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Estimating Density Dependence, Environmental Variance, and Long-Term Selection on a Stage-Structured Life History

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ABSTRACT: A method for analyzing long-term demographic data on density-dependent stage-structured populations in a stochastic environment is derived to facilitate comparison of populations and species with different life histories. We assume that a weighted sum of stage abundances, N, exerts density dependence on stage-specific vital rates of survival and reproduction and that N has a small or moderate coefficient of variation. The dynamics of N are approximated as a univariate stochastic process governed by three key parameters: the density-independent growth rate, the net density dependence, and environmental variance in the life history. We show how to estimate the relative weighs of stages in N and the key parameters. Life history evolution represents a stochastic maximization of a simple function of the key parameters. The long-term selection gradient on the life history can be expressed as a vector of sensitivities of this function with respect to density-independent, density-dependent, and stochastic components of the vital rates. To illustrate the method, we analyze 38 years of demographic data on a great tit population, estimating the key parameters, which accurately predict the observed mean, coefficient of variation, and fluctuation rate of N; we also evaluate the long-term selection gradient on the life history.

Keywords: demography, density dependence, environmental variance, great tit, selection, sensitivity.

Introduction

Following the classical debate on the occurrence of density dependence in natural populations (Turchin 1995), a variety of ad hoc statistical methods were developed to detect density dependence and assess its prevalence among species from univariate time series of population size (Bulmer 1975; Pollard 1987; Holyoak 1993; Dennis and Taper 1994). These methods generally have low statistical power to detect density dependence, producing frequent type I and II errors, even for long time series of accurately estimated population sizes (Murdoch 1994; Shenk et al. 1998; Brook and Bradshaw 2006; Freckleton et al. 2006).

Initial attempts to develop more realistic methods incorporated time delays implicitly caused by life history and interspecific interactions (Turchin 1990, 1995; Royama 1992; Turchin and Taylor 1992; Woiwood and Hanski 1992). A basic stage-structured life history was incorporated in a time-delay autoregression to analyze univariate time series of adult population size for several vertebrate species (Lande et al. 2002*a*, 2002*b*, 2003), revealing that interpreting time-delay coefficients as caused solely by density dependence is erroneous because they are created by developmental delays in the life history (Lande et al. 2002*a*, 2002*b*, 2003).

Fluctuations in total population size are driven by environmental stochasticity and density dependence in stage-specific vital rates of reproduction and survival (op. cit.) but also are influenced by transient fluctuations in stage structure (Caswell 2001; Lande et al. 2003; Engen et al. 2009). Accurate analysis of the interaction of density dependence and environmental stochasticity therefore requires the use of stage-structured demographic models. However, current theory and application of stochastic stage-structured population dynamics generally ignores density dependence (Tuljapurkar 1990; Caswell 2001), which then becomes unrealistically conflated with environmental stochasticity. A wide variety of stage-structured demographic models including both density dependence and environmental stochasticity have been fitted to particular populations or life histories, making it difficult to compare them (Constantino and Desharnais 1991; Takada and Nakashizuka 1996; Grant and Benton 2000; Coulson et al. 2001, 2008; Lande et al. 2006; Gamelon et al. 2016, 2019).

Here, we analyze a density-dependent stage-structured population in a stochastic environment, assuming that all density dependence in the vital rates is exerted by a function, $g(N)$, of a weighted sum of stage abundances, N,

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undergoing small or moderate fluctuations around a deterministically stable equilibrium, the carrying capacity, K. We outline statistical methods for estimating the relative weights of stage abundances contributing to N and density-independent, density-dependent, and stochastic parameters of the stage-specific vital rates. The numerous parameters of the vital rates are summarized in three key demographic parameters governing a univariate approximation for the stochastic dynamics of N. These are the density-independent population growth rate, $\alpha - 1$, and the net density dependence, γ, and environmental variance, σ_e^2, in the life history. These key parameters facilitate comparison among populations and species that differ in life history and also have a fundamental connection to life history evolution.

For a density-dependent population in a constant environment, MacArthur (1962) showed that evolution maximizes the population carrying capacity, K. This was extended to density-dependent age- and stage-structured populations by Charlesworth (1973, 1994) and Takada and Nakajima (1992, 1998), revealing that evolution maximizes the equilibrium abundance of the critical age or stage class(es), a linear combination of stage abundances that causes density dependence in the vital rates.

We show here that in a stochastic environment, life history evolution maximizes the expected value of the density dependence function affecting the vital rates, expressed using the key demographic parameters, $\mathrm{E}[g(N)] = s/\gamma$, where $s = \alpha - 1 - \sigma_e^2/2$ is the density-independent stochastic growth rate of the population and γ is the net density dependence in the life history. This reveals that evolution tends to maximize the stochastic growth rate and minimize the net density dependence, constrained by ecological and genetic trade-offs. The long-term selection gradient on the life history has elements proportional to derivatives of s/γ with respect to density-independent, density-dependent, and stochastic parameters of the vital rates. Selection gradient elements can be expressed as a sum of contributions from sensitivities of the three key demographic parameters with respect to components of the vital rates.

To illustrate these concepts, we apply the theory to estimate the net density dependence, environmental variance, and long-term selection gradient on a great tit life history, using 38 years of demographic data on fluctuations in the vital rates.

Stochastic Demography of a Density-Dependent Stage-Structured Life History

We first show how the stochastic demography of a density-dependent stage-structured population in a fluctuating environment can be approximated by a one-dimensional process for the weighted population size, N, that exerts density dependence on the vital rates.

The dynamics of abundances in the column vector of stage classes, n, are

$$n(t+1) = L(g(N), t)n(t), \tag{1a}$$

where $L(g(N), t) = [l_{ij}(g(N)) + \xi_{ij}(t)]$. The projection matrix $L(g(N), t)$ has nonnegative elements, the vital rates of stage-specific annual survival and reproduction, and is assumed to be irreducible, with distinct nonzero eigenvalues. The expected projection matrix, $l(g(N))$, has elements $l_{ij}(g(N))$ involving a density-dependent function $g(N)$, where $N = \sum_i b_i n_i$ is a linear combination of stage abundances with nonnegative weights contained in the row vector $b = (b_1, b_2, \ldots)$, governing competition for a limiting resource. The largest weight may be set to 1, or the sum of the weights could be scaled to a given number, such as the number of stage classes; if all coefficients are unity, then N is the actual total population size.

The density dependence function $g(N)$ is assumed to increase monotonically with N, so that an Allee effect, or unstable equilibrium at small population size, either does not exist or can be neglected by assuming that the population size remains well above the unstable equilibrium population size. Thus, we suppose that $g(0) \to 0$ as $N \to 0$ and that density-dependent elements of $l(g(N))$ typically decrease with increasing N.

We analyze a population subject to an environment with a stationary distribution and no serial autocorrelation. Environmental stochasticity in the vital rates has means $\mathrm{E}[\xi_{ij}(t)] = 0$ and covariances $C_{ij,i'j'} = \mathrm{E}[\xi_{ij}(t)\xi_{i'j'}(t)]$. The population size is assumed to remain large enough (usually at least a few hundred individuals) that demographic stochasticity, due to random independent events of individual births and deaths, can be neglected in comparison to environmental stochasticity, which affects all genotypes (or phenotypes) in the same or similar way (Lande et al. 2003).

The carrying capacity of the population, K, is set by the deterministic equilibrium projection matrix, $l(g(K))$, such that its leading eigenvalue is unity, $\lambda(g(K)) = 1$. The stable stage distribution and reproductive values are the corresponding right (column) eigenvector, u, and the left (row) eigenvector, v, normalized so that $\sum_i u_i = 1$ and $vu = 1$, which solve the eigenvalue equations

$$l(g(K))u = u \quad \text{and} \quad vl(g(K)) = v. \tag{1b}$$

Further analysis of stochastic population dynamics and evolution is based on linearization of the expected projection matrix to separate density-independent and density-dependent components of the vital rates by Taylor expansion in powers of $g(N)$:

$$l_{ij}(g(N)) \approx \alpha_{ij} - \gamma_{ij} g(N) \quad \text{with } \gamma_{ij} = -\left.\frac{\partial l_{ij}}{\partial g(N)}\right|_{N=K}. \tag{2a}$$

Substituting the linearized vital rates (eq. [2a]) into the first eigenvalue equation (1b) and premultiplying both sides by v yields $\lambda(g(K)) = \alpha - \gamma g(K) = 1$, so

$$g(K) = \frac{\alpha - 1}{\gamma}, \quad \text{where } \alpha = vAu \text{ and } \gamma = v\Gamma u, \tag{2b}$$

with $A = (\alpha_{ij})$ and $\Gamma = (\gamma_{ij})$ representing matrices of density-independent and density-dependent components of the vital rates.

For an element of the deterministic equilibrium projection matrix, $l_{ij}(g(K))$, denote perturbations due to fluctuating population size and environment as $\delta l_{ij}(g(K)) = \gamma_{ij}[g(N) - g(K)] + \xi_{ij}(t)$. The sensitivity of $\lambda(g(K))$ to such perturbations is $v_i u_j$ (Caswell 2001, eq. [9.12]). Thus, the leading eigenvalue of the stochastic projection matrix, $L(g(N), t)$, is approximately

$$\begin{aligned}\lambda(g(N), t) &\approx \lambda(g(K)) + \sum_{ij} v_i u_j \delta l_{ij}(g(K)) \\ &= \alpha - \gamma g(N) + \xi(t), \text{ where } \xi(t) = v\Xi(t)u.\end{aligned} \tag{3a}$$

The term $\xi(t)$ is the environmental stochasticity in net reproductive value, and $\Xi(t) = (\xi_{ij}(t))$ represents the matrix of environmental stochasticity in the vital rates (eq. [1a]).

