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

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11 **Estimating Density Dependence, Environmental Variance and**
12 **Long-term Selection on a Stage-structured Life History**

13

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22

23 **Abstract**

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

39

40

41 **Keywords:** demography, density dependence, environmental variance, great tit, reproductive
42 value, sensitivity

43 Following the classical debate on the occurrence of density dependence in natural populations
44 (Turchin 1995), a variety of *ad hoc* statistical methods were developed to detect density depen-
45 dence and assess its prevalence among species from univariate time series of population size
46 (Bulmer 1975, Pollard 1987, Holyoak 1993, Dennis and Taper 1994). These methods generally
47 have low statistical power to detect density dependence, producing frequent Type 1 and Type 2
48 errors, even for long time series of accurately estimated population sizes (Murdoch 1994, Shenk
49 et al. 1998, Brook and Bradshaw 2006, Freckleton et al. 2006).

50 Initial attempts to develop more realistic methods incorporated time delays implicitly caused
51 by life history and interspecific interactions (Turchin 1990, 1995, Royama 1992, Turchin and Taylor
52 1992, Woiwood and Hanski 1992). A basic stage-structured life history was incorporated in a
53 time-delay autoregression to analyze univariate time series of adult population size for several
54 vertebrate species (Lande et al. 2002a,b, 2003), revealing that interpreting time-delay coefficients
55 as caused solely by density dependence is erroneous, because they are created by developmental
56 delays in the life history (Lande et al. 2002a,b, 2003).

57 Fluctuations in total population size are driven by environmental stochasticity and density
58 dependence in stage-specific vital rates of reproduction and survival (*op. cit.*), but also are influ-
59 enced by transient fluctuations in stage-structure (Caswell 2001, Lande et al. 2003, Engen et al.
60 2009). Accurate analysis of the interaction of density dependence and environmental stochastic-
61 ity therefore requires the use of stage-structured demographic models. However, current theory
62 and application of stochastic stage-structured population dynamics generally ignores density de-
63 pendence (Tuljapurkar 1990, Caswell 2001), which then becomes unrealistically conflated with
64 environmental stochasticity. A wide variety of stage-structured demographic models including
65 both density dependence and environmental stochasticity have been fit to particular populations
66 or life histories, making it difficult to compare them (Constantino and Desharnais 1991, Takada
67 and Nakashizuka 1996, Grant and Benton 2000, Coulson et al. 2001, 2008, Lande et al. 2006,
68 Gamelon et al. 2016, 2019).

69 Here we analyze a density-dependent stage-structured population in a stochastic environ-

70 ment, assuming that all density dependence in the vital rates is exerted by a function, $g(N)$, of
71 a weighted sum of stage abundances, N , undergoing small or moderate fluctuations around a
72 deterministically stable equilibrium, the carrying capacity, K . We outline statistical methods for
73 estimating the relative weights of stage abundances contributing to N , and density-independent,
74 density-dependent and stochastic parameters of the stage-specific vital rates. The numerous pa-
75 rameters of the vital rates are summarized in three key demographic parameters governing a
76 univariate approximation for the stochastic dynamics of N . These are the density-independent
77 population growth rate in the average environment, $\alpha - 1$, and the net density dependence, γ ,
78 and environmental variance, σ_e^2 , in the life history. These key parameters facilitate comparison
79 among populations and species that differ in life history, and also have a fundamental connection
80 to life history evolution.

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

87 Here we show that in a stochastic environment life history evolution maximizes the expected
88 value of the density-dependence function affecting the vital rates expressed using the key demo-
89 graphic parameters, $E[g(N)] = s/\gamma$, where $s = \alpha - 1 - \sigma_e^2/2$ is the density-independent stochastic
90 growth rate of the population, and γ is the net density dependence in the life history. This reveals
91 that evolution tends to maximize the stochastic growth rate and minimize the net density depen-
92 dence, constrained by ecological and genetic tradeoffs. The long-term selection gradient on the
93 life history has elements proportional to derivatives of s/γ with respect to density-independent,
94 density-dependent, and stochastic parameters of the vital rates. Selection gradient elements can
95 be expressed as a sum of contributions from sensitivities of the three key demographic parame-
96 ters with respect to components of the vital rates.

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

100

101 **Stochastic demography of a density-dependent stage-structured life history**

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

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

$$n(t+1) = L(g(N), t)n(t) \text{ where } L(g(N), t) = \left[l_{ij}(g(N)) + \xi_{ij}(t) \right]. \quad (1a)$$

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

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

119 We analyze a population subject to an environment with a stationary distribution and no
120 serial autocorrelation. Environmental stochasticity in the vital rates has means $E[\xi_{ij}(t)] = 0$

121 and covariances $C_{ij,i'j'} = E[\xi_{ij}(t)\xi_{i'j'}(t)]$. The population size is assumed to remain large enough
 122 (usually at least a few hundred individuals) that demographic stochasticity, due to random inde-
 123 pendent events of individual births and deaths, can be neglected in comparison to environmental
 124 stochasticity, which affects all genotypes (or phenotypes) in the same or similar way (Lande et
 125 al. 2003).

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

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

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

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

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

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

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

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

141 eigenvalue of the stochastic projection matrix, $L(g(N), t)$, is approximately

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

142 $\zeta(t)$ is the environmental stochasticity in net reproductive value, and $\Xi(t) = (\zeta_{ij}(t))$ represents
143 the matrix of environmental stochasticity in the vital rates (eq. 1a).

144 Premultiplying both sides of eq. (1a) by v , the dynamics of fluctuations around the deter-
145 ministic equilibrium can be reduced to a stochastic process for net reproductive value, $V(t) =$
146 $vn(t)$, using the approximate eigenvalue equation $vL(g(N), t) \approx \lambda(g(N), t)v$, giving $V(t+1) =$
147 $\lambda(g(N), t)V(t)$ in which neglected terms are net second order (Engen et al. 2009, Lion 2018).
148 Transforming to a log scale, denoting $\Delta \ln V = \ln V(t+1) - \ln V(t)$, and expanding $\ln \lambda(g(N), t)$
149 in a Taylor series around the deterministic equilibrium, $\lambda(g(K)) = 1$, produces

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

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

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

152

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

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

154 The expected change in eq. (3c) differs in three ways from the approximate stochastic growth
155 rate of a density-independent population, $r - \sigma_e^2/2$ (Tuljapurkar 1982, 1990, Caswell 2001), most
156 importantly by the last term, the product of the net density dependence in the life history, γ ,

157 and the density-dependence function, $g(N)$. The environmental variance σ_e^2 (eq. 3d) differs from
 158 that of Tuljapurkar (1982, 1990) which includes a factor of $1/\lambda^2$, but with density dependence
 159 $\lambda(g(K)) = 1$, so this factor vanishes. Finally, $\alpha - 1$ is the deterministic density-independent
 160 growth rate in the average environment; this replaces r , and corresponds to the deterministic
 161 growth rate of a density-independent population in discrete-time, $e^r - 1 = r + r^2/2 + \dots$, but
 162 here $\alpha = vAu$ involves eigenvectors v and u of the deterministic projection matrix evaluated at
 163 $N = K$, whereas $e^r = vAu$ with v and u evaluated at $N \ll K$.

