticity of λ with respect to population size, evaluated at K , the equilibrium population size, $\gamma = -(\partial \ln \lambda / \partial \ln N)_K$.

To compare the present general model of density dependence with previous approaches, we derive an expression for γ in the general model. Under weak or moderate density dependence, the leading eigenvalue $1 - \gamma$ of the stability matrix $\tilde{\mathbf{L}} - \mathbf{D}$ can be approximated by regarding \mathbf{D} as a perturbation of the equilibrium projection matrix $\tilde{\mathbf{L}}$, which has leading eigenvalue $\lambda = 1$. The strength of density dependence then takes the form derived in the appendix, $\gamma = \mathbf{v}\mathbf{D}\mathbf{u}$, which can also be expressed as

$$\gamma = - \sum_j \left(\frac{\partial \ln \lambda}{\partial \ln n_j} \right). \quad (10)$$

This still allows every age or stage class to exert any density dependence on all the vital rates.

If we assume that all density dependence is exerted by a single linear combination of age classes, $N = \sum_j c_j n_j$, then λ depends on n_j only through its contribution to N , and as shown in the appendix, equation (10) becomes $\gamma = -(\partial \ln \lambda / \partial \ln N)_K$, in agreement with previous approaches. Although this result assumes weak or moderate density dependence, that is not an assumption of either this model or that of Lande et al. (2002a, 2002b).

Estimation of Density Dependence

Estimation of key population parameters is based on equation (2), which can be written as $\mathbf{n}_{t+1} = \tilde{\mathbf{L}}\mathbf{n}_t + \boldsymbol{\omega} + \boldsymbol{\delta}_t$. Here $\tilde{\mathbf{L}}$ is an unknown matrix, $\boldsymbol{\omega}$ is an unknown vector ($= [\mathbf{I} - \tilde{\mathbf{L}}]\mathbf{K}\mathbf{u}$ in eq. [2]), while $\boldsymbol{\delta}_t$ is a vector of stochastic environmental effects ($\mathbf{K}\boldsymbol{\epsilon}_t\mathbf{u}$ in eq. [2]) with zero expectation. We assume that the age classes in the population are fully censused in years $t = 1, 2, \dots, t_0$. Writing $n_{i,t}$ for the i th component of \mathbf{n}_t and a similar notation for $\delta_{i,t}$, equation (2) for $i = 0, 1 \dots k$ becomes $\delta_{i,t} = n_{i,t+1} - \sum_j \tilde{L}_{ij} n_{j,t} - \omega_i$. From this, we see that the \tilde{L}_{ij} and ω_i can be estimated using least squares by minimizing $\sum_{t=1}^{t_0-1} \delta_{i,t}^2$. (This can be done using standard statistical packages for general linear models.) Then $\tilde{\lambda}$ is estimated as the dominant eigenvalue of the estimate of $\tilde{\mathbf{L}}$. The carrying capacity and stable age distribution can also be estimated from the above dynamic equation at equilibrium by setting $\delta_t = 0$ and $\mathbf{n}_{t+1} = \mathbf{n}_t = \hat{\mathbf{n}} = \mathbf{K}\mathbf{u}$ and solving for $\hat{\mathbf{n}} = (\mathbf{I} - \tilde{\mathbf{L}})^{-1}\boldsymbol{\omega}$. Finally, the covariance matrix of the residual vectors $\delta_{i,t}$ gives the environmental covariance matrix $\mathbf{K}^2\mathbf{S}$.

The uncertainty in the estimates can be evaluated by bootstrapping, simulating bootstrap replicates of the time

series observations by drawing residuals at random with replacement each year, a technique often used in regression analysis (Efron and Tibshirani 1993). The components of residual vectors $\delta_{i,t}$ at a given time are likely to be dependent because they are affected by the same environmental factors, so it is important that the complete vector of residuals, and not single components, are drawn at random. A bootstrap replicate is finally constructed by starting with the initial observations at time 1 and recursively using the relation $\mathbf{n}_{t+1} = \tilde{\mathbf{L}}\mathbf{n}_t + \boldsymbol{\omega} + \boldsymbol{\delta}_t$, where the components of $\tilde{\mathbf{L}}$ and $\boldsymbol{\omega}$ are those estimated from the data and the index τ for the residual vector is randomly chosen with replacement from the set $(1, 2, \dots, t_0)$ of indices representing the observations. From each bootstrap replicate of the complete time series, a bootstrap replicate of $\tilde{\mathbf{L}}$ and $\boldsymbol{\omega}$ as well as $\tilde{\lambda}$, K , and \mathbf{u} are found by using the same estimation procedure as for the actual data.