Premultiplying both sides of equation (1a) by v, the dynamics of fluctuations around the deterministic equilibrium can be reduced to a stochastic process for net reproductive value, $V(t) = vn(t)$, using the approximate eigenvalue equation $vL(g(N), t) \approx \lambda(g(N), t)v$, giving $V(t+1) = \lambda(g(N), t)V(t)$, in which neglected terms are net second order (Engen et al. 2009; Lion 2018). Transforming to a log scale, denoting $\Delta \ln V = \ln V(t+1) - \ln V(t)$, and expanding $\ln \lambda(g(N), t)$ in a Taylor series around the deterministic equilibrium, $\lambda(g(K)) = 1$, produces

$$\begin{aligned}\Delta \ln V &= \ln \lambda(g(N), t) \\ &= 0 + \lambda(g(N), t) - 1 - \frac{1}{2}[\lambda(g(N), t) - 1]^2 + \cdots\end{aligned} \tag{3b}$$

Assuming small fluctuations of N around K (so that $[\alpha - \gamma g(N) - 1]^2 \ll 1$ and $\mathrm{E}\xi^2(t) = \sigma_e^2 \ll 1$), this yields a stochastic process with approximate moments

$$\mathrm{E}[\Delta \ln V | N] = \alpha - 1 - \sigma_e^2/2 - \gamma g(N), \quad \mathrm{Var}[\Delta \ln V | N] = \sigma_e^2 \tag{3c}$$

$$\text{where } \sigma_e^2 = \sum_{ij} \sum_{i'j'} v_i u_j v_{i'} u_{j'} C_{ij,i'j'}. \tag{3d}$$

The term σ_e^2 is the environmental variance in the growth rate of net reproductive value.

The expected change in equation (3c) differs in three ways from the approximate stochastic growth rate of a density-independent population, $r - \sigma_e^2/2$ (Tuljapurkar 1982, 1990; Caswell 2001), most importantly by the last term, the product of the net density dependence in the life history, γ, and the density dependence function, $g(N)$. The environmental variance σ_e^2 (eq. [3d]) differs from that of Tuljapurkar (1982, 1990), which includes a factor of $1/\lambda^2$ but with density dependence $\lambda(g(K)) = 1$, so this factor vanishes. Finally, instead of r, the deterministic density-independent growth rate here, $\alpha - 1 = vAu - 1$, is for a population in discrete time, corresponding to $e^r - 1 = r + r^2/2 + \cdots$ but with eigenvectors v and u of the expected projection matrix evaluated at $N = K$ instead of $N \ll K$.

The corresponding stochastic difference equation is

$$\Delta \ln V = \alpha - 1 - \sigma_e^2/2 - \gamma g(N) + \xi(t), \tag{3e}$$

with $\mathrm{E}[\xi(t)] = 0$ and $\mathrm{Var}[\xi(t)] = \sigma_e^2$. This motivates the statistical method described below for estimating the key demographic parameters.

In the long run, the expected change in $\ln V$ is zero, and averaging both sides of equation (3e) through time gives the expected value of the density dependence function:

$$\mathrm{E}[g(N)] = \frac{\alpha - 1 - \sigma_e^2/2}{\gamma}. \tag{4}$$

Comparison with the deterministic equilibrium in a constant environment (eq. [2b]) shows that environmental stochasticity decreases the expected population size below K, in agreement with previous theory (Lande et al. 2003, 2009, 2017; Engen et al. 2013).

Other statistics of the population distribution can be derived by reducing the process to a single dimension. Appendix A shows that the log of any positive linear combination of stage abundances increases at the approximate asymptotic rate of the log of the leading eigenvalue of the stochastic projection matrix. Similarly, it was previously known for density-independent populations that any positive linear combination of stages increases asymptotically at the density-independent stochastic growth rate (Tuljapurkar 1982; Caswell 2001; Engen et al. 2007, 2009). We can therefore replace V with N in equations (3b), (3c),

and (3e), rendering the process one dimensional while maintaining the correct density dependence function:

$$\mathrm{E}[\Delta \ln N|N] = \alpha - 1 - \sigma_e^2/2 - \gamma g(N), \ \mathrm{Var}[\Delta \ln N|N] = \sigma_e^2. \tag{5a}$$

The stationary distribution of N and its moments can be derived using a continuous-time diffusion approximation (Karlin and Taylor 1981; Lande et al. 2003) with infinitesimal mean and variance in equation (5a), as for the stochastic theta-logistic model (Diserud and Engen 2000). Simulations show that this approach accurately describes the stationary distribution of N for $r \leq 0.1$ (Lande et al. 2017). The present theory using $\alpha - 1$ instead of r should remain accurate under higher density-independent growth rates, $\alpha - 1 < 2$, with the upper limit set by the requirement for deterministic stability of K. The diffusion approximation is not employed in equation (4) or in the statistical procedure below for estimating the demographic parameters.

Neglecting demographic stochasticity and Allee effects at small population sizes, the stationary distribution exists when the density-independent stochastic growth rate is positive, $s = \alpha - 1 - \sigma_e^2/2 > 0$. With linear density dependence, $g(N) = N$, the stationary distribution of N has mean, variance, and coefficient of variation (Lande et al. 2017)

$$\begin{aligned} \mathrm{E}[N] &= (1-a)K, \quad \sigma_N^2 = a(1-a)K^2, \\ \mathrm{CV}_N &= \sqrt{\frac{a}{1-a}}, \quad \text{where } a = \frac{\sigma_e^2}{2(\alpha - 1)}. \end{aligned} \tag{5b}$$

The diffusion formula for $E[N]$ agrees with the discrete-time formula (eq. [4]) under linear density dependence with $K = (\alpha - 1)/\gamma$ (eq. [2b]).

Statistics for Parameter Estimation

We outline a basic three-step procedure for estimating parameters of the linearized density-dependent projection matrix (eq. [2a]).

Step 1: Establish net density dependence and estimate relative weights. Before conducting a detailed analysis of long-term demographic data, it is necessary to first establish that significant net density dependence exists in the life history. A simple regression analysis based on the discrete-time recursion (eq. [3e]) suffices to estimate the net density dependence, γ, and the relative weights, b_i, of stages in the weighted population size, $N = \sum_i b_i n_i$. Assuming the density dependence function is linear, $g(N) = N$, and writing $\Delta \ln V = \ln \lambda(N, t)$, equation (3e) becomes a linear multiple regression of annual values of $\ln \lambda$ on the corresponding stage abundances, n_i:

$$\ln \lambda = s - \gamma \sum_i b_i n_i + \epsilon. \tag{6a}$$

Annual values of $\ln \lambda$ in this regression should be calculated from the dominant eigenvalue λ of the projection matrix estimated from annual demographic data. The regression constant, s, is the density-independent stochastic growth rate, and ϵ is a random residual with mean 0 that includes both environmental and demographic variance. The partial regression coefficient of n_i is $-\gamma b_i$, and one of the weights, b_i (or their sum), can be chosen arbitrarily as a scaling factor, determining γ and the relative weights from the estimated partial regression coefficients. If the fraction of the variance in $\ln \lambda$ among years explained by the regression, R^2, is significant, then net density dependence exists in the life history, justifying a more detailed analysis. We emphasize that this is not an autoregression of a population time series and only uses stage abundances as independent variables to explain annual variation in $\ln \lambda$ from projection matrices containing vital rates estimated separately each year.

Step 2: Estimate density dependence in stage-specific vital rates. The estimated relative weights, b_i, can be used in a separate univariate regression of annual estimates for each vital rate on annual values of N to estimate the density-independent and density-dependent coefficients α_{ij} and γ_{ij} using the linearized form (eqq. [1a], [2a]):

$$L_{ij} = \alpha_{ij} - \gamma_{ij} N + \epsilon_{ij}, \tag{6b}$$

where ϵ_{ij} is a stage-specific residual with mean 0 that includes environmental and demographic variance. The stage-specific regressions must be checked to ensure that they do not predict negative vital rates (or survival rates exceeding 1) within the observed range of N.

The carrying capacity, K, is obtained from the leading eigenvalue of the expected projection matrix at equilibrium $l(g(K)) = A - \Gamma g(K)$, solving $\lambda(g(K)) = 1$ using $g(K) = K$ (eq. [2b]). The right and left eigenvectors of $l(g(K))$ are respectively the stable stage distribution u and reproductive values v, normalized so that $\sum_i u_i = 1$ and $vu = 1$. The net density dependence (eq. [2b]) is then $\gamma = v\Gamma u$, which should agree closely with the initial estimate from step 1.