164 The corresponding stochastic difference equation is

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

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

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

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

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

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

179 maintaining the correct density dependence function,

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

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

188 Neglecting demographic stochasticity and Allee effects at small population sizes, the sta-
 189 tionary distribution exists when the density-independent stochastic growth rate is positive, $s =$
 190 $\alpha - 1 - \sigma_e^2/2 > 0$. With linear density-dependence, $g(N) = N$, the stationary distribution of N has
 191 mean, variance, and coefficient of variation (Lande et al. 2017)

$$E[N] = (1 - a)K, \quad \sigma_N^2 = a(1 - a)K^2,$$

$$CV_N = \sqrt{\frac{a}{1 - a}} \quad \text{where} \quad a = \frac{\sigma_e^2}{2(\alpha - 1)}. \quad (5b)$$

192
 193 The diffusion formula for $E[N]$ agrees with the discrete-time formula (eq. 4) under linear density
 194 dependence with $K = (\alpha - 1)/\gamma$ (eq. 2b).

195

196 **Statistics for parameter estimation**

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

199 *Step 1. Establish net density dependence and estimate relative weights.* Before conducting a detailed

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

$$\ln \lambda = s - \gamma \sum_i b_i n_i + \epsilon. \quad (6a)$$

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

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

$$L_{ij} = \alpha_{ij} - \gamma_{ij} N + \epsilon_{ij} \quad (6b)$$

221 where ϵ_{ij} is a stage-specific residual with mean 0 that includes environmental and demographic

222 variance. The stage-specific regressions must be checked to ensure that they do not predict
 223 negative vital rates (or survival rates exceeding 1) within the observed range of N .

224 The carrying capacity, K , is obtained from the leading eigenvalue of the expected projection
 225 matrix at equilibrium $l(g(K)) = A - \Gamma g(K)$, solving $\lambda(g(K)) = 1$ using $g(K) = K$ (eq. 2b).
 226 The right and left eigenvectors of $l(g(K))$, are respectively the stable stage distribution u , and
 227 reproductive values v , normalized so that $\sum_i u_i = 1$ and $vu = 1$. The net density dependence (eq.
 228 2b) is then $\gamma = v\Gamma u$, which should agree closely with the initial estimate from *Step 1*.

229 Nonlinear regression or Generalized Linear Models with nonlinear link functions (log re-
 230 production and logit survival) could be employed to guarantee that fitted vital rates are non-
 231 negative (with survival not exceeding 1) across the observed range of N . For example, Takada
 232 and Nakashizuka (1996) use log-linear regression to fit exponential density-dependence func-
 233 tions for the vital rates. Taylor expansion of the vital rates around the deterministic equilibrium
 234 at $N = K$ as a linear function of $g(N)$ would then be necessary to estimate the coefficients α_{ij} , γ_{ij} ,
 235 and $C_{ij,ij}$ (eqs. 1a, 2a, 3d) required to calculate the key demographic parameters, $\alpha - 1$, γ , and σ_e^2 .

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

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

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

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

242 $\sigma_{d,ij}^2$ is the variance of individual survival or fecundity for vital rate l_{ij} in each year, and n_j is
 243 the corresponding stage abundance. Because n_j is in the denominator, large sampling errors in

244 the estimated environment variances can be avoided by combining into a single terminal stage
 245 the oldest, rarest age classes with age-specific abundances too small to accurately estimate vital
 246 rates and density dependence. This procedure is common in demographic models of species with
 247 determinate growth where stages are defined by age and fecundity plateaus or declines at mature
 248 ages, as in many birds and mammals (Caswell 2001). Excessive condensation into fewer stages
 249 can, however, produce inaccurate population dynamics because it ignores heterogeneity among
 250 ages combined in a single stage, particularly for species with indeterminate growth where stages
 251 are defined by size and fecundity continually increases with size, as in many plants (Maloney
 252 1986, Rojas-Sandoval, J. and E. Meléndez-Ackerman 2013, Doak et al. 2021).

253 These ANOVA estimates are unbiased, but for life histories with more than a few vital rates
 254 this method is likely to produce a physically impossible estimate of C , with some negative eigen-
 255 values (Hill and Thompson 1978). We therefore employed a maximum likelihood method using
 256 the covariance matrix of residuals and the vector of demographic stochasticities, with Cholesky
 257 decomposition of the environmental correlation matrix, to guarantee a positive semi-definite es-
 258 timate of C (Stan Reference Manual v2.29, TMB Documentation v1.8.1).

259

260 **Standardized density dependence**

261 To compare populations or species with different carrying capacity, Lande et al. (2002a,b, 2003,
 262 2006) defined the net density dependence per unit time as the negative elasticity of the lead-
 263 ing eigenvalue, λ , to change in population size, N , at demographic equilibrium in the average
 264 environment. From the eigenvalue of the projection matrix (eq. 3a), this is

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

265 Because our statistical method assumes a linear (or linearized) density dependence function, the
 266 standardized net density dependence is simply $\gamma' = K\gamma$. The same standardized scaling can be
 267 applied to density dependence in the vital rates, $\gamma'_{ij} = K\gamma_{ij}$. If the actual density dependence

268 function is nonlinear, but linear regressions on N are used in estimation (eq. 6b), then the factor
 269 $\frac{dg(K)}{dK}$ is implicitly incorporated in the estimates of density dependence coefficients and their
 270 standardized values.

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

276 For interspecific comparisons of net density dependence, when species differ in life history,
 277 further scaling by generation time, T , may be used to give the net density dependence per gener-
 278 ation, $T\gamma' = TK\gamma$ (Lande et al. 2002a,b, 2003, 2006, Gaillard et al. 2005, Sæther et al. 2005), where
 279 T is the mean age of mothers of a newborn cohort at the deterministic equilibrium. Caswell
 280 (2001, Chap. 5) summarizes how to calculate T for a general stage-structured demography.

281 A simple expression for T can be derived for a commonly used stage structure similar to
 282 the Leslie matrix, with age-specific fecundities f_τ in the first row, annual survival probabilities
 283 s_τ on the subdiagonal, and ages $\tau \geq \omega$ combined in a terminal stage with survival s_ω in the
 284 last row and column (e.g., eq. 8). Using a prebreeding census, first year survival s_0 implicitly
 285 multiplies all fecundities (avoiding for most species the description of sibling competition), and
 286 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
 287 $\lambda = 1$ at demographic equilibrium, the generation time is

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

288

289 Demographic parameter estimates for a great tit life history

290 Demographic data were collected over 38 years on a population of great tits (*Parus major* L.) in
 291 Hoge Veluwe National Park in The Netherlands (Sæther et al. 2016a, Gamelon et al. 2016). The

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

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

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

306 Recruitment rates in the first row represent the product of fecundity and survival to age 1
 307 (Caswell 2001). Total recruits of both sexes were counted and then multiplied by 1/2 to pro-
 308 duce female recruits per adult female in each age class, assuming an even sex ratio at fledging
 309 and no sex difference in survival. Observed recruitment rates across all years were multiplied by
 310 a common immigration factor, $m = 2.988024$, to balance emigration of nearly 3/4 of fledglings
 311 out of the study area, determined by setting the long-run density-dependent growth rate of the
 312 population to zero, $E \ln \lambda = 0$, consistent with the observed lack of trend in the time series of
 313 actual population size for breeding females in Fig. 1. For statistical analysis of the demographic
 314 data we used a linear density-dependence function, $g(N) = N$, which is justified because the

315 observed fluctuations in actual population size were not very large; moreover, the regressions of
316 $\ln \lambda$ and the vital rates on N in Fig. 2 and Fig. 3 appear to be approximately linear.