Demographic and Effective Total Stochasticity

Our theory assumes small or moderate fluctuations of total population size around an average population size or carrying capacity K sufficiently large to neglect demographic stochasticity in comparison to environmental stochasticity. For a density-independent age-structured population in a fluctuating environment, Engen et al. (2005) derived formulas for the demographic variance σ_d^2 influencing population size N and showed that the total stochasticity affecting N can be approximated as in simple models without age structure by $\sigma_e^2 + \sigma_d^2/N$. As already emphasized above, in a density-dependent population, the environmental variance σ_e^2 cannot be estimated in the same way as for density-independent populations (Tuljapurkar 1982; Tuljapurkar and Lee 1997; S. Engen, R. Lande, and B.-E. Sæther, unpublished manuscript) because observed temporal fluctuations in vital rates among years are partly caused by density dependence. In contrast, the demographic variance is estimated from the observed variation in survival and reproduction among individuals within years and thus can be accurately estimated regardless of density dependence, although in general σ_d^2 may be a function of population size (Lande et al. 2003; Engen et al. 2005). Assuming a small or moderate coefficient of variation in population size through time, we can therefore assess the importance of demographic stochasticity in contributing to fluctuations in population size around carrying capacity by comparing the total stochasticity at $N = K$ to the contribution from demographic stochasticity σ_d^2/K , using the average value of the demographic variance through time.

The density-dependent projection matrix $\mathbf{L}(\mathbf{n})$ has elements L_{ij} as in equation (1). Writing the demographic variance in this vital rate as $\sigma_d^2[L_{ij}]$ and assuming no de-

mographic covariance among the vital rates, the net demographic variance influencing total population size is

$$\sigma_d^2 = \lambda^{-2} \sum_i \sum_j v_i u_j \sigma_d^2[L_{ij}] \quad (11)$$

(Engen et al. 2005). Here v_i and u_j are elements of the left and right eigenvalues of the equilibrium projection matrix $\hat{\mathbf{L}}$, respectively Fisher's reproductive value and the stable age distribution, normalized as above so that $\sum_j u_j = 1$ and $\mathbf{v}\mathbf{u} = 1$, corresponding to the leading eigenvalue λ . In practice, $\hat{\mathbf{L}}$ must be estimated by the average projection matrix across years, $\bar{\mathbf{L}}$. For a population in which females give birth to at most one daughter per year, both survival and reproduction have the binomial variance $\sigma_d^2[L_{ij}] = \hat{L}_{ij}(1 - \hat{L}_{ij})$, and the net demographic variance can be simply estimated from the average projection matrix.

Direct comparison of the demographic variance in N to the environmental variance in the density-dependent reproductive value is problematic for two reasons. First, this variance component neglects covariances with the other left eigenvectors of the stability matrix, which add power to explain the stationary variance in N (eq. [8]). Second, if $\tilde{\lambda}$ is complex, so is the density-dependent reproductive value Z , formed from the corresponding left eigenvector of the stability matrix. Environmental stochasticity influences both the real and imaginary parts of Z , which interact to influence the stationary variance of the real part of Z (since eq. [3] then represents a pair of coupled equations).

A linear model with no age structure offers the simplest description of population fluctuations around an equilibrium, excluding short-term oscillations due to age-structure, and should be reasonably accurate provided that the density-dependent reproductive value explains a large fraction of the stationary variance in population size (eq. [8]). An effective total stochasticity appropriate for use in such a model can be derived to be consistent with the estimated rate of return of population size toward equilibrium and the estimated stationary variance in N , as in Sæther et al. (2005). The rate of return of population size toward the carrying capacity, as elaborated above, is $\gamma = 1 - \|\tilde{\lambda}\|$. Given a small or moderate coefficient of variation of population size, the total stochasticity near equilibrium is approximately constant, $\sigma_e^2 + \sigma_d^2/K$. This would appear in a linear model with no age structure, analogous to equations (3) and (5) but with Z replaced by N and with the environmental variance replaced by the effective total stochasticity, giving

$$\sigma_e^2 + \frac{\sigma_d^2}{K} = (2\gamma - \gamma^2) \left(\frac{\sigma_N}{K} \right)^2 \quad (12)$$

The contribution of demographic variance near equilibrium, σ_d^2/K , can be calculated from equation (11) and an estimate of K , and then compared with the effective total stochasticity in equation (12).