Nonlinear regression or generalized linear models with nonlinear link functions (log reproduction and logit survival) could be employed to guarantee that fitted vital rates are nonnegative (with survival not exceeding 1) across the observed range of N. For example, Takada and Nakashizuka (1996) use log-linear regression to fit exponential density dependence functions for the vital rates. Taylor expansion of the vital rates around the deterministic equilibrium at $N = K$ as a linear function of $g(N)$ would then

be necessary to estimate the coefficients α_{ij}, γ_{ij}, and $C_{ij,ij}$ (eqq. [1a], [2a], [3d]) required to calculate the key parameters, $\alpha - 1$, γ, and σ_e^2.

Step 3: Estimate environmental covariance matrix of vital rates. For distinct vital rates l_{ij} and $l_{i'j'}$, the estimated environmental covariance is simply the observed covariance of residuals from the regressions (eq. [6b]), assuming that demographic stochasticity operates independently among the vital rates (Engen et al. 1998; Lande et al. 2003; Sæther et al. 2004):

$$C_{ij,i'j'} = \mathrm{E}[\epsilon_{ij}\epsilon_{i'j'}] \quad \text{for } ij \neq i'j'. \tag{6c}$$

The environmental variance of each vital rate, l_{ij}, can be estimated from the variance of residuals in the regression minus the average demographic stochasticity:

$$C_{ij,ij} = \mathrm{E}[\epsilon_{ij}^2] - \mathrm{E}[\sigma_{d,ij}^2/n_j]. \tag{6d}$$

The term $\sigma_{d,ij}^2$ is the variance of individual survival or fecundity for vital rate l_{ij} in each year, and n_j is the corresponding stage abundance. Because n_j is in the denominator, large sampling errors in the estimated environment variances can be avoided by combining into a single terminal stage the oldest, rarest age classes with age-specific abundances too small to accurately estimate vital rates and density dependence. This procedure is common in demographic models of species with determinate growth, where stages are defined by age and fecundity plateaus or declines at mature ages, as in many birds and mammals (Caswell 2001). Excessive condensation into fewer stages can, however, produce inaccurate population dynamics because it ignores heterogeneity among ages combined in a single stage, particularly for species with indeterminate growth, where stages are defined by size and fecundity continually increases with size, as in many plants (Maloney 1986; Rojas-Sandoval and Meléndez-Ackerman 2013; Doak et al. 2021).

These ANOVA estimates are unbiased, but for life histories with more than a few vital rates this method is likely to produce a physically impossible estimate of C, with some negative eigenvalues (Hill and Thompson 1978). We therefore employed a maximum likelihood method using the covariance matrix of residuals and the vector of demographic stochasticities, with Cholesky decomposition of the environmental correlation matrix, to guarantee a positive semidefinite estimate of C (Chen and Dunson 2003; Pourahmadi 2007).

Standardized Density Dependence

To compare populations or species with different carrying capacity, Lande et al. (2002*a*, 2002*b*, 2003, 2006) defined the net density dependence per unit time as the negative elasticity of the leading eigenvalue, λ, to change in population size, N, at the deterministic demographic equilibrium. From the eigenvalue of the projection matrix (eq. [3a]), this is

$$\gamma' = -\frac{\partial \ln\lambda}{\partial \ln N}\bigg|_{N=K,\lambda=1} = -K\frac{\partial\lambda}{\partial N}\bigg|_{N=K} = K\gamma\frac{dg(K)}{dK}. \tag{7a}$$

Because our statistical method assumes a linear (or linearized) density dependence function, the standardized net density dependence is simply $\gamma' = K\gamma$. The same standardized scaling can be applied to density dependence in the vital rates, $\gamma'_{ij} = K\gamma_{ij}$. If the actual density dependence function is nonlinear but linear regressions on N are used in estimation (eq. [6b]), then the factor $dg(K)/dK$ is implicitly incorporated in the estimates of density dependence coefficients and their standardized values.

Standardized net density dependence, γ', gives the expected rate of return of N to its equilibrium or average size (Lande et al. 2002*a*, 2002*b*, 2003, 2006). This entails a condition for deterministic stability of K in discrete time, $\gamma' = \alpha - 1 < 2$ (eq. [5a]). Standardized density dependence measures also have the advantage that whatever arbitrary scaling is chosen for the relative weights, b_i, determining N (after eq. [1a]), this cancels out after multiplying by K.

For interspecific comparisons of net density dependence, when species differ in life history, further scaling by generation time, T, may be used to give the net density dependence per generation, $T\gamma' = TK\gamma$ (Lande et al. 2002*a*, 2002*b*, 2003, 2006; Gaillard et al. 2005; Sæther et al. 2005), where T is the mean age of mothers of a newborn cohort at the deterministic equilibrium. Caswell (2001, chap. 5) summarizes how to calculate T for a general stage-structured demography.

A simple expression for T can be derived for a commonly used stage structure similar to the Leslie matrix, with age-specific fecundities f_τ in the first row, annual survival probabilities s_τ on the subdiagonal, and ages $\tau \geq \omega$ combined in a terminal stage with survival s_ω in the last row and column (e.g., eq. [8]). Using a prebreeding census, first-year survival s_0 implicitly multiplies all fecundities (avoiding for most species the description of sibling competition), and the probability of survival to age τ is $l_\tau = \prod_{i=1}^{\tau-1} s_i$ for $\tau > 1$, defining $l_1 = 1$ (Caswell 2001). Since $\lambda = 1$ at demographic equilibrium, the generation time is

$$T = \sum_{\tau=1}^{\omega-1} \tau l_\tau f_\tau + \frac{l_\omega f_\omega}{1 - s_\omega}\left(\omega + \frac{s_\omega}{1 - s_\omega}\right). \tag{7b}$$

Demographic Parameter Estimates for a Great Tit Life History

Demographic data were collected over 38 years on a population of great tits (*Parus major* L.) in Hoge Veluwe

National Park in the Netherlands (Sæther et al. 2016*b*; Gamelon et al. 2016). The area consists of mixed pine-deciduous woodland on poor sandy soils. To ensure that availability of artificial nest sites did not limit population size, a surplus of nest boxes was provided (Grøtan et al. 2009). The adult survival rate of great tits in this population is strongly dependent on the beech crop cycle (Perdeck et al. 2000), and population fluctuations in this species are caused by a combination of density dependence and environmental stochasticity, especially due to variation in beech crops and winter temperatures (Perrins 1965; Slagsvold 1975; Sæther et al. 2007). In this population there is density-dependent selection on reproductive traits (Sæther et al. 2016*b*), and immigrants strongly affect population dynamics (Grøtan et al. 2009).

The minimal sex dimorphism, as well as the similarity of male and female mean life histories in great tits (Clobert et al. 1988), justifies focusing on female life history as the main determinant of population dynamics, as usual in female-biased demography (Caswell 2001). The data were analyzed using an annual prebreeding census common in avian demography. The oldest ages were combined in a terminal stage, producing a projection matrix with three stages, for individuals aged 1, 2, and 3 or more years, with the projection matrix

$$L = \begin{pmatrix} f_1 & f_2 & f_3 \\ s_1 & 0 & 0 \\ 0 & s_2 & s_3 \end{pmatrix}. \tag{8}$$

Recruitment rates in the first row represent the product of fecundity and survival to age 1 (Caswell 2001). Total recruits of both sexes were counted and then multiplied by 0.5 to produce female recruits per adult female in each age class, assuming an even sex ratio at fledging and no sex difference in survival. Observed recruitment rates across all years were multiplied by a common immigration factor, $m = 2.988024$, to balance emigration of nearly three-fourths of fledglings out of the study area, determined by setting the long-run density-dependent growth rate of the population to zero, $\mathrm{E}\ln\lambda = 0$, consistent with the observed lack of trend in the time series of actual population size for breeding females in figure 1. For statistical analysis of the demographic data, we used a linear density dependence function, $g(N) = N$, which is justified because the observed fluctuations in actual population size were not very large; moreover, the regressions of $\ln\lambda$ and the vital rates on N in figures 2 and 3 appear to be approximately linear.

Step 1: Net density dependence and relative weights. Multiple regression of $\ln\lambda$ from annual projection matrices on $-\gamma\sum_{i=1}^{3} b_i n_i$ (eq. [6a]) for 38 years of data from the great tit population showed that the initial estimate $\gamma b_3 = -0.00396647$ was slightly negative but far from significant ($P = .64$); because the initial estimate was negative, which is biologically unrealistic, we set $b_3 = 0$ and reran the regression, which only slightly changed the remaining estimates: $\gamma b_1 = 0.01354864$ ($P = .00009$) and $\gamma b_2 = 0.00886644$ ($P = .21$). A maximum likelihood method applied to $\ln(\gamma b_i)$, constraining the weight coefficients to be nonnegative, produced nearly the same results. We scaled the relative weights so that their sum equaled 3 (the number of stages), giving the relative weights $(b_1, b_2, b_3) = (1.813329, 1.186671, 0)$.

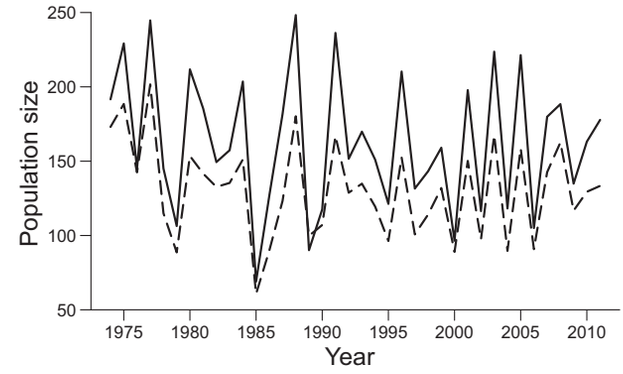

Figure 1: Weighted population size, $N = \sum_{i=1}^{3} b_i n_i$ (solid line), and actual population size, $N_a = \sum_{i=1}^{3} n_i$ (dashed line), over 38 years in the great tit population.