317 *Step 1. Net density dependence and relative weights.* Multiple regression of $\ln \lambda$ from annual
318 projection matrices on $-\gamma \sum_{i=1}^3 b_i n_i$ (eq. 6a) for 38 years of data from the great tit population
319 showed that the initial estimate $\gamma b_3 = -0.00396647$ was slightly negative but far from significant
320 ($p = 0.64$); because the initial estimate was negative, which is biologically unrealistic, we set
321 $b_3 = 0$ and reran the regression, which only slightly changed the remaining estimates, $\gamma b_1 =$
322 0.01354864 , ($p = 0.00009$) and $\gamma b_2 = 0.00886644$ ($p = 0.21$). A maximum likelihood method
323 applied to $\ln(\gamma b_i)$, constraining the weight coefficients to be non-negative, produced nearly the
324 same results. We scaled the relative weights so that their sum equaled 3 (the number of stages),
325 giving the relative weights $(b_1, b_2, b_3) = (1.813329, 1.186671, 0)$.

326 Univariate regression of $\ln \lambda$ on weighted N , illustrated in Fig. 2, was very highly significant
327 ($slope = -0.00747169$, $p = 0.00004$, adj. $R^2 = 0.36$), indicating substantial density dependence
328 in the great tit life history, measured by the estimated slope, $\gamma = 0.00747169$, with 95% CI
329 $(0.01069, 0.00426)$. This prompted us to complete the demographic sensitivity analysis. The
330 intercept of the univariate regression estimating the density-independent stochastic growth rate
331 (eq. 6a), $s = 1.2191$, also was very highly significant ($p = 0.00004$). Fig. 1 illustrates the time
332 series for actual population size, N_a and weighted population size, N , over 38 years for the great
333 tit population.

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

340 The deterministic projection matrix $l(g(K)) = A - \Gamma g(K)$ with leading eigenvalue $\lambda(g(K)) =$
341 1 was used with $g(K) = K$ to determine the carrying capacity. Non-zero elements of A and

342 Γ appear in Table 1, and we obtain the estimated carrying capacity $K = 183.62$. The right
 343 and left eigenvectors of $l(g(K))$, are the stable stage distribution u , and reproductive values
 344 v , normalized so that $\sum_i u_i = 1$ and $vu = 1$. These were estimated as the column vector $u =$
 345 $(0.601587, 0.239026, 0.159387)^\top$ where superscript \top indicates transpose, and the row vector $v =$
 346 $(0.974525, 1.15287, 0.866898)$. The deterministic density-independent growth rate, and the net
 347 density dependence (eq. 2b), were then estimated as $\alpha - 1 = vAu - 1 = 1.39665$ and $\gamma = v\Gamma u =$
 348 0.00760619 .

349 **Table 1.** Estimated density-independent and -dependent parameters, α_{ij} and γ_{ij} ,
 350 of recruitment and survival rates, f_i and s_i , from regressions on weighted N .
 351

rate	α_{ij}	γ_{ij}	p	adj. R^2
f_1	1.72366	0.00650092	0.0002	0.306
f_2	1.83804	0.00585470	0.0116	0.141
f_3	1.64701	0.00553938	0.0039	0.187
s_1	0.707262	0.00168792	0.0006	0.265
s_2	0.742178	0.00147056	0.0169	0.125
s_3	0.418691	0.00069034	0.1779	0.024

352

354 *Step 3. Environmental variance-covariance matrix.* Initially, all demographic variances for stage-
 355 specific recruitment (eq. 6d) were multiplied by the square of the immigration factor, m^2 , because
 356 up to this point only the stage-specific mean recruitments in each year had been corrected for
 357 immigration (see after eq. 8). The environmental covariance matrix, C , estimated by analysis of
 358 (co)variance (eqs. 6c, 6d) produced a matrix with two small negative eigenvalues. The maximum
 359 likelihood estimate using Cholesky decomposition produced a positive semi-definite estimate of
 360 C with two eigenvalues near zero. Estimated environmental (co)variances of vital rates, with
 361 corresponding correlations, are displayed in Table 2. Environmental variances in stage-specific
 362 recruitment are considerably larger than variances in survival, which can be partly, but not

363 fully, explained as a scale effect because the mean values of recruitment are larger than those of
 364 survival (Fig. 3). Environmental correlations among the vital rates are all substantially positive.
 365 The environmental covariance matrix produced an estimate of the environmental variance in
 366 population growth rate (eq. 3d), $\sigma_e^2 = 0.199707$.

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

rate	f_1	f_2	f_3	s_1	s_2	s_3
f_1	0.149405	0.151463	0.139466	0.023770	0.016787	0.016061
f_2	0.76	0.264974	0.140525	0.027208	0.032312	0.025764
f_3	0.97	0.73	0.138002	0.020572	0.019900	0.014642
s_1	0.67	0.58	0.60	0.008413	0.006604	0.005870
s_2	0.41	0.60	0.51	0.68	0.010982	0.006069
s_3	0.61	0.73	0.58	0.94	0.85	0.004667

370

372

373 Accuracy of the theory and parameter estimates

374 As a check on the accuracy of the theory and adequacy of the data, estimates of the net density
 375 dependence, γ , and the density-independent stochastic growth rate, s , obtained in *Step 1* are
 376 compared to formulas using the density-independent and density-dependent parameters of the
 377 expected vital rates estimated in *Step 2* and their environmental (co)variances estimated in *Step*
 378 *3*. We then estimate from the theory the mean and coefficient of variation of N , and the expected
 379 rate of fluctuations around the mean, and compare these predictions with observed population
 380 statistics in the 38 years of observation.

381 The net density dependence in the life history was estimated from the univariate regression
 382 in *Step 1* as $\gamma = 0.00747169$. This agrees within 2% compared to $\gamma = v\Gamma u = 0.00760619$ estimated
 383 in *Step 2* (eq. 2b).

384 The estimated carrying capacity, $K = 183.62$, is obtained from the leading eigenvalue of the
385 deterministic equilibrium projection matrix, setting $\lambda(g(K)) = 1$ using linear density-dependence
386 $g(K) = K$. This necessarily matches exactly the identity $K = (\alpha - 1)/\gamma$ (eq. 2b) using the estimates
387 of α and γ from *Step 2*.

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

391 The standardized net density dependence (eq. 7a), using the estimated γ from *Step 2*, is
392 $\gamma' = K\gamma = 1.39665$. In a constant environment, values in the range $1 < \gamma' < 2$ predict damped
393 oscillations in N with successive diminishing overshoot and undershoot of K , on a time scale
394 for expected return of N to its average value, $1/\gamma'$, less than 1 year. This strong net density
395 dependence accords with observed rapid fluctuations of N around its average value (Fig. 1).