Red Deer Population Dynamics

We used data from a food-limited population of red deer living in the North Block of Rum, Scotland. All resident individuals within the population are uniquely marked, and life-history data have been collected on the marked individuals since 1971. We use data on age-specific female performance records in each year; for each female within the population, we recorded her age, whether she survived from May 15 in year t to May 14 in year $t + 1$, and the number of female offspring she produced in May/June of year t that survived to May 14 the following year. In this population, females can give birth to only one offspring per year, and most females of reproductive age do not reproduce every year. The population was released from culling in 1972 and increased in size until the early 1980s when ecological carrying capacity was reached. Since then, the population has fluctuated around carrying capacity (Coulson et al. 2004). We use data for the period 1981–2001. Full details of data collection have been published elsewhere (Clutton-Brock et al. 1982). The solid trajectory in figure 1 presents a simplified three-dimensional plot of fluctuations in the age structure of the population, with three life stages: 1 and 2 years old, 3 and 4 years old, and 5 years and older. The heavy solid line in figure 2 depicts fluctuations in total population size.

Our quantitative analysis of the data deals with five age classes of individuals ages 1, 2, 3, 4, and 5 or more years old. The mean projection matrix over 20 annual transitions, $\bar{\mathbf{L}}$, with leading eigenvalue 1.026, only approximates the equilibrium projection matrix $\hat{\mathbf{L}}$, which must have a leading eigenvalue of unity (table 1).

The estimated stability matrix, $\tilde{\mathbf{L}} = \hat{\mathbf{L}} - \mathbf{D}$ in table 1, has eigenvalues displayed in table 2. The leading eigenvalue is complex with modulus $\|\tilde{\lambda}\| = 0.789$, so the strength of density dependence is $\gamma = 1 - \|\tilde{\lambda}\| = 0.211$ (0.0289, 0.385), with an approximate 95% confidence interval (in parentheses) based on 10,000 bootstrap replicates, showing that the estimate is significantly different from 0. Corresponding to the leading eigenvalue are the right eigenvector \mathbf{w} and transposed left eigenvector \mathbf{v}' , the density-dependent reproductive value vector (table 2). This has a timescale for return toward equilibrium of $1/\gamma = 5$ years, with damped oscillations at a period of 12 years. The estimated carrying capacity $K = 187.8$ (174.3, 200.8) has fairly narrow confidence limits. Elements of the estimated stable age distribution, \mathbf{u} , necessarily decrease with age until the last stage of 5 years and older (table 2).