Univariate regression of $\ln\lambda$ on weighted N, illustrated in figure 2, was very highly significant (slope $= -0.00747169$, $P = .00004$, adj. $R^2 = 0.36$), indicating substantial density dependence in the great tit life history, measured by the estimated slope, $\gamma = 0.00747169$ (95% confidence interval: 0.00426–0.01069). This prompted us to complete the demographic sensitivity analysis. The intercept of the univariate regression estimating the density-independent

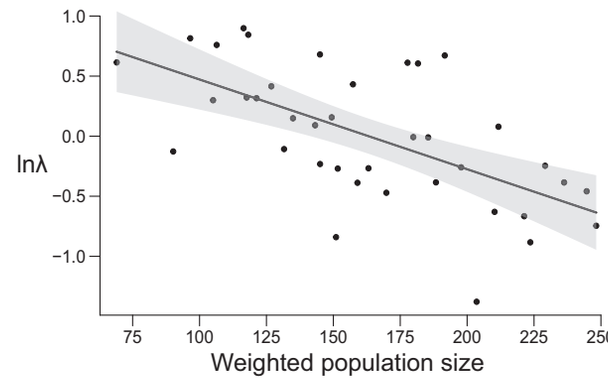

Figure 2: Regression of $\ln\lambda$ from annual projection matrices on weighted N for the great tit population. The gray area is the 95% confidence region for the regression line.

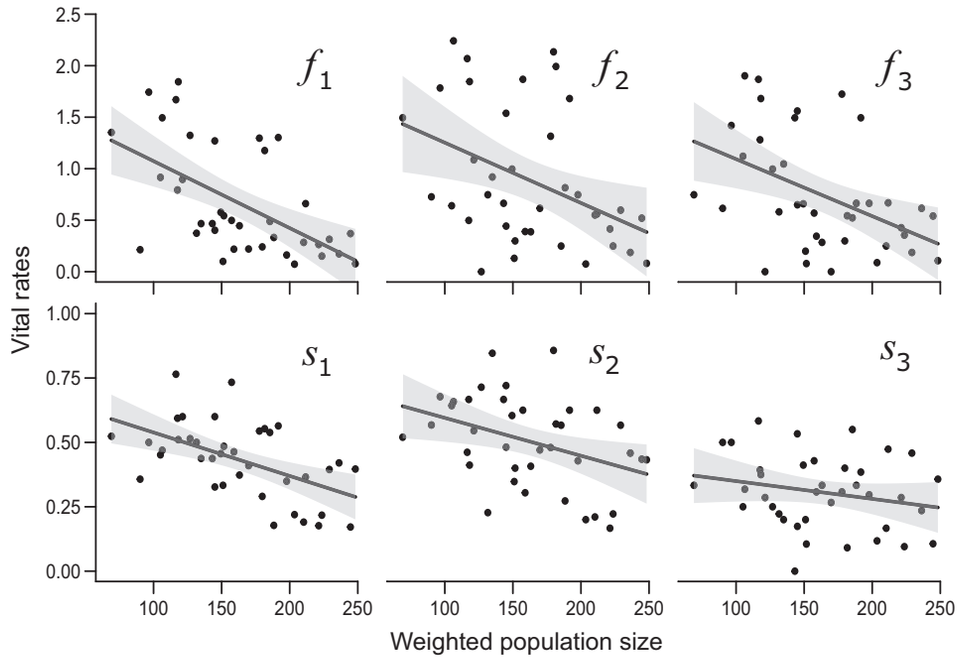

Figure 3: Regressions of recruitment and survival rates, f_i and s_i, on weighted N for the great tit population. Gray areas are 95% confidence regions for the regression lines.

stochastic growth rate (eq. [6a]), $s = 1.2191$, also was very highly significant ($P = .00004$). Figure 1 illustrates the time series for actual population size, N_a, and weighted population size, N, over 38 years for the great tit population.

Step 2: Density dependence in stage-specific vital rates. Univariate regressions of vital rates on weighted N all had highly significant positive intercepts, the density-independent components, α_{ij}. Estimated slopes, $-\gamma_{ij}$, were all negative, reflecting density dependence that in all but one case was significant, with adjusted R^2 and P values in table 1. Density dependence of the vital rates is depicted in figure 3. Density dependence in the stage-specific recruitments is much stronger than in the survival rates.

The deterministic projection matrix $l(g(K)) = A - \Gamma g(K)$ with leading eigenvalue $\lambda(g(K)) = 1$ was used with $g(K) = K$ to determine the carrying capacity. Nonzero elements of A and Γ appear in table 1, and we obtain the estimated carrying capacity $K = 183.62$. The right and left eigenvectors of $l(g(K))$ are the stable stage distribution u and reproductive values v, normalized so that $\sum_i u_i = 1$ and $vu = 1$. These were estimated as the column vector $u = (0.601587, 0.239026, 0.159387)^\top$, where the superscript $\top$ indicates transpose, and the row vector $v = (0.974525, 1.15287, 0.866898)$. The deterministic density-independent growth rate and the net density dependence (eq. [2b]) were then estimated as $\alpha - 1 = vAu - 1 = 1.39665$ and $\gamma = v\Gamma u = 0.00760619$.

Step 3: Environmental variance-covariance matrix. Initially, all demographic variances for stage-specific recruitment (eq. [6d]) were multiplied by the square of the immigration factor, m^2, because up to this point only the stage-specific mean recruitments in each year had been corrected for immigration (see after eq. [8]). The environmental covariance matrix, C, estimated by analysis

Table 1: Estimated density-independent and density-dependent parameters, α_{ij} and γ_{ij}, of recruitment and survival rates, f_i and s_i, from regressions on weighted N

Rate	α_{ij}	γ_{ij}	P	Adj. R^2
f_1	1.72366	.00650092	.0002	.306
f_2	1.83804	.00585470	.0116	.141
f_3	1.64701	.00553938	.0039	.187
s_1	.707262	.00168792	.0006	.265
s_2	.742178	.00147056	.0169	.125
s_3	.418691	.00069034	.1779	.024

of (co)variance (eqq. [6c], [6d]), produced a matrix with two small negative eigenvalues. The maximum likelihood estimate using Cholesky decomposition produced a positive semidefinite estimate of C with two eigenvalues near zero. Estimated environmental (co)variances of vital rates, with corresponding correlations, are displayed in table 2. Environmental variances in stage-specific recruitment are considerably larger than variances in survival, which can be partly, but not fully, explained as a scale effect because the mean values of recruitment are larger than those of survival (fig. 3). Environmental correlations among the vital rates are all substantially positive. The environmental covariance matrix produced an estimate of the environmental variance in population growth rate (eq. [3d]), $\sigma_e^2 = 0.199707$.

Accuracy of the Theory and Parameter Estimates

As a check on the accuracy of the theory and adequacy of the data, estimates of the net density dependence, γ, and the density-independent stochastic growth rate, s, obtained in step 1 were compared with formulas using the density-independent and density-dependent parameters of the expected vital rates estimated in step 2 and their environmental (co)variances estimated in step 3. We then estimated from the theory the mean and coefficient of variation of N and the expected rate of fluctuations around the mean and compared these predictions with observed population statistics in the 38 years of observation.

The net density dependence in the life history was estimated from the univariate regression in step 1 as $\gamma = 0.00747169$. This agrees within 2% compared with the $\gamma = v\Gamma u = 0.00760619$ estimated in step 2 (eq. [2b]).

The estimated carrying capacity, $K = 183.62$, was obtained from the leading eigenvalue of the deterministic equilibrium projection matrix, setting $\lambda(g(K)) = 1$ using linear density dependence $g(K) = K$. This necessarily matches exactly the identity $K = (\alpha - 1)/\gamma$ (eq. [2b]) using the estimates of α and γ from step 2.

The density-independent stochastic growth rate, s, estimated from the univariate regression in step 1 was $s = 1.21906$. This is about 6% smaller than $s = \alpha - 1 - \sigma_e^2/2 = 1.29679$ estimated using $\alpha - 1 = 1.39665$ from step 2 and $\sigma_e^2 = 0.199893$ from step 3.

The standardized net density dependence (eq. [7a]), using the estimated γ from step 2, is $\gamma' = K\gamma = 1.39665$. In a constant environment, values in the range $1 < \gamma' < 2$ predict damped oscillations in N with successive diminishing overshoot and undershoot of K, on a timescale for expected return of N to its average value, $1/\gamma'$, less than 1 year. This strong net density dependence accords with observed rapid fluctuations of N around its average value (fig. 1).

The expected weighted population size, $\mathrm{E}[N]$, is less than its deterministic equilibrium, K, because of environmental and demographic stochasticity (Lande et al. 2003). Accounting only for environmental stochasticity (eqq. [4], [5b]), using $\sigma_e^2 = 0.199707$ estimated in step 3, the expected population size predicted by equation (4) is $\mathrm{E}[N] = 170.48$. Including the demographic stochasticities with the environmental variances (eqq. [6c], [6d]; Lande et al. 2003; Sæther et al. 2004; Engen et al. 2009) slightly reduced the prediction to 168.86. These predictions of $\mathrm{E}[N]$ are within about 4% of the observed mean weighted population size, $\bar{N} = 163.16$.