396 The expected weighted population size, $E[N]$, is less than its deterministic equilibrium, K ,
397 because of environmental and demographic stochasticity (Lande et al. 2003). Accounting only
398 for environmental stochasticity (eqs. 4, 5b), using $\sigma_e^2 = 0.199707$ estimated in *Step 3*, the expected
399 population size predicted by eq. (4) is $E[N] = 170.48$. Including the demographic stochasticities
400 with the environmental variances (eqs. 6c, 6d) (Lande et al. 2003, Sæther et al. 2004, Engen et al.
401 2009), slightly reduced the prediction to 168.86. These predictions of $E[N]$ are within about 4%
402 of the observed mean weighted population size, $\bar{N} = 163.16$.

403 The coefficient of variation of N predicted from diffusion theory (eq. 5b), using the estimates
404 of α and σ_e^2 , is $CV_N = 0.2776$. The observed $CV_N = 0.2828$ is within 2% of the estimate.

405

406 **Life history evolution in a stochastic environment**

407 Evolution in fluctuating (st)age-structured populations is generally described most accurately
408 using reproductive value weighted mean phenotype to remove transient effects of age structure
409 fluctuations (Fisher 1958, Engen et al. 2014, Lion 2018). This is precluded by defining the mean
410 life history phenotype in a population as the vector, \bar{z} , of stage-specific vital rate parameters,

411 α_{ij} , γ_{ij} and $C_{ij,i'j'}$, or quantitative traits underlying them. Coupled to the stochastic demographic
 412 process (eq. 5a), the expected rate of evolution of the mean phenotype, \bar{z} , is (Lande 1982, 2007,
 413 Engen et al. 2013, Lande et al. 2017)

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

414 G is the additive genetic covariance matrix of the phenotypes, T is the generation time (average
 415 age of mothers of newborns at the deterministic demographic equilibrium), ∇ is the selection
 416 gradient operator (column vector of partial derivatives with respect to elements of \bar{z}), and $E \ln \lambda \approx$
 417 $\alpha - 1 - \sigma_e^2/2 - \gamma g(N)$ is the density-dependent stochastic growth rate of the population (eqs.
 418 3b, 3c). This can be re-expressed using the density-independent stochastic growth rate $s =$
 419 $\alpha - 1 - \sigma_e^2/2$,

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

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

423 Assuming that evolution of the mean phenotype is slow compared to the time scale for pop-
 424 ulation fluctuations, averaging the expected evolution over the stationary distribution of pop-
 425 ulation size, and substituting $E[g(N)]$ from eq. (4), produces the expected selection gradient
 426 governing long-term evolution of the life history, conditioned only on \bar{z} ,

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

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

431 logistic density dependence, $\theta = 1$, evolution maximizes $E[N]$ (Lande et al. 2017).

432 Under a stationary distribution of environments, the long-term average growth rate of a
433 density-dependent population must be zero, which after an initial transient period can be im-
434 proved slowly if at all by evolution. The long-term average rate of evolution (eq. 9c) also must
435 be near zero, but nevertheless there may be a substantial long-term average selection gradient on
436 the life history. This can occur if the G matrix is singular, lacking additive genetic variance in the
437 prevailing direction of selection, when G incorporates ecological tradeoffs manifested in genetic
438 constraints among characters. A genetic correlation between characters that opposes their direc-
439 tions of selection retards evolution and is known as antagonistic selection. Genetic constraints
440 for life history characters often appear as negative genetic correlations between major compo-
441 nents of fitness selected in the same direction, such as survival and reproduction, or early and
442 late reproduction; a positive genetic correlation constrains the evolution of characters selected in
443 opposite directions, such as intrinsic rate of increase and environmental variance (Lande 1982,
444 Charlesworth 1994, Mueller 1997, Travis et al. 2013, Sæther et al. 2016a, Lande et al. 2009, 2017).
445 Even in the absence of additive genetic variance for a combination of characters in the direction
446 of the selection gradient, measurable natural selection can occur based on on non-heritable phe-
447 notypic variance caused by the environment and developmental noise (Haldane 1954, Lande and
448 Arnold 1983).

449

450 Demographic sensitivities in the long-term selection gradient

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

457 evolutionary interpretation of demographic sensitivities as selection coefficients to life history of
 458 a density-dependent population in a stochastic environment.

459

460 Long-term selection gradient

461 For evolution of the life history, the elements in the long-term average selection gradient $\gamma \nabla(s/\gamma)$
 462 are demographic sensitivities to perturbations in the vital rate parameters (eq. 9c). Focusing on
 463 a single element in the long-term selection gradient, and substituting $\alpha - 1 = g(K)\gamma$ in $s =$
 464 $\alpha - 1 - \sigma_e^2/2$, the sensitivity to a vital rate parameter, $x = \alpha_{ij}$, γ_{ij} , or $C_{ij,i'j'}$, is

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

465 Simple formulas are given below for the sensitivity of $g(K)$ to change in α_{ij} or γ_{ij} , and the
 466 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
 467 complex, involving eigenvector sensitivities, and appear in Appendix B. Numerical sensitivities
 468 also can be obtained by perturbing x to $x + \delta x$, recomputing perturbed values of K , u , and v to
 469 find $\gamma + \delta\gamma$, approximating the sensitivity by $\delta\gamma/\delta x$, and similarly for $\delta\sigma_e^2/\delta x$.

470

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

472 The sensitivities of $g(K)$ to perturbation in α_{ij} or γ_{ij} are derived in the Appendix,

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

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

477

478 Sensitivity of σ_e^2 to $C_{ij,i'j'}$

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

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

481 where $\delta_{ij,i'j'} = 1$ if $ij = i'j'$ and zero otherwise, which accounts for symmetry of the environ-
 482 mental covariance matrix, $C_{ij,i'j'} = C_{i'j',ij}$ (Caswell 2001 eqs. 14.110-111). The simplicity of this
 483 formula arises because the eigenvectors, u and v , at the deterministic equilibrium do not depend
 484 on environmental stochasticity.

485

486 Sensitivity analysis of the great tit life history

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

491 **Table 3.** Sensitivities to α_{ij} in the long-term selection gradient,
 492 and their components (eq. 10).

493

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	0.58626	-0.03913	0.01801		0.56512
f_2	0.23294	0.01255	-0.00312		0.24236
f_3	0.15533	0.03777	-0.01566		0.17743
s_1	0.69355	-0.04031	0.00402		0.65726
s_2	0.20721	0.01130	-0.00543		0.21309
s_3	0.13817	0.03369	-0.01570		0.15616

494

496

497

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

498

499

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

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Table 5. Sensitivities to $C_{ij,i'j'}$ in the long-term selection gradient,

$$-\frac{1}{2} \frac{\partial \sigma_e^2}{\partial C_{ij,i'j'}}.$$

rate	f_1	f_2	f_3	s_1	s_2	s_3
f_1	-0.17185	-0.13656	-0.09106	-0.40660	-0.12148	-0.08101
f_2		-0.02713	-0.03618	-0.16155	-0.04827	-0.03219
f_3			-0.01206	-0.10773	-0.03219	-0.02146
s_1				-0.24051	-0.14371	-0.09583
s_2					-0.02147	-0.02863
s_3						-0.00955

512

513 The last column in Tables 3 and 4, and the diagonal entries in Table 5, reveal that within
 514 each group of sensitivities those to parameters of first year survival and recruitment are the
 515 largest. This occurs primarily because all three age classes have similar reproductive values, but
 516 the abundance of one year olds far exceeds that of two year olds or the three year and older class
 517 (see *Step 2* of great tit parameter estimates).