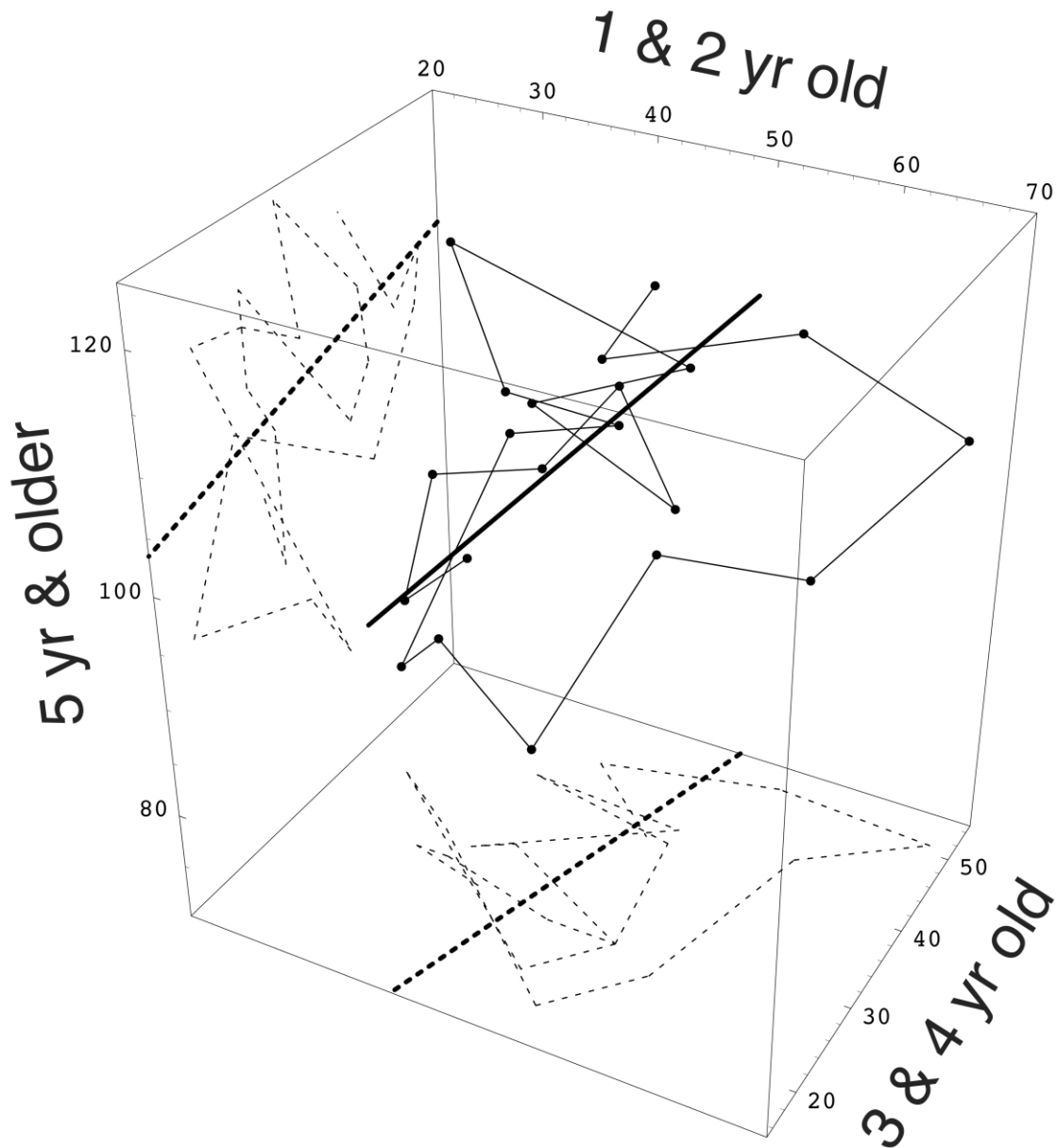


Figure 1: Annual fluctuations in age structure of female red deer on the Isle of Rum from 1981 to 2001 for a simplified life history grouped into three stages: 1 and 2 years old, 3 and 4 years old, and 5 years and older. Thin solid line shows trajectory in three dimensions, with heavy straight line through the equilibrium age structure at (46.85, 38.27, 108.68) in the direction of the real part of the scaled left eigenvector of the stability matrix (density-dependent reproductive value vector; tables 1, 2). Dashed lines show two-dimensional projections onto the left and bottom faces of the box.

The real parts of the density-dependent reproductive value vector \mathbf{v} and the rescaled vector $c\mathbf{v}$ have all positive elements and are nearly colinear (table 2). Variance in the real part of the density-dependent reproductive value Z and its covariance with the real parts of the other eigenvectors explain 79.5% of the variance in the stationary distribution of population size (eq. [8]). In contrast, any

of the other eigenvectors explains at most 30% of the variance in N . It is therefore not surprising that the rescaled density-dependent reproductive value Z^* fits fairly well to fluctuations in the total population size N (fig. 2).