The coefficient of variation of N predicted from diffusion theory (eq. [5b]), using the estimates of α and σ_e^2, is $\mathrm{CV}_N = 0.2776$. The observed $\mathrm{CV}_N = 0.2828$ is within 2% of the estimate.

Life History Evolution in a Stochastic Environment

Evolution in fluctuating (st)age-structured populations is generally described most accurately using reproductive-value-weighted mean phenotype to remove transient effects of age structure fluctuations (Fisher 1958; Engen et al. 2014; Lion 2018). This is precluded by defining the mean life history phenotype in a population as the vector, $\bar{z}$, of stage-specific vital rate parameters, α_{ij}, γ_{ij}, and $C_{ij,i'j'}$, or the quantitative traits underlying them. Coupled to the stochastic demographic process (eq. [5a]), the expected rate

Table 2: Estimated environmental (co)variances of vital rates, $C_{ij,i'j'}$, in upper triangular matrix, with two-digit correlations below the diagonal

Rate	f_1	f_2	f_3	s_1	s_2	s_3
f_1	.149405	.151463	.139466	.023770	.016787	.016061
f_2	.76	.264974	.140525	.027208	.032312	.025764
f_3	.97	.73	.138002	.020572	.019900	.014642
s_1	.67	.58	.60	.008413	.006604	.005870
s_2	.41	.60	.51	.68	.010982	.006069
s_3	.61	.73	.58	.94	.85	.004667

of evolution of the mean phenotype, $\bar{z}$, is (Lande 1982, 2007; Engen et al. 2013; Lande et al. 2017)

$$\mathrm{E}[\Delta\bar{z}|\bar{z}, N] = \frac{G}{T}\nabla \mathrm{E}\ln\lambda. \tag{9a}$$

The term G is the additive genetic covariance matrix of the phenotypes, T is the generation time (average age of mothers of newborns at the deterministic demographic equilibrium), ∇ is the selection gradient operator (column vector of partial derivatives with respect to elements of $\bar{z}$), and $\mathrm{E}\ln\lambda \approx \alpha - 1 - \sigma_e^2/2 - \gamma g(N)$ is the density-dependent stochastic growth rate of the population (eqq. [3b], [3c]). This can be reexpressed using the density-independent stochastic growth rate $s = \alpha - 1 - \sigma_e^2/2$:

$$\mathrm{E}[\Delta\bar{z}|\bar{z}, N] = \frac{G}{T}[\nabla s - g(N)\nabla\gamma]. \tag{9b}$$

The first term in brackets, ∇s, appears identical to the selection gradient for fluctuating density-independent selection (Lande 2007) but with density-dependent selection and stage structure; s contains eigenvectors u and v of the deterministic equilibrium projection matrix, $l(g(K))$.

Assuming that evolution of the mean phenotype is slow compared with the timescale for population fluctuations, averaging the expected evolution over the stationary distribution of population size, and substituting $\mathrm{E}[g(N)]$ from equation (4) produces the expected selection gradient governing long-term evolution of the life history, conditioned only on $\bar{z}$:

$$\mathrm{E}[\Delta\bar{z}|\bar{z}] = \frac{G}{T}\gamma\nabla\left(\frac{s}{\gamma}\right). \tag{9c}$$

This shows that the long-term average selection gradient is $\gamma\nabla(s/\gamma)$. Because γ must be positive, the expected long-term evolution of a density-dependent population in a fluctuating environment is a stochastic maximization of $\mathrm{E}[g(N)] = s/\gamma$, as illustrated by simulations in Engen et al. (2013). For theta-logistic density dependence, $g(N) = N^\theta$, life history evolution maximizes $\mathrm{E}[N^\theta]$, and for logistic density dependence, $\theta = 1$, evolution maximizes $E[N]$ (Lande et al. 2017).

Under a stationary distribution of environments, the long-term average growth rate of a density-dependent population must be zero, which after an initial transient period can be improved slowly if at all by evolution. The long-term average rate of evolution (eq. [9c]) also must be near zero, but nevertheless there may be a substantial long-term average selection gradient on the life history. This can occur if the G matrix is singular, lacking additive genetic variance in the prevailing direction of selection, when G incorporates ecological trade-offs manifested in genetic constraints among characters. A genetic correlation between characters that opposes their directions of selection retards evolution and is known as antagonistic selection. Genetic constraints for life history characters often appear as negative genetic correlations between major components of fitness selected in the same direction, such as survival and reproduction, or early and late reproduction; a positive genetic correlation constrains the evolution of characters selected in opposite directions, such as intrinsic rate of increase and environmental variance (Lande 1982; Charlesworth 1994; Mueller 1997; Travis et al. 2013; Sæther et al. 2016*b*; Lande et al. 2009, 2017). Even in the absence of additive genetic variance for a combination of characters in the direction of the selection gradient, measurable natural selection can occur based on nonheritable phenotypic variance caused by the environment and developmental noise (Haldane 1954; Lande and Arnold 1983).

Demographic Sensitivities in the Long-Term Selection Gradient

Sensitivity analysis is an important tool in demography, describing how population growth rate responds to small changes in age- or stage-specific vital rates of survival and reproduction (Caswell 2001, 2019). Previous theory for density-independent age-structured populations in a constant environment established that evolution maximizes the population growth rate, λ, and that the selection gradient governing life history evolution is composed of demographic sensitivities of λ to changes in the vital rates (Lande 1982; van Tienderen 2000). Here, we extend these evolutionary interpretation of demographic sensitivities as selection coefficients to life history of a density-dependent population in a stochastic environment.

Long-Term Selection Gradient

For evolution of the life history, the elements in the long-term average selection gradient $\gamma\nabla(s/\gamma)$ are demographic sensitivities to perturbations in the vital rate parameters (eq. [9c]). Focusing on a single element in the long-term selection gradient and substituting $\alpha - 1 = g(K)\gamma$ in $s = \alpha - 1 - \sigma_e^2/2$, the sensitivity to a vital rate parameter—$x = \alpha_{ij}$, γ_{ij}, or $C_{ij,i'j'}$—is

$$\gamma\frac{\partial(s/\gamma)}{\partial x} = \gamma\frac{\partial g(K)}{\partial x} - \frac{1}{2}\frac{\partial\sigma_e^2}{\partial x} + \frac{\sigma_e^2}{2\gamma}\frac{\partial\gamma}{\partial x}. \tag{10}$$

Simple formulas are given below for the sensitivity of $g(K)$ to change in α_{ij} or γ_{ij} and for the sensitivity of σ_e^2 to change in $C_{ij,i'j'}$. Sensitivities of γ and σ_e^2 to perturbation in α_{ij} or γ_{ij} are more complex, involving eigenvector sensitivities (app. B). Numerical sensitivities also can be obtained by perturbing x to $x + \delta x$; recomputing perturbed values of

K, u, and v to find $\gamma + \delta\gamma$; and approximating the sensitivity by $\delta\gamma/\delta x$ and similarly for $\delta\sigma_e^2/\delta x$.

Sensitivity of $g(K)$ to α_{ij} and γ_{ij}

The sensitivities of $g(K)$ to perturbation in α_{ij} or γ_{ij} are derived in appendix B:

$$\frac{\partial g(K)}{\partial \alpha_{ij}} = \frac{v_i u_j}{\gamma} \quad \text{and} \quad \frac{\partial g(K)}{\partial \gamma_{ij}} = -g(K)\frac{v_i u_j}{\gamma}. \tag{11a}$$

The first formula agrees with the sensitivity of K derived by Takada and Nakajima (1998) and Caswell (2001, eq. [16.111]), who included a factor $dg(K)/dK$ in γ_{ij} (as after eq. [7a]). They did not distinguish perturbations in α_{ij} and γ_{ij}. The sensitivity of $g(K)$ to perturbation in γ_{ij} is $-g(K)$ times the sensitivity to α_{ij}, as evident from equation (2a).

Sensitivity of σ_e^2 to $C_{ij,i'j'}$

The sensitivity of the environmental variance to a perturbation in the environmental (co)variance of vital rate(s), $C_{ij,i'j'}$, is

$$\frac{\partial \sigma_e^2}{\partial C_{ij,i'j'}} = (2 - \delta_{ij,i'j'})v_i u_j v_{i'} u_{j'}, \tag{11b}$$

where $\delta_{ij,i'j'} = 1$ if $ij = i'j'$ and zero otherwise, which accounts for the symmetry of the environmental covariance matrix, $C_{ij,i'j'} = C_{i'j',ij}$ (Caswell 2001, eqq. [14.110], [14.111]). The simplicity of this formula arises because the eigenvectors, u and v, at the deterministic equilibrium do not depend on environmental stochasticity.

Sensitivity Analysis of the Great Tit Life History

Using the estimated density-independent and density-dependent coefficients of the vital rates, α_{ij} and γ_{ij} in table 1, we calculated elements in the long-term selection gradient on the great tit life history, the sensitivities to each these coefficients, and their component contributions (eq. [10]), as shown in tables 3 and 4.