518 For sensitivities to deterministic parameters of the vital rates, α_{ij} and γ_{ij} , the largest contri-
 519 bution arises from sensitivity of carrying capacity, which in Table 3 is simply $v_i u_j$, and in Table 4
 520 $-K v_i u_j$ (eq. 11a). Sensitivities to environmental (co)variances, $C_{ij,i'j'}$, in Table 5 for the variances
 521 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 envi-
 522 ronmental variances are about equal, the sensitivity for their corresponding covariance is about
 523 twice as large. This explains why in Table 5 the largest sensitivity is that for the covariance of
 524 first year survival and recruitment.

525

526 **Relative sensitivities in the long-term selection gradient**

527 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,
 528 4 and 5, the sensitivities to density-dependence coefficients γ_{ij} dominate all the other sensitivities.
 529 This occurs because γ_{ij} , and the net density dependence γ , are rather small when K is large.

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

534 Logarithms are valid only for positive parameters. All non-zero density-independent coef-
 535 ficients α_{ij} must be positive, but density-dependent coefficients γ_{ij} can be negative with social
 536 facilitation of reproduction or survival in highly social species, or because of Allee effects in
 537 small populations. Even if some γ_{ij} are negative, a stable deterministic $K > 0$ still exists when
 538 the net density dependence is positive, $\gamma > 0$. Environmental variances must be positive; and
 539 environmental covariances usually will be positive (as in Table 2), but in some cases may be

540 negative. A small increase in an environmental covariance $C_{ij,i'j'}$ increases σ_e^2 regardless whether
 541 $C_{ij,i'j'}$ is positive or negative. For negative demographic parameters, $x < 0$, the relative sensitivity
 542 measure that preserves the sign of the sensitivity is $\gamma|x|\frac{\partial(s/\gamma)}{\partial x}$.

543 Elements in the long-term selection gradient are derivatives of the density-dependent stochas-
 544 tic growth rate, $E \ln \lambda$, averaged over the stationary distribution of N (eqs. 9a-9c). Thus, without
 545 further scale transformation, relative sensitivities in the long-term selection gradient correspond
 546 to traditional elasticities, $\frac{\partial \ln \lambda}{\partial \ln x} = \frac{x}{\lambda} \frac{\partial \lambda}{\partial x}$ (Caswell 2001, 2019, van Tienderen 2000, Hereford et al.
 547 2004, Matsumura et al. 2012).

548

549

Relative sensitivities in the great tit life history

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

557

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

558

559

rate	$\gamma \frac{\partial(s/\gamma)}{\partial \ln \alpha_{ij}}$	$\gamma \frac{\partial(s/\gamma)}{\partial \ln \gamma_{ij}}$
f_1	0.97407	-0.62450
f_2	0.44548	-0.24263
f_3	0.29223	-0.16917
s_1	0.46485	-0.18833
s_2	0.15815	-0.05353
s_3	0.06538	-0.01854

561

560

Table 7. Relative sensitivities to $\ln C_{ij,i'j'}$ in the long-term selection

$$\text{gradient, } -\frac{1}{2} \frac{\partial \sigma_e^2}{\partial \ln C_{ij,i'j'}}.$$

rate	f_1	f_2	f_3	s_1	s_2	s_3
f_1	-0.02568	-0.02068	-0.01270	-0.00966	-0.00204	-0.00130
f_2		-0.00719	-0.00508	-0.00440	-0.00156	-0.00083
f_3			-0.00166	-0.00222	-0.00064	-0.00031
s_1				-0.00202	-0.00095	-0.00056
s_2					-0.00024	-0.00017
s_3						-0.00004

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 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 $CV_N \lesssim 0.3$.

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,

582 α_{ij} and γ_{ij} , and the environmental (co)variances, $C_{ij,i'j'}$, of the vital rates. These coefficients deter-
583 mine the population carrying capacity, K , the stable age distribution and reproductive values, u
584 and v at equilibrium when $N = K$, and the key demographic parameters. Estimation of the key
585 parameters facilitates quantitative comparison of populations and species with different carrying
586 capacities and life histories.

587 Most previous studies assuming that a weighted population size, N , exerts density depen-
588 dence on the vital rates made *a priori* assumptions about the weights, b_i (Takada and Nakashizuka
589 1996, Grant and Benton 2000, Coulson et al. 2001, 2008, Lande et al. 2002a,b, Sæther et al. 2005,
590 2016b). In contrast, our statistical analysis (*Step 1*, eq. 6a) employs multiple regression of $\ln \lambda$ on
591 stage abundances to estimate the relative weights, γb_i . If the regression is significant, then net
592 density dependence exists and the relative weights can be determined by choosing an arbitrary
593 scale factor, e.g. fixing their sum, which becomes incorporated in N (*Step 2*). The inverse of this
594 scale factor is absorbed in γ , and in density-dependent coefficients for the vital rates, γ_{ij} . The
595 arbitrary scale factor vanishes in the standardized net density dependence, $\gamma' = K\gamma$, giving the
596 expected rate of return of N to equilibrium after a small perturbation (eq. 7a).

597 For the great tit population the estimated relative weights of stages in N decrease strongly
598 for the older stages, $(b_1, b_2, b_3) = (1.813329, 1.186671, 0)$, indicating that one-year-olds exert the
599 strongest density dependence on population growth, two-year-olds exert an intermediate density
600 dependence, and individuals three or more years old exert no density dependence. Gamelon et
601 al. (2016) analyzed the same data divided into four life history stages, using Bayesian methods
602 and allowing all possible inter-class density-dependent effects, obtaining similar results, which
603 they interpreted as caused by young first-time breeders competing most strongly for breeding
604 territories, compared to older individuals with established territories. In contrast, our analysis
605 assumes that a single linear combination of stages exerts all the density dependence, and con-
606 denses the description of the stochastic dynamics of N into a few key demographic parameters
607 revealing more information on population dynamics and selection on the life history, discussed
608 below. Our great tit data analysis employed a linear density-dependence function, $g(N) = N$,

609 entailing that $\alpha - 1 = K\gamma$ (corresponding to $r = \gamma$ in the classical logistic model [Lande et al.
610 2003]). Thus there are only two independent key parameters describing the great tit population
611 dynamics, the standardized net density dependence, γ' and the environmental variance σ_e^2 .

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

625 Estimates of the key demographic parameters predicted with remarkable accuracy the ob-
626 served mean and coefficient of variation of the weighted population size of the great tits, given
627 that the population is not closed (and neglecting stochasticity in emigration and immigration).
628 The accuracy of these predictions is not a tautology, because the parameters were estimated by
629 regressing the vital rate fluctuations on N , with observed stage abundances used as independent
630 variables only in determining the relative weights of stages in N . These results reflect the high
631 quality and length of the data, and help to confirm the accuracy of the univariate approximation
632 to the stage-structured dynamics, even for populations with a strong net density dependence
633 and large environmental stochasticity.