Although the density-dependent reproductive value must be the linear combination of age classes with the weakest restoring force toward equilibrium, γ , for the red

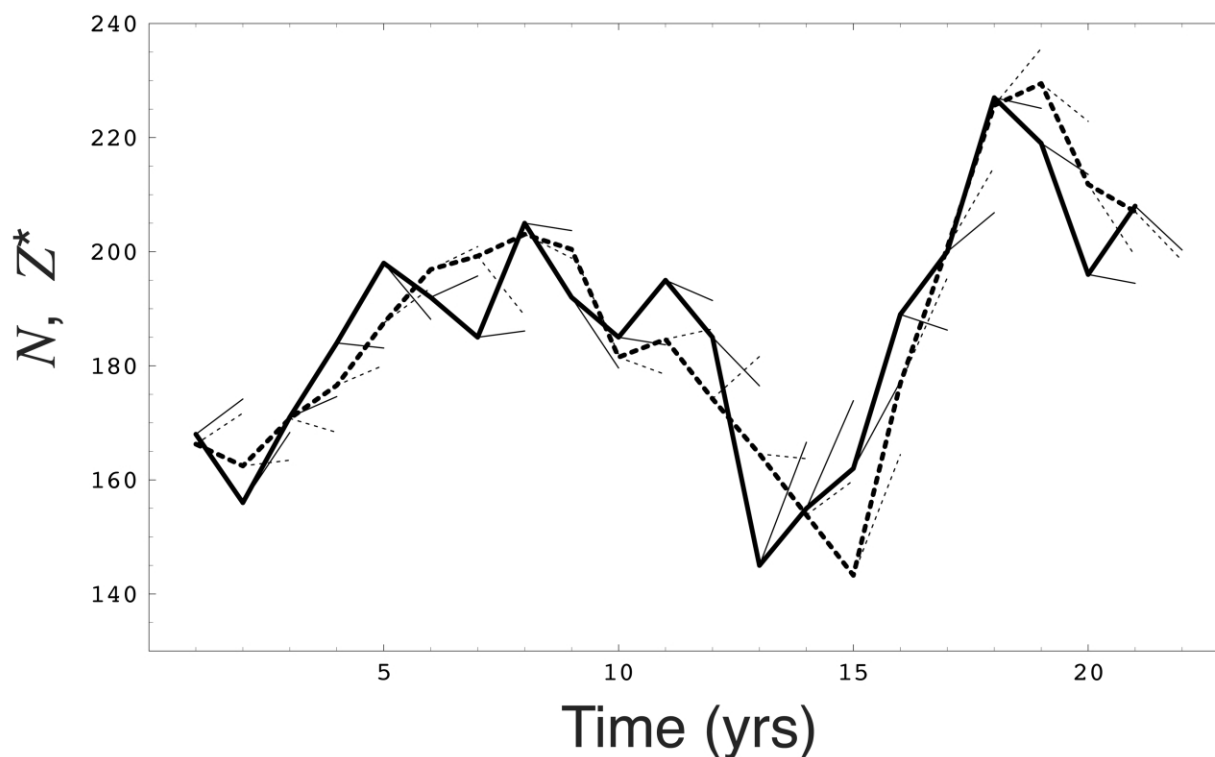


Figure 2: Total population size N (heavy solid line) and real part of the scaled density-dependent reproductive value $Z^* = \mathbf{zn}/(\mathbf{zu})$ (heavy dashed line) for female red deer on the Isle of Rum from 1981 to 2001. Short solid lines and short dashed lines give annual predictions of N and Z^* , respectively, projected using equations (2) and (9).

deer the other eigenvalues have comparable modulus (table 2). Thus, the primary reason why variance in Z explains a high proportion of σ_N^2 is that the real part of the density-dependent reproductive value vector has all positive components (table 2), implying that it experiences the largest environmental stochasticity (see “Strength of Density Dependence”). Figure 2 also shows that predicted annual changes in the real part of Z^* (eq. [9]) are about equally accurate in comparison to using the full stability matrix (eq. [2]) to predict annual changes in N , although both are subject to substantial stochasticity.

The small observed coefficient of variation in population size, $\sigma_N/\bar{N} = 11\%$, helps to justify the application of our linearized model to this population. However, 20 years of observed changes are at best barely adequate to describe the stationary distribution of age structure in five dimensions (condensed to three dimensions in fig. 1). Bootstrap sampling of the residual vectors therefore provides only a rough approximation of the statistical accuracy of the parameter estimates. Nevertheless, symmetry of the bootstrap confidence intervals around the estimates of γ and K indicates that the estimates of the strength of density dependence and the carrying capacity are nearly unbiased.