Table 5 displays sensitivities to environmental (co)variances in the long-term selection gradient, $\gamma\partial(s/\gamma)/\partial C_{ij,i'j'} = -(1/2)\partial\sigma_e^2/\partial C_{ij,i'j'}$ (eq. [10]). Off-diagonal sensitivities include a factor of 2, accounting for symmetry of C including contributions from $C_{ij,i'j'}$ and $C_{i'j',ij}$ (eq. [11b]); the lower off-diagonal terms are not shown because they are included in the upper off-diagonal terms.

The last column of tables 3 and 4 and the diagonal entries in table 5 reveal that within each group of sensitivities, those to parameters of first-year survival and recruitment are the largest. This occurs primarily because all three age classes have similar reproductive values, but the abundance of 1-year-olds far exceeds that of 2-year-olds or the 3-year-and-older class (see step 2 of great tit parameter estimates).

For sensitivities to deterministic parameters of the vital rates, α_{ij} and γ_{ij}, the largest contribution arises from the sensitivity of carrying capacity, which in table 3 is simply $v_i u_j$ and in table 4 is $-Kv_i u_j$ (eq. [11a]). Sensitivities to environmental (co)variances, $C_{ij,i'j'}$, in table 5 for the variances are $-(v_i u_j)^2/2$ and for the covariances are $-v_i u_j v_i u_j$. Thus, when the sensitivities for two environmental variances are about equal, the sensitivity for their corresponding covariance is about twice as large. This explains why in table 5 the largest sensitivity is that for the covariance of first-year survival and recruitment.

Relative Sensitivities in the Long-Term Selection Gradient

The sensitivity of $g(K)$ to γ_{ij} is larger than that to α_{ij} by a factor of $g(K)$ (eq. [11a]), and in tables 3–5 the sensitivities to density dependence coefficients γ_{ij} dominate all the other sensitivities. This occurs because γ_{ij} and the net density dependence γ are rather small when K is large.

To better compare the selection intensity acting on demographic parameters and to render them all dimensionless, the long-term selection gradient acting on the logarithms of demographic parameters can be employed. Instead of the element of the long-term selection gradient $\gamma\partial(s/\gamma)/\partial x$ (eq. [10]), one would use $\gamma\partial(s/\gamma)/\partial \ln x = \gamma x\partial(s/\gamma)/\partial x$.

Table 3: Sensitivities to α_{ij} in the long-term selection gradient and their components (eq. [10])

Rate	$\gamma\frac{\partial g(K)}{\partial \alpha_{ij}}$	$-\frac{1}{2}\frac{\partial \sigma_e^2}{\partial \alpha_{ij}}$	$+\frac{\sigma_e^2}{2\gamma}\frac{\partial \gamma}{\partial \alpha_{ij}}$	$= \gamma\frac{\partial(s/\gamma)}{\partial \alpha_{ij}}$
f_1	.58626	−.03913	.01801	.56512
f_2	.23294	.01255	−.00312	.24236
f_3	.15533	.03777	−.01566	.17743
s_1	.69355	−.04031	.00402	.65726
s_2	.20721	.01130	−.00543	.21309
s_3	.13817	.03369	−.01570	.15616

Table 4: Sensitivities to γ_{ij} in the long-term selection gradient and their components (eq. [10])

Rate	$\gamma \frac{\partial g(K)}{\partial \gamma_{ij}}$	$-\frac{1}{2}\frac{\partial \sigma_e^2}{\partial \gamma_{ij}}$	$+\frac{\sigma_e^2}{2\gamma}\frac{\partial \gamma}{\partial \gamma_{ij}}$	$=\gamma \frac{\partial (s/\gamma)}{\partial \gamma_{ij}}$
f_1	−107.649	7.1887	4.3969	−96.064
f_2	−42.772	−2.3045	3.6343	−41.442
f_3	−28.521	−6.9345	4.9166	−30.539
s_1	−127.350	7.4021	8.3756	−111.572
s_2	−38.048	−2.0753	3.7192	−36.404
s_3	−25.371	−6.1855	4.6979	−26.859

Logarithms are valid only for positive parameters. All nonzero density-independent coefficients α_{ij} must be positive, but density-dependent coefficients γ_{ij} can be negative with social facilitation of reproduction or survival in highly social species or because of Allee effects in small populations. Even if some γ_{ij} are negative, a stable deterministic $K > 0$ still exists when the net density dependence is positive, $\gamma > 0$. Environmental variances must be positive; environmental covariances usually will be positive (as in table 2) but in some cases may be negative. A small increase in an environmental covariance $C_{ij,i'j'}$ increases σ_e^2 regardless of whether $C_{ij,i'j'}$ is positive or negative. For negative demographic parameters, $x < 0$, the relative sensitivity measure that preserves the sign of the sensitivity is $\gamma|x|\partial(s/\gamma)/\partial x$.

Elements in the long-term selection gradient are derivatives of the density-dependent stochastic growth rate, $\mathrm{E}\ln\lambda$, averaged over the stationary distribution of N (eqq. [9a]–[9c]). Thus, without further scale transformation, relative sensitivities in the long-term selection gradient correspond to traditional elasticities, $\partial \ln\lambda/\partial \ln x = (x/\lambda)\partial\lambda/\partial x$ (Caswell 2001, 2019; van Tienderen 2000; Hereford et al. 2004; Matsumura et al. 2012).

Relative Sensitivities in the Great Tit Life History

For the great tit population, all of the demographic parameters in tables 1 and 2 are positive. We therefore compare their relative sensitivities in the long-term selection gradient on their logarithms in tables 6 and 7. The relative sensitivities for the density-independent parameters, the elements of the selection gradient on $\ln\alpha_{ij}$, are all positive and of larger magnitude than those on the density-dependent parameters $\ln\gamma_{ij}$, which are all negative. The relative sensitivities on the environmental (co)variances are all negative with yet-smaller magnitudes. Relative sensitivities for first-year recruitment and survival have magnitudes larger than those for age 2 or stage 3.

Discussion

We analyzed the dynamics of a density-dependent stage-structured population, assuming a stationary distribution of environments, with density dependence in the vital rates exerted by a function $g(N)$ of a weighted sum of stage abundances, $N = \sum_i b_i n_i$. The multivariate dynamics of stage abundances, n_i, can be approximated by a univariate stochastic process for N governed by three key demographic factors: the density-independent growth rate $\alpha - 1$; the net density dependence, γ; and environmental variance, σ_e^2, in the life history. Similar results were previously derived for populations with small density-independent growth rate, $r \leq 0.1$, and weak density dependence and were shown by simulation to be accurate for small or moderate fluctuations in N (Lande et al. 2017). More generally, the present theory allows any density-independent growth rate and strength of density dependence, still assuming small or moderate fluctuations around a deterministically stable equilibrium, with coefficient of variation $\mathrm{CV}_N \lesssim 0.3$.

These results motivate a novel statistical analysis for long-term demographic data to estimate the relative weights of stages in N; the density-independent and density-dependent parameters, α_{ij} and γ_{ij}; and the environmental (co)variances, $C_{ij,i'j'}$, of the vital rates. These coefficients determine the population carrying capacity, K; the stable age distribution and reproductive values, u and v, at equilibrium when $N = K$;

Table 5: Sensitivities to $C_{ij,i'j'}$ in the long-term selection gradient, $-(1/2)\partial\sigma_e^2/\partial C_{ij,i'j'}$

Rate	f_1	f_2	f_3	s_1	s_2	s_3
f_1	−.17185	−.13656	−.09106	−.40660	−.12148	−.08101
f_2		−.02713	−.03618	−.16155	−.04827	−.03219
f_3			−.01206	−.10773	−.03219	−.02146
s_1				−.24051	−.14371	−.09583
s_2					−.02147	−.02863
s_3						−.00955

Table 6: Relative sensitivities to $\ln\alpha_{ij}$ and $\ln\gamma_{ij}$ in the long-term selection gradient

Rate	$\gamma\frac{\partial(s/\gamma)}{\partial\ln\alpha_{ij}}$	$\gamma\frac{\partial(s/\gamma)}{\partial\ln\gamma_{ij}}$
f_1	.97407	−.62450
f_2	.44548	−.24263
f_3	.29223	−.16917
s_1	.46485	−.18833
s_2	.15815	−.05353
s_3	.06538	−.01854

and the key demographic parameters. Estimation of the key parameters facilitates quantitative comparison of populations and species with different carrying capacities and life histories.

Most previous studies assuming that a weighted population size, N, exerts density dependence on the vital rates made a priori assumptions about the weights, b_i (Takada and Nakashizuka 1996; Grant and Benton 2000; Coulson et al. 2001, 2008; Lande et al. 2002*a*, 2002*b*; Sæther et al. 2005, 2016*a*). In contrast, our statistical analysis (step 1; eq. [6a]) employs multiple regression of $\ln\lambda$ on stage abundances to estimate the relative weights, γb_i. If the regression is significant, then net density dependence exists and the relative weights can be determined by choosing an arbitrary scale factor (e.g., fixing their sum), which becomes incorporated in N (step 2). The inverse of this scale factor is absorbed in γ and in density-dependent coefficients for the vital rates, γ_{ij}. The arbitrary scale factor vanishes in the standardized net density dependence, $\gamma' = K\gamma$, giving the expected rate of return of N to equilibrium after a small perturbation (eq. [7a]).