634 Life history evolution maximizes $E[g(N)] = s/\gamma$ where $s = \alpha - 1 - \sigma_e^2/2$ is the density-
635 independent stochastic growth rate (eq. 9c). For the theta-logistic model of density depen-

636 dence, $g(N) = N^\theta$ (Gilpin and Ayala 1973), evolution maximizes $E[N^\theta]$. For $\theta = 1$ the density
637 dependence is logistic (linear) and evolution maximizes $E[N]$. This extends to stochastic stage-
638 structured populations the finding of MacArthur (1962) that evolution in a constant environment
639 maximizes the population carrying capacity, K .

640 Long-term demographic data can be used to estimate demographic sensitivities, which are
641 elements in the long-term selection gradient on the life history, $\gamma \frac{\partial(s/\gamma)}{\partial x}$, where $x = \alpha_{ij}$, γ_{ij} , or
642 $C_{ij,i'j'}$. Each of these elements is the sum of component sensitivities for the key demographic
643 parameters (eqs. 2b, 10).

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

652 Sensitivities to density-dependent parameters, γ_{ij} , have much larger magnitude (and oppo-
653 site sign) than those to density-independent parameters, α_{ij} (Tables 3, 4), primarily because γ_{ij} is
654 much smaller in magnitude than α_{ij} for the great tits (Table 1). This must occur when the carrying
655 capacity is large, as evident in the main component of these sensitivities: the sensitivity of K to
656 γ_{ij} is $-K$ times as large as that to α_{ij} (eq. 11a). To compare sensitivities for parameters of different
657 magnitude, we calculated relative sensitivities using the logarithms, $\gamma \frac{\partial(s/\gamma)}{\partial \ln x}$ (Tables 6 and 7). The
658 largest relative sensitivities to $\ln \alpha_{ij}$ and $\ln \gamma_{ij}$ are still those for first year survival and recruitment.
659 However, for every vital rate the relative sensitivity to the density-independent parameter $\ln \alpha_{ij}$
660 has a larger magnitude than that to the density-dependent parameter $\ln \gamma_{ij}$. Relative sensitivi-
661 ties to $\ln C_{ij,i'j'}$ are generally smaller than those to $\ln \alpha_{ij}$ and $\ln \gamma_{ij}$, but among the environmental
662 (co)variances the largest relative sensitivities are to the variance of first year recruitment and its

663 covariance with the other recruitments and first year survival. These results show that for the
664 great tits the density-independent and density-dependent parameters of first year survival and
665 recruitment, and the environmental variance of first year survival, are subject to the strongest
666 long-term selection in the life history, with density-independent and density-dependent param-
667 eters of the vital rates more strongly selected than their environmental (co)variances.

668

669 **Extensions and limitations**

670 Environmental stochasticity parameterized as noise around a deterministic equilibrium, inter-
671 acting with nonlinear density dependence (when $g(N)$ has sufficient negative curvature), can
672 increase the means of vital rates, the long-run growth rate (Lande et al. 2003), and mean popu-
673 lation size. Environmental stochasticity itself also may be density dependent (Lande et al. 2003).
674 However, when parameterized as noise around the mean vital rates, even with nonlinear density
675 dependence, environmental stochasticity always decreases the long-run growth rate compared to
676 that of the average projection matrix (eq. 3c) (Caswell 2001, Lande et al. 2003), reducing the mean
677 population size. In any case, the assumption of linear density dependence in vital rates, approx-
678 imated by Taylor expansion around their mean values, estimated using linear regression (*Step 2*)
679 allows estimation of a few key demographic parameters that accurately describe the dynamics of
680 populations with small or moderate coefficient of variation.

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

689

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697
698 **Statement of Authorship**

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

702
703 **Data Availability**

704 The great tit demographic data used in the paper are archived, along with R code for statisti-
705 cal analysis and Mathematica code for sensitivity analysis, at [https://datadryad.org/stash/
706 share/PXim1A-ymLIydCxNOw4vb2HD7ZsWwCdpNG3shSNAR3k](https://datadryad.org/stash/share/PXim1A-ymLIydCxNOw4vb2HD7ZsWwCdpNG3shSNAR3k).

707
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871

872 **Appendix A:** *Asymptotic growth rate of $\ln N$*

873 The stochastic projection matrix $L(g(N), t)$ has eigenvalues denoted as $\lambda_i(g(N), t)$, with associated
874 right (column) eigenvectors $u^{(i)}$ and left (row) eigenvectors $v^{(i)}$ normalized so that $v^{(i)}u^{(j)} = 1$ if
875 $i = j$ and zero otherwise. The Perron-Frobenius theorem for real matrices with non-negative ele-
876 ments guarantees that the leading eigenvalue with the largest modulus, $\lambda(g(N), t) = \lambda_1(g(N), t)$
877 is real and positive, and the associated eigenvalues $u = u^{(1)}$ and $v = v^{(1)}$ have real non-negative

878 elements. Some of the other eigenvalues may be complex, occurring in complex conjugate pairs,
 879 with associated complex eigenvectors.

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

$$\lambda_i(g(N), t) \approx \alpha^{(i)} - \gamma^{(i)}g(N) + \zeta^{(i)}(t) \quad \text{where} \quad (\text{A1a})$$

$$885 \quad \alpha^{(i)} = v^{(i)} A u^{(i)}, \quad \gamma^{(i)} = v^{(i)} \Gamma u^{(i)}, \quad \zeta^{(i)}(t) = v^{(i)} \Xi(t) u^{(i)}.$$

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

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

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

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

891 This with eq. (A1b) produces

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

892 where the weighted population size, $N = bn$, also implicitly changes with time. Environmental
 893 stochasticity and fluctuation in N (eqs. 1a, 2a), can cause some of the eigenvalues at any time to

894 violate the usual ordering by decreasing modulus, compared to the fixed order of eigenvectors
 895 associated with eigenvalues of the deterministic equilibrium projection matrix. However, the
 896 stochastic eigenvalue associated with the leading eigenvectors, u and v , must always have the
 897 largest modulus (with expectation 1), giving the asymptotic result

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

898 Transforming this to a log scale yields the stochastic difference equation

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

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

903

904 **Appendix B: Sensitivities in the long-term selection gradient**

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

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

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

910 Rearranging, and using the eigenvalue equations (1b), produces

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

911

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

912 The first two terms are the derivative of $vu = 1$, so they sum to 0, yielding the first solution, and
 913 an analogous derivation produces the second solution, as evident from eq. (2a),

$$\frac{\partial g(K)}{\partial \alpha_{ij}} = \frac{v_i u_j}{\gamma} \quad \text{and} \quad \frac{\partial g(K)}{\partial \gamma_{ij}} = -g(K) \frac{v_i u_j}{\gamma}. \quad (\text{A4})$$