Because female red deer on Rum produce at most one offspring per year, the demographic variance near equilibrium can be calculated directly from the equilibrium projection matrix $\hat{\mathbf{L}}$ using the binomial variance for individual survival and reproduction in equation (11). Employing the average projection matrix in table 1 as an estimate of $\hat{\mathbf{L}}$ gives $\sigma_a^2 = 0.170$ near equilibrium. The contribution of the demographic variance to the total stochasticity near equilibrium, calculated using the estimated carrying capacity, is $\sigma_a^2/K = 0.000907$. The effective total stochasticity calculated from the estimated rate of return toward equilibrium γ and the observed coefficient of variation of population size (eq. [12]) is $\sigma_e^2 + \sigma_a^2/K = 0.0048$. Thus, demographic stochasticity contributes about one-fifth of the effective total stochasticity near equilibrium.

Discussion

For annual time series of vertebrate populations over a few decades, it is usually possible to detect statistically significant density dependence (Lande et al. 2002a, 2002b; Sæther et al. 2005). Beginning with a general life history and allowing density dependence within and among age

Table 1: Average projection matrix $\bar{\mathbf{L}}$ and estimated stability matrix $\tilde{\mathbf{L}}$ for red deer on the Isle of Rum, 1981–2001

$\bar{\mathbf{L}}$					$\tilde{\mathbf{L}}$				
0	0	.0590	.2192	.2170	-.0379	.2674	.0441	.0473	-.2251
.8729	0	0	0	0	.7867	-.0384	-.0616	-.0580	.0121
0	.9124	0	0	0	.0616	.9734	.1328	-.1421	-.0725
0	0	.9196	0	0	.0198	-.1337	.9034	-.0604	-.0167
0	0	0	.9069	.8665	.1974	-.2387	-.2539	1.3562	.5185

Note: Based on 20 annual transitions of age structure.

classes, we propose that the total density dependence in the life history should be measured by the rate of return to the equilibrium or average age structure. Assuming small or moderate fluctuations in population size and age structure, we linearize the stochastic dynamics around the equilibrium point. This facilitates estimation of key demographic parameters of age- or stage-structured population dynamics for species with different life histories.

For density-dependent populations, the key demographic parameters are the expected population size (or carrying capacity) and the overall strength of density dependence in the life history. We also show how to assess the contribution of demographic variance to the total stochasticity near equilibrium. Our approach contrasts with other methods of analyzing stochastic population dynamics that focus on partitioning the variance in annual population growth rate into contributions from variation in age-specific vital rates and age-structure fluctuations (van Tienderen 1995; Albon et al. 2000; Caswell 2000; Coulson et al. 2005). Finally, we consider simplified models for describing and predicting the dynamics of population size.

The present definition of the strength of density dependence is based on the leading eigenvalue of the density-dependent stability matrix for age-structured population dynamics. This determines the asymptotic rate of return to the equilibrium age structure following a perturbation and also approximates in a stochastic context the rate of return of the expected age structure to its equilibrium. Application of our general model to population data requires detailed time series on the full age or stage structure to estimate elements of the stability matrix $\tilde{\mathbf{L}}$. The strength of density dependence per year, γ , is obtained as 1 minus the modulus of the dominant eigenvalue $\tilde{\lambda}$ of the stability matrix.

The data requirement of this model for multivariate time series on population age structure is much more stringent than for a related method of measuring density dependence in a simplified life history, which requires only a univariate time series of the adult population and basic information on the life history (Lande et al. 2002a, 2002b). Nevertheless, both methods consistently estimate the

strength of density dependence by the rate of return to the equilibrium age structure γ .

If $\tilde{\lambda}$ is real and positive, the dynamics of population size may be accurately described by a one-dimensional Markovian process for the density-dependent reproductive value, assuming no temporal autocorrelation in the environment. But if $\tilde{\lambda}$ is complex, so is the density-dependent reproductive value, and the description of environmental stochasticity and population prediction then require at least a two-dimensional process to account for interaction between the real and imaginary parts of the complex reproductive value. Under strong density dependence, an accurate description of population fluctuations may involve multiple eigenvectors, depending on the pattern of environmental stochasticity.