For the great tit population, the estimated relative weights of stages in N decrease strongly for the older stages, $(b_1, b_2, b_3) = (1.813329, 1.186671, 0)$, indicating that 1-year-olds exert the strongest density dependence on population growth, 2-year-olds exert an intermediate density dependence, and individuals three or more years old exert no density dependence. Gamelon et al. (2016) analyzed the same data divided into four life history stages, using Bayesian methods and allowing all possible interclass density-dependent effects, and obtained similar results, which they interpreted as being caused by young first-time breeders competing most strongly for breeding territories, compared with older individuals with established territories. In contrast, our analysis assumes that a single linear combination of stages exerts all the density dependence and condenses the description of the stochastic dynamics of N into a few key parameters, revealing additional information on population dynamics and selection on the life history, discussed below. Our great tit data analysis employed a linear density dependence function, $g(N) = N$, entailing that $\alpha - 1 = K\gamma$ (corresponding to $r = \gamma$ in the classical logistic model; Lande et al. 2003). Thus, there are only two independent key parameters describing the great tit population dynamics, the standardized net density dependence, γ', and the environmental variance σ_e^2.

Previous analyses of stage-structured density dependence (Takada and Nakashizuka 1996; Grant and Benton 2000; Coulson et al. 2001, 2008; Gamelon et al. 2016, 2019) did not estimate environmental (co)variance in the vital rates separated from fluctuations caused by density dependence and demographic stochasticity. The environmental covariance matrix of vital rates estimated for the great tit population (table 2) displays substantial environmental variance in all of the vital rates, with moderate or high correlations especially among stage-specific recruitments and among stage-specific survival rates. We estimated a large environmental variance in population growth rate, with standard deviation $\sigma_e = 0.447$. We also found strong standardized net density dependence, $\gamma' = 1.397$, corresponding deterministically to damped oscillations around a stable equilibrium, consistent with the observed rapid rate of population fluctuations in figure 1. The great tit population has a moderate coefficient of variation (observed $CV_N = 0.2828$) because strong net density dependence limits the impact of high environmental variance in population growth rate (eq. [5b]).

Estimates of the key parameters predicted with remarkable accuracy the observed mean and coefficient of variation of the weighted population size of the great tits, given that the population is not closed (and neglecting stochasticity

Table 7: Relative sensitivities to $\ln C_{ij,i'j'}$ in the long-term selection gradient, $-(1/2)\partial\sigma_e^2/\partial\ln C_{ij,i'j'}$

Rate	f_1	f_2	f_3	s_1	s_2	s_3
f_1	−.02568	−.02068	−.01270	−.00966	−.00204	−.00130
f_2		−.00719	−.00508	−.00440	−.00156	−.00083
f_3			−.00166	−.00222	−.00064	−.00031
s_1				−.00202	−.00095	−.00056
s_2					−.00024	−.00017
s_3						−.00004

in dispersal). These results reflect the high quality and long time span of the data and help to confirm the accuracy of the univariate approximation to the stage-structured dynamics, even for populations with a strong net density dependence and large environmental stochasticity.

Life history evolution maximizes $\mathrm{E}[g(N)] = s/\gamma$, where $s = \alpha - 1 - \sigma_e^2/2$ is the density-independent stochastic growth rate (eq. [9c]). For the theta-logistic model of density dependence, $g(N) = N^\theta$ (Gilpin and Ayala 1973), evolution maximizes $\mathrm{E}[N^\theta]$. For $\theta = 1$, the density dependence is logistic (linear) and evolution maximizes $E[N]$. This extends to stochastic stage-structured populations the finding of MacArthur (1962) that evolution in a constant environment maximizes the population carrying capacity, K.

Long-term demographic data can be used to estimate demographic sensitivities, which are elements in the long-term selection gradient on the life history, $\gamma\partial(s/\gamma)/\partial x$, where $x = \alpha_{ij}$, γ_{ij}, or $C_{ij,i'j'}$. Each of these elements is the sum of component sensitivities for the key demographic parameters (eqq. [2b], [10]).

In the great tit data, the dominant component of the sensitivities to α_{ij} or γ_{ij} is contributed by the sensitivity of carrying capacity, K (tables 3, 4). The largest sensitivities are those for first-year recruitment and survival, f_1 and s_1. In view of the simple formulas for sensitivities of K (eq. [11a]), which are proportional to $v_i u_j$, this occurs mainly because the individual reproductive values at the three stages are similar but the stable stage distribution has many more individuals of age 1 than age 2 or stage 3 (great tit parameter estimates step 2). The largest sensitivities to $C_{ij,i'j'}$ in the great tits are those for the variances and covariance in first-year survival and recruitment (table 5), for the same reason (eq. [11b]).

Sensitivities to density-dependent parameters, γ_{ij}, have much larger magnitude (and opposite sign) than those to density-independent parameters, α_{ij} (tables 3, 4), primarily because γ_{ij} is much smaller than α_{ij} for the great tits (table 1). This must occur when the carrying capacity is large, as evident in the main component of these sensitivities: the sensitivity of K to γ_{ij} is $-K$ times as large as that to α_{ij} (eq. [11a]). To compare sensitivities for parameters of different magnitude, we calculated relative sensitivities using the logarithms, $\gamma\partial(s/\gamma)/\partial \ln x$ (tables 6, 7). The largest relative sensitivities to $\ln\alpha_{ij}$ and $\ln\gamma_{ij}$ are still those for first-year survival and recruitment. However, for every vital rate the relative sensitivity to the density-independent parameter $\ln\alpha_{ij}$ is larger than that to the density-dependent parameter $\ln\gamma_{ij}$. Relative sensitivities to $\ln C_{ij,i'j'}$ are generally smaller than those to $\ln\alpha_{ij}$ and $\ln\gamma_{ij}$, but among the environmental (co)variances the largest relative sensitivities are to the variance of first-year recruitment and its covariance with the other recruitments and first-year survival.

These results show that for the great tits the density-independent and density-dependent parameters of first-year survival and recruitment, as well as the environmental variance of first-year survival, are subject to the strongest long-term selection in the life history, with density-independent and density-dependent parameters of the vital rates more strongly selected than their environmental (co)variances.

Extensions and limitations. Environmental stochasticity parameterized as noise around a deterministic equilibrium, interacting with nonlinear density dependence (when $g(N)$ has sufficient negative curvature), can increase the means of vital rates, the long-run growth rate (Lande et al. 2003), and mean population size. Environmental stochasticity itself also may be density dependent (Lande et al. 2003). However, when parameterized as noise around the mean vital rates, even with nonlinear density dependence, environmental stochasticity always decreases the long-run growth rate compared with that of the average projection matrix (eq. [3c]; Caswell 2001; Lande et al. 2003), reducing the mean population size. In any case, the assumption of linear density dependence in vital rates, approximated by Taylor expansion around their mean values, estimated using linear regression (step 2) allows estimation of a few key demographic parameters that accurately describe the dynamics of populations with a small or moderate coefficient of variation.

We expect additional insights into population dynamics and life history evolution to emerge from application of our methods to comparative demography among species with simple life cycles. When life history differs between the sexes, with density dependence in their vital rates depending on a single combination of female and male stage abundances, the foregoing methods can be applied to a two-sex projection matrix (Caswell 2001; Engen et al. 2005). The present theory is not applicable to species with complex life cycles involving distinct density dependence functions at different stages (e.g., Berven 2009), for which the population dynamics cannot generally be approximated as a univariate process.

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Statement of Authorship

R.L., B.-E.S., and S.E. designed the research. R.L. derived the theory. R.L., S.E., and V.G. developed statistical methods. M.E.V. collected and compiled great tit data. V.G. calculated statistics and made graphs. R.L. calculated sensitivities and wrote the manuscript with input from all authors.

Data and Code Availability

The great tit demographic data used in the article have been archived, along with R code for statistical analysis and Mathematica code for sensitivity analysis, in the Dryad Digital Repository (https://doi.org/10.5061/dryad.37pvmcvnn; Lande et al. 2022).

APPENDIX A

Asymptotic Growth Rate of $\ln N$

The stochastic projection matrix $L(g(N), t)$ has eigenvalues denoted as $\lambda_i(g(N), t)$, with associated right (column) eigenvectors $u^{(i)}$ and left (row) eigenvectors $v^{(i)}$ normalized so that $v^{(i)}u^{(j)} = 1$ if $i = j$ and zero otherwise. The Perron-Frobenius theorem for real matrices with nonnegative elements guarantees that the leading eigenvalue with the largest modulus, $\lambda(g(N), t) = \lambda_1(g(N), t)$, is real and positive, and the associated eigenvalues $u = u^{(1)}$ and $v = v^{(1)}$ have real nonnegative elements. Some of the other eigenvalues may be complex, occurring in complex conjugate pairs, with associated complex eigenvectors.