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

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

919 Perturbation of $x = \alpha_{ab}$ or γ_{ab} , influences the environmental variance through the eigenvector
 920 sensitivities derived below (eqs. A9a-A9c),

$$\frac{\partial \sigma_e^2}{\partial x} = 2 \sum_{ij} \sum_{i'j'} \left[\frac{\partial v_i}{\partial x} u_j + v_i \frac{\partial u_j}{\partial x} \right] v_{i'} u_{j'} C_{ij,i'j'}. \quad (\text{A5})$$

921 *Sensitivity of γ .* The sensitivity of γ to perturbations in a component of a single vital rate,
 922 $x = \alpha_{ab}$ or γ_{ab} , can be obtained from

$$\frac{\partial \gamma}{\partial \alpha_{ab}} = \frac{\partial v}{\partial \alpha_{ab}} \Gamma u + v \Gamma \frac{\partial u}{\partial \alpha_{ab}} \quad (\text{A6a})$$

923

$$\frac{\partial \gamma}{\partial \gamma_{ab}} = \frac{\partial v}{\partial \gamma_{ab}} \Gamma u + v \Gamma \frac{\partial u}{\partial \gamma_{ab}} + v_a u_b. \quad (\text{A6b})$$

924 This requires eigenvector sensitivities $\partial u / \partial x$ and $\partial v / \partial x$ accounting for density-dependent con-

925 straints among elements of $l(g(K))$, contained in the perturbation matrices $\partial l/\partial x$ (Caswell 2001
 926 eqs. 9.131, 9.132)

$$\frac{\partial u}{\partial x} = \sum_{m>1} \frac{v^{(m)} \frac{\partial l}{\partial x} u^{(m)}}{1 - \lambda_m} \quad \text{and} \quad \frac{\partial v}{\partial x} = \sum_{m>1} \frac{v \frac{\partial l}{\partial x} u^{(m)}}{1 - \lambda_m} v^{(m)}. \quad (\text{A7})$$

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

931 A change in a parameter of a vital rate, $x = \alpha_{ab}$ or γ_{ab} , perturbs not only that vital rate but
 932 also all other vital rates that are density-dependent. Using eqs. (2a) and (A4), the perturbation
 933 matrices are

$$\frac{\partial l}{\partial \alpha_{ab}} = \left(\delta_{ij,ab} - \frac{\gamma_{ij}}{\gamma} v_a u_b \right) \quad \text{and} \quad \frac{\partial l}{\partial \gamma_{ab}} = -g(K) \frac{\partial l}{\partial \alpha_{ab}}. \quad (\text{A8})$$

934 where $\delta_{ij,ab} = 1$ if $ij = ab$ and zero otherwise. Substituting $\partial l/\partial \alpha_{ab}$ into eqs. (A7) yields the
 935 eigenvector sensitivities,

$$\frac{\partial u}{\partial \alpha_{ab}} = \sum_{m>1} \frac{v_a^{(m)} u_b - \frac{v^{(m)} \Gamma u}{\gamma} v_a u_b}{1 - \lambda_m} u^{(m)} \quad (\text{A9a})$$

$$\frac{\partial v}{\partial \alpha_{ab}} = \sum_{m>1} \frac{v_a u_b^{(m)} - \frac{v \Gamma u^{(m)}}{\gamma} v_a u_b}{1 - \lambda_m} v^{(m)}. \quad (\text{A9b})$$

937 A similar derivation using eqs. (A6b) and (A7) with $\partial l/\partial \gamma_{ab}$ shows that

$$\frac{\partial u}{\partial \gamma_{ab}} = -g(K) \frac{\partial u}{\partial \alpha_{ab}} \quad \text{and} \quad \frac{\partial v}{\partial \gamma_{ab}} = -g(K) \frac{\partial v}{\partial \alpha_{ab}}. \quad (\text{A9c})$$

938 These eigenvector sensitivities complete the solutions for sensitivities of σ_c^2 (eq. A5) and γ (eqs.
 939 A6a, A6b).

Figure Captions

940

941 **Fig. 1.** Weighted population size, $N = \sum_{i=1}^3 b_i n_i$ (solid line), and actual population size,
942 $N_a = \sum_{i=1}^3 n_i$ (dashed line), over 38 years in the great tit population.

943

944 **Fig. 2.** Regression of $\ln \lambda$ from annual projection matrices on weighted N for the great tit popu-
945 lation. Grey area is the 95% confidence region for the regression line.

946

947 **Fig. 3.** Regressions of recruitment and survival rates, f_i and s_i , on weighted N for the great tit
948 population. Grey areas are 95% confidence regions for the regression lines.