We analyzed a 21-year time series of age structure for red deer on the Isle of Rum with a small coefficient of variation of total population size to estimate the stability matrix (table 1). Despite the high accuracy of population censuses within years, by comparison with the average projection matrix (table 1) it appears that the matrix of density-dependent coefficients \mathbf{D} is subject to substantial sampling error, with some estimated elements being negative instead of positive. Key parameters are more accurately estimated, however, including the overall strength of density dependence in the life history, $\gamma = 0.211$, which is statistically significant, and the estimated carrying capacity, $K = 188$, which has a rather narrow confidence interval. The strength of density dependence in red deer is comparable to that previously estimated from time series of adult populations of birds and mammals (Lande et al. 2002a, 2002b; Sæther et al. 2005). Density dependence is strong enough through the life history so that the leading eigenvalue is estimated as complex (table 2), showing a tendency for oscillations with a period of 12 years. However, this oscillation has only marginal statistical significance ($P = .055$ that bootstrap estimates of $\tilde{\lambda}$ are real) and would not be readily observed because any fluctuations are damped on a timescale of 5 years. The estimated demographic variance $\sigma_a^2 = 0.170$ is comparable to that found for other long-lived vertebrate species (Sæther et

Table 2: Eigenvalues $\tilde{\lambda}_j$, leading right and left eigenvectors \mathbf{w} and \mathbf{z}' of the stability matrix $\tilde{\mathbf{L}}$ (table 1), estimated stable age distribution \mathbf{u} , and rescaled density-dependent reproductive value vector $c\mathbf{z}'$

$\tilde{\lambda}_j$	\mathbf{w}	\mathbf{z}'	\mathbf{u}	$c\mathbf{z}'^a$
.6852 + .3915 <i>i</i>	.0652 + .2014 <i>i</i>	.0168 - .9130 <i>i</i>	.1245	.1145 - 2.3485 <i>i</i>
.6852 - .3915 <i>i</i>	.1100 + .1310 <i>i</i>	.2982 - .9073 <i>i</i>	.1090	.8384 - 2.3119 <i>i</i>
-.7477	.2051 + .1656 <i>i</i>	.7667 - .1816 <i>i</i>	.0980	1.9877 - .4075 <i>i</i>
-.0541 + .6858 <i>i</i>	.2546 + .0614 <i>i</i>	.6729 + .2971 <i>i</i>	.0898	1.7088 + .8172 <i>i</i>
-.0541 - .6858 <i>i</i>	.3650 - .5593 <i>i</i>	.3767 + .3316 <i>i</i>	.5787	.9437 + .8828 <i>i</i>

Note: Five eigenvalues listed in order of decreasing modulus.

^a Complex scaling factor $c = 1/(\mathbf{z}\mathbf{u})$.

al. 2004). Although the average population size is not large, the demographic variance contributes only about one-fifth of the effective total stochasticity influencing population size near equilibrium, $\sigma_e^2 + \sigma_a^2/K$, the great majority of which is due to environmental variance.

The real parts of the scaled density-dependent reproductive value vector are all positive, so variation in this direction should account for much of the environmental stochasticity influencing total population size. The real part of the total scaled density-dependent reproductive value provides a fairly good approximation to the dynamics of population size, giving 1-year predictions nearly as accurate as using the full stability matrix (fig. 2). This occurs because the real part of the density-dependent reproductive value explains a large fraction of the variance in the stationary distribution of population size (eq. [8]). The real parts of the scaled and unscaled density-dependent reproductive value vector are nearly colinear, with the scaling factor c magnifying environmental stochasticity (above eq. [9]), compensating for the unexplained variance in population size.

Our analysis of the red deer data demonstrates the feasibility of estimating the overall strength of density dependence in a life history from time series data on population size and age structure. With a carrying capacity near 200, demographic stochasticity contributes a small fraction of the effective total stochasticity near equilibrium. We show that the density-dependent reproductive value can provide a simplified description and prediction of population dynamics for a general life history in a stochastic environment, similar to that developed for density-independent populations (S. Engen, R. Lande, and B.-E. Sæther, unpublished manuscript).

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