For small fluctuations in the weighted population size, N, around its deterministic equilibrium, K, the eigenvectors of $L(g(N), t)$ can be approximated by those for the deterministic equilibrium projection matrix, $l(g(K)) = A - \Gamma g(K)$ (eq. [2a]), with deterministic eigenvalues ordered by decreasing modulus. A derivation analogous to that for equation (3a) produces the approximation for the associated eigenvalues,

$$\lambda_i(g(N), t) \approx \alpha^{(i)} - \gamma^{(i)} g(N) + \xi^{(i)}(t), \quad \text{where}$$

$$\alpha^{(i)} = v^{(i)} A u^{(i)}, \gamma^{(i)} = v^{(i)} \Gamma u^{(i)}, \xi^{(i)}(t) = v^{(i)} \Xi(t) u^{(i)}. \quad \text{(A1a)}$$

These eigenvalues satisfy the approximate eigenvalue equations $v^{(i)} L(g(N), t) \approx \lambda_i(g(N), t) v^{(i)}$, so premultiplying both sides of the projection equation (1a) by $v^{(i)}$ gives

$$V^{(i)}(t+1) = \lambda_i(g(N), t) V^{(i)}(t), \quad \text{with } V^{(i)}(t) = v^{(i)} n(t). \quad \text{(A1b)}$$

The dynamics of any positive linear combination of stage abundances, $N_c = cn$, can derived by premultiplying both sides of equation (1a) by the row vector $c = (c_1, c_2, \ldots)$, using the eigen decomposition of the projection matrix, $L(g(N), t) = \sum_i \lambda_i(g(N), t) u^{(i)} v^{(i)}$, yielding

$$N_c(t+1) = \sum_i c u^{(i)} \lambda_i(g(N), t) V^{(i)}(t).$$

This with equation (A1b) produces

$$N_c(t) = \sum_i c u^{(i)} \prod_{\tau=0}^{t-1} \lambda_i(g(N), \tau) V^{(i)}(0),$$

where the weighted population size, $N = bn$, also implicitly changes with time. Environmental stochasticity and fluctuation in N (eqq. [1a], [2a]) can cause some of the eigenvalues at any time to violate the usual ordering by decreasing modulus, compared with the fixed order of eigenvectors associated with eigenvalues of the deterministic equilibrium projection matrix. However, the stochastic eigenvalue associated with the leading eigenvectors, u and v, must always have the largest modulus (with expectation 1), giving the asymptotic result

$$\lim_{t \to \infty} N_c(t) = c u \prod_{\tau=0}^{t-1} \lambda(g(N), \tau) V(0). \quad \text{(A2)}$$

Transforming this to a log scale yields the stochastic difference equation

$$\lim_{t \to \infty} \Delta \ln N_c = \ln \lambda(g(N), t). \quad \text{(A3)}$$

Thus, in the long run, the growth rate of the log of any positive linear combination of stage abundances approximately equals the log of the leading eigenvalue of the stochastic projection matrix. We can then choose $c = b$ and $N_c = N$ to produce a one-dimensional stochastic difference equation (5a) useful for analysis of the stationary distribution of N.

APPENDIX B

Sensitivities in the Long-Term Selection Gradient

Sensitivities of $g(K)$, σ_e^2, and γ to perturbations in parameters of the vital rates are components of elements in the long-term selection gradient (eq. [10]), derived below.

Sensitivity of g(K). The deterministic projection matrix at equilibrium, $l(g(K)) = A - \Gamma g(K)$ (eq. [2a]), has leading eigenvalue $\lambda(g(K)) = \alpha - g(K)\gamma = 1$ (eq. [2b]), and differentiating this with respect to α_{ij} gives

$$\frac{\partial v}{\partial \alpha_{ij}} A u + v A \frac{\partial u}{\partial \alpha_{ij}} + v_i u_j - g(K) \left(\frac{\partial v}{\partial \alpha_{ij}} \Gamma u + v \Gamma \frac{\partial u}{\partial \alpha_{ij}} \right) - \gamma \frac{\partial g(K)}{\partial \alpha_{ij}} = 0.$$

Rearranging and using the eigenvalue equations (1b) produces

$$\frac{\partial v}{\partial \alpha_{ij}} l(g(K))u + vl(g(K))\frac{\partial u}{\partial \alpha_{ij}} + v_i u_j - \gamma \frac{\partial g(K)}{\partial \alpha_{ij}} = 0$$
$$\text{and} \quad \frac{\partial v}{\partial \alpha_{ij}} u + v\frac{\partial u}{\partial \alpha_{ij}} + v_i u_j - \gamma \frac{\partial g(K)}{\partial \alpha_{ij}} = 0.$$

The first two terms are the derivative of $vu = 1$, so they sum to zero, yielding the first solution, and an analogous derivation produces the second solution, as evident from equation (2a):

$$\frac{\partial g(K)}{\partial \alpha_{ij}} = \frac{v_i u_j}{\gamma} \quad \text{and} \quad \frac{\partial g(K)}{\partial \gamma_{ij}} = -g(K)\frac{v_i u_j}{\gamma}. \tag{B1}$$

The first formula agrees with the sensitivity of K derived by Takada and Nakajima (1998) and Caswell (2001, eq. [16.111]), who included a factor $dg(K)/dK$ in γ_{ij} (as after eq. [7a]). They did not distinguish perturbations in α_{ij} and γ_{ij}.

Sensitivity of σ_e^2. The sensitivity of the environmental variance (eq. [3d]) to a perturbation in the environmental (co)variance of vital rate(s), $C_{ij,i'j'}$, is given by equation (11b).

Perturbation of $x = \alpha_{ab}$ or γ_{ab}, influences the environmental variance through the eigenvector sensitivities derived below (eqq. [B6a]–[B6c]):

$$\frac{\partial \sigma_e^2}{\partial x} = 2\sum_{ij}\sum_{i'j'}\left[\frac{\partial v_i}{\partial x}u_j + v_i\frac{\partial u_j}{\partial x}\right]v_{i'}u_{j'}C_{ij,i'j'}. \tag{B2}$$

Sensitivity of γ. The sensitivity of γ to perturbations in a component of a single vital rate, $x = \alpha_{ab}$ or γ_{ab}, can be obtained from

$$\frac{\partial \gamma}{\partial \alpha_{ab}} = \frac{\partial v}{\partial \alpha_{ab}}\Gamma u + v\Gamma\frac{\partial u}{\partial \alpha_{ab}}, \tag{B3a}$$

$$\frac{\partial \gamma}{\partial \gamma_{ab}} = \frac{\partial v}{\partial \gamma_{ab}}\Gamma u + v\Gamma\frac{\partial u}{\partial \gamma_{ab}} + v_a u_b. \tag{B3b}$$

This requires eigenvector sensitivities $\partial u/\partial x$ and $\partial v/\partial x$, accounting for density-dependent constraints among elements of $l(g(K))$, contained in the perturbation matrices $\partial l/\partial x$ (Caswell 2001, eqq. [9.131], [9.132]):

$$\frac{\partial u}{\partial x} = \sum_{m>1}\frac{v^{(m)}\dfrac{\partial l}{\partial x}u}{1-\lambda_m}u^{(m)} \quad \text{and} \quad \frac{\partial v}{\partial x} = \sum_{m>1}\frac{v\dfrac{\partial l}{\partial x}u^{(m)}}{1-\lambda_m}v^{(m)}. \tag{B4}$$

These formulas involve λ_m, the eigenvalues of l ordered by decreasing modulus. Associated left and right eigenvectors denoted by superscript (m) are scaled so that $v^{(i)}u^{(j)} = \delta_{ij}$, where $\delta_{ij} = 1$ if $i = j$ and zero otherwise. We suppress the subscript for the leading eigenvalue and the superscript for the leading eigenvectors, writing $\lambda_1 = \lambda = 1$, with $v^{(1)} = v$ and $u^{(1)} = u$.

A change in a parameter of a vital rate, $x = \alpha_{ab}$ or γ_{ab}, perturbs not only that vital rate but also all other vital rates that are density dependent. Using equations (2a) and (B1), the perturbation matrices are

$$\frac{\partial l}{\partial \alpha_{ab}} = \left(\delta_{ij,ab} - \frac{\gamma_{ij}}{\gamma}v_a u_b\right) \quad \text{and} \quad \frac{\partial l}{\partial \gamma_{ab}} = -g(K)\frac{\partial l}{\partial \alpha_{ab}}. \tag{B5}$$

where $\delta_{ij,ab} = 1$ if $ij = ab$ and zero otherwise. Substituting $\partial l/\partial \alpha_{ab}$ into equations (B4) yields the eigenvector sensitivities:

$$\frac{\partial u}{\partial \alpha_{ab}} = \sum_{m>1}\frac{v_a^{(m)}u_b - \dfrac{v^{(m)}\Gamma u}{\gamma}v_a u_b}{1-\lambda_m}u^{(m)}, \tag{B6a}$$

$$\frac{\partial v}{\partial \alpha_{ab}} = \sum_{m>1}\frac{v_a u_b^{(m)} - \dfrac{v\Gamma u^{(m)}}{\gamma}v_a u_b}{1-\lambda_m}v^{(m)}. \tag{B6b}$$

A similar derivation using equations (B3b) and (B4) with $\partial l/\partial \gamma_{ab}$ shows that

$$\frac{\partial u}{\partial \gamma_{ab}} = -g(K)\frac{\partial u}{\partial \alpha_{ab}} \quad \text{and} \quad \frac{\partial v}{\partial \gamma_{ab}} = -g(K)\frac{\partial v}{\partial \alpha_{ab}}. \tag{B6c}$$

These eigenvector sensitivities complete the solutions for sensitivities of σ_e^2 (eq. [B2]) and γ (eqq. [B3a], [B3b]).

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