949

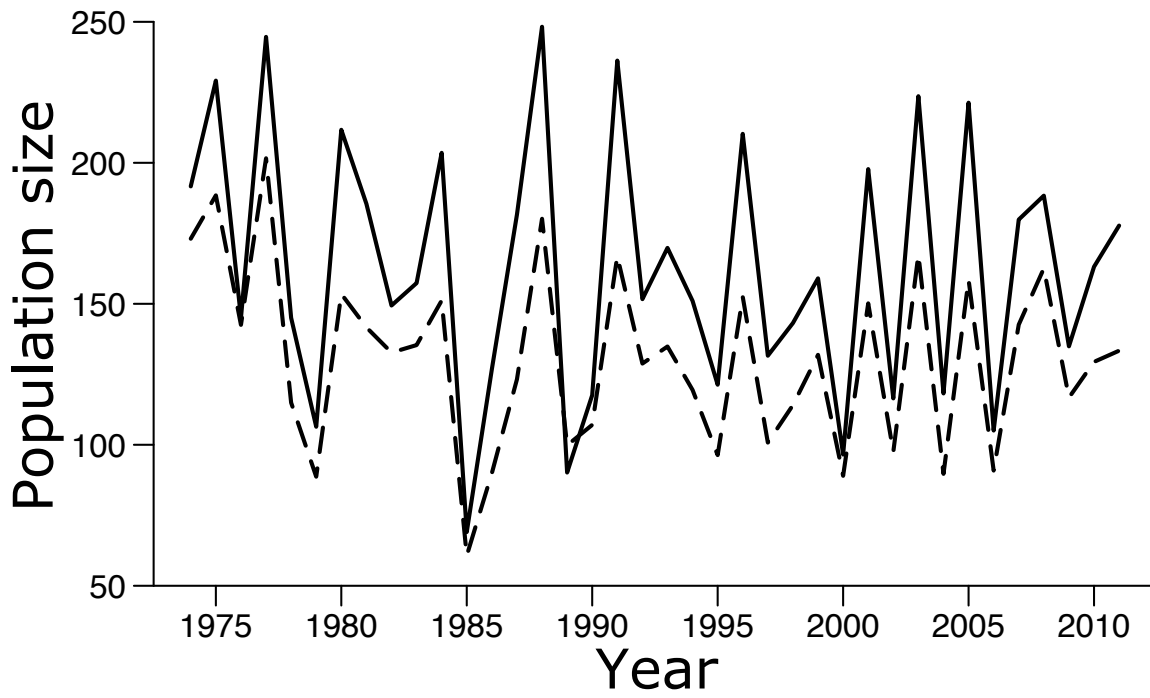


Fig. 1

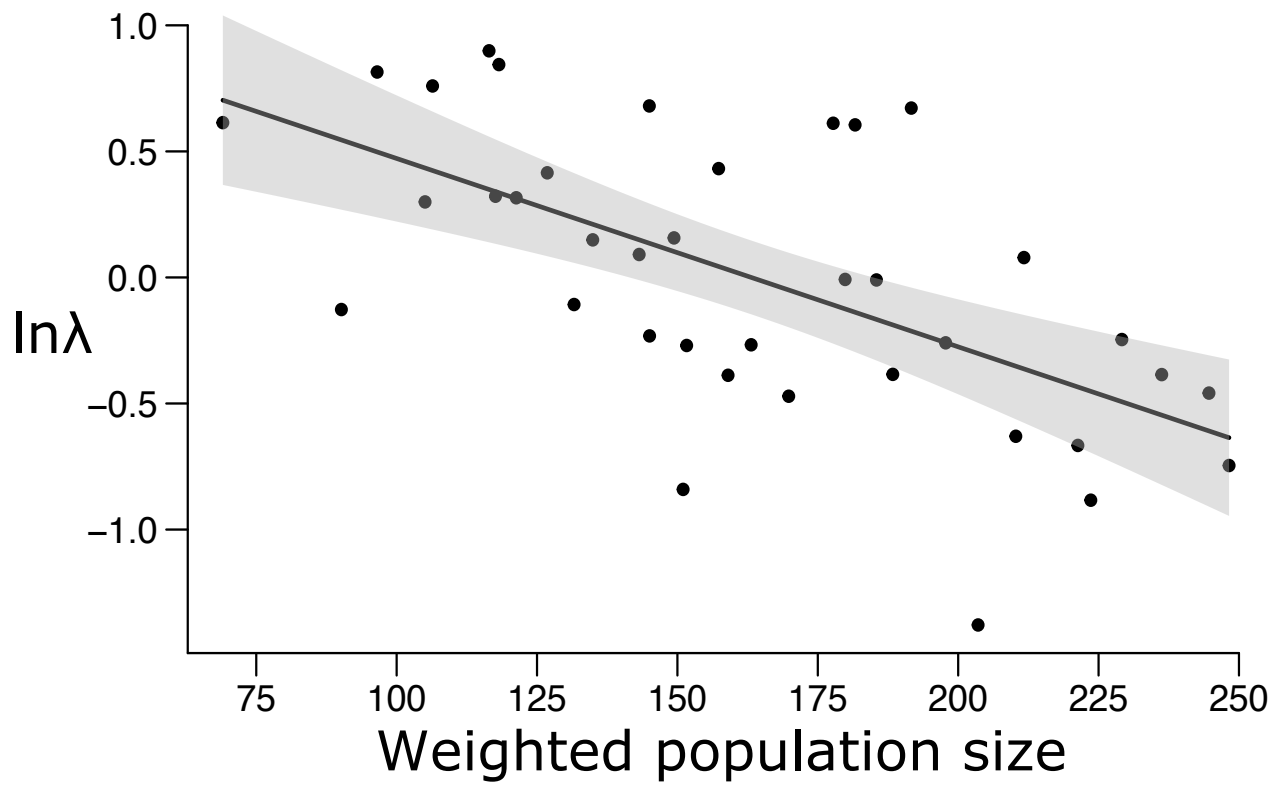


Fig. 2

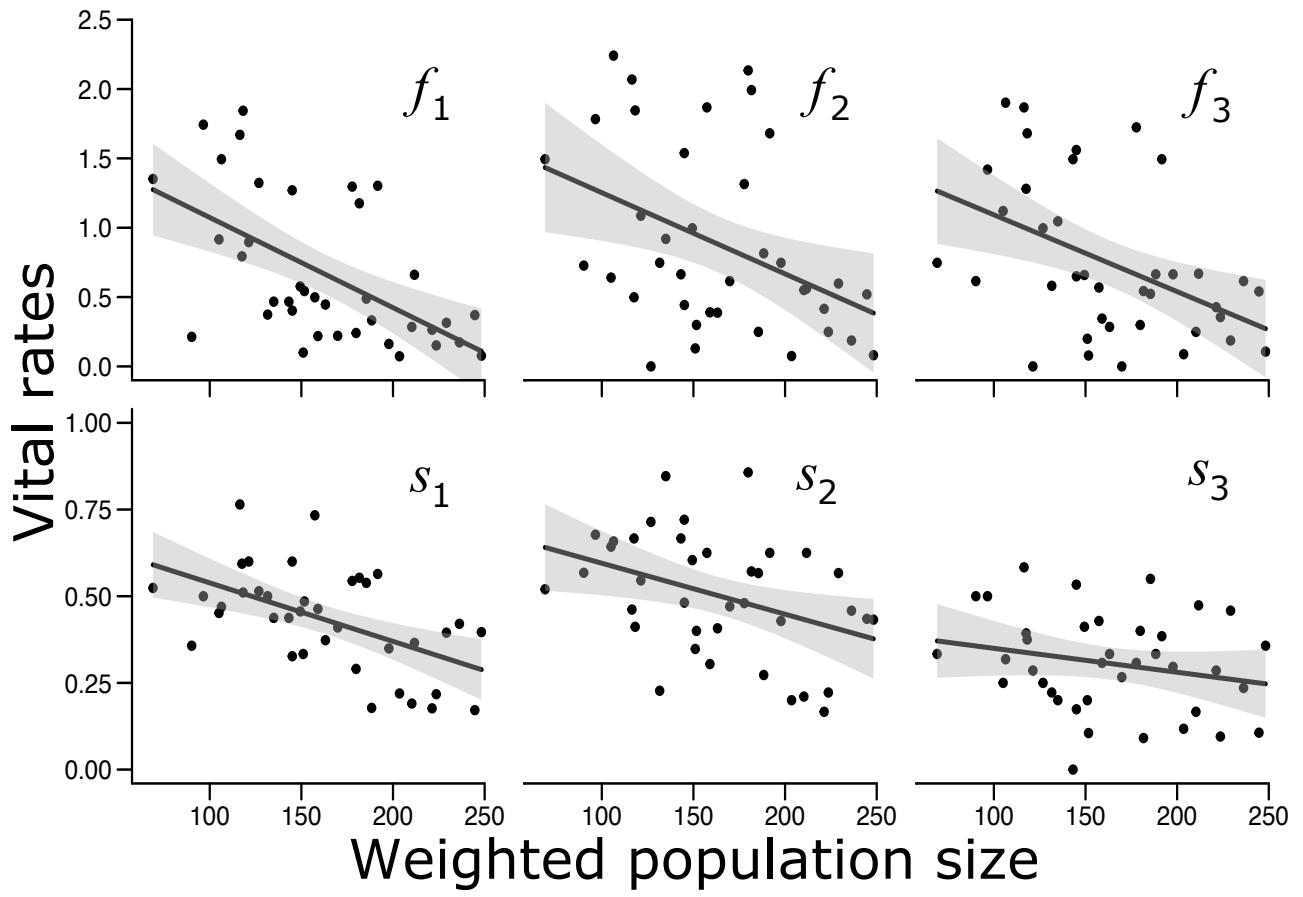


Fig. 3