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REPORT

Sensitivity analysis of equilibrium in density-dependent matrix population models

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Abstract

We consider the effects of parameter perturbations on a density-dependent population at equilibrium. Such perturbations change the dominant eigenvalue λ of the projection matrix evaluated at the equilibrium as well as the equilibrium itself. We show that, regardless of the functional form of density dependence, the sensitivity of λ is equal to the sensitivity of an effective equilibrium density $\tilde{N}$, which is a weighted combination of the equilibrium stage densities. The weights measure the contributions of each stage to density dependence and their effects on demography. Thus, $\tilde{N}$ is in general more relevant than total density, which simply adds all stages regardless of their ecological properties. As $\log \lambda$ is the invasion exponent, our results show that successful invasion will increase $\tilde{N}$, and that an evolutionary stable strategy will maximize $\tilde{N}$. Our results imply that eigenvalue sensitivity analysis of a population projection matrix that is evaluated near equilibrium can give useful information about the sensitivity of the equilibrium population, even if no data on density dependence are available.

Keywords

Density dependence, elasticity analysis, equilibrium, evolutionary stable strategy, invasion exponent, matrix population models, nonlinear, sensitivity analysis, territory limitation, *Tribolium*.

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INTRODUCTION

A density-independent population in a constant environment will eventually grow exponentially. If population growth is described by a population projection matrix **A**, then the rate of population growth (λ) is given by the dominant eigenvalue of **A**. This population growth rate measures the potential performance of the population in the environment, giving rise to the entries in **A**. The sensitivities and elasticities (i.e. proportional sensitivities) of λ to changes in parameters are useful for studying the effects of environmental change, the action of natural selection and the efficacy of management strategies (e.g., Caswell 1978, 2001; de Kroon *et al.* 1986, 2000; Crouse *et al.* 1987; Roff 1992; Hunter *et al.* 2000).

In contrast, the dynamics of a density-dependent population are not characterized by exponential growth. Instead, trajectories typically converge to an attracting invariant set (an equilibrium point, cycle, invariant loop or strange attractor) on which the long-term average growth rate is 1. It is natural to look for indices of population performance related to that attractor, and to explore their sensitivity and elasticity to changes in parameters. Ideally, these sensitivities and elasticities would also have interpretations useful for studying environmental change, natural selection and management.

Two such indices have been examined. One is the invasion exponent, $\log \lambda_I$, which measures the rate at which an invading phenotype would grow if introduced into an environment where a resident phenotype is at its attractor (Metz *et al.* 1992; Rand *et al.* 1994; Ferriére & Gatto 1995). The second index is some measure of population density (Grant 1998; Grant & Benton 2000, 2003; Yearsley *et al.* 2003). When the attractor is an equilibrium point, important relationships between these two indices are known for some special cases. This paper provides a general formula. Its importance is that it links effects on population growth with effects on equilibrium population density; such relationships are useful in evolutionary and management questions.

The Takada–Nakajima theorem

Takada & Nakajima (1992, 1998; for related earlier special cases see Hastings 1978 and Charlesworth 1980) proved

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some important results about the sensitivity analysis of density-dependent matrix models. Suppose that population dynamics are given by

$$\mathbf{n}(t+1) = \mathbf{A}_{N(t)}\mathbf{n}(t), \tag{1}$$

where the entries of $\mathbf{A}_{N(t)}$ are functions of an effective density $N(t)$, which is a weighted sum of stage densities

$$N(t) = \mathbf{c}^{\mathsf{T}}\mathbf{n}(t), \tag{2}$$

where $\mathbf{c} \geq 0$ and $\mathbf{c}^{\mathsf{T}}$ is the transpose of $\mathbf{c}$. What we call the effective density was called the biologically active density by Caswell (2001). At an equilibrium $\hat{\mathbf{n}}$, the projection matrix satisfies

$$\hat{\mathbf{n}} = \mathbf{A}_{\hat{N}}\hat{\mathbf{n}}. \tag{3}$$

The dominant eigenvalue of the matrix $\mathbf{A}_{\hat{N}}$ is denoted by λ, and satisfies $\lambda=1$. Takada & Nakajima (1998) proved that

$$\frac{\partial \hat{N}}{\partial a_{ij}} = \frac{\left.\frac{\partial \lambda}{\partial a_{ij}}\right|_{\hat{N}}}{-\mathbf{v}^{\mathsf{T}}\left.\frac{\partial \mathbf{A}}{\partial N}\right|_{\hat{N}}\mathbf{w}} \tag{4}$$

where $\mathbf{w}$ and $\mathbf{v}$ are the right and left eigenvectors of $\mathbf{A}_{\hat{N}}$ scaled so that their scalar product is 1, and the sensitivity $\partial\lambda/\partial a_{ij}=v_i w_j$.

This result has several implications:

(1) The sensitivities (and also the elasticities; see Caswell 2001, p. 560) of λ to the a_{ij} at equilibrium are proportional to the corresponding sensitivities (and elasticities) of $\hat{N}$.
(2) If density dependence is non-positive, so that $\partial a_{ij}/\partial N \leq 0$ for all i and j, then any perturbation that increases λ will also increase $\hat{N}$.
(3) If $\hat{\mathbf{n}}$ is a stable equilibrium, then $\log \lambda$ is the invasion exponent. For an alternative phenotype to invade, it must have a higher value of λ than the resident (Metz *et al.* 1992). Thus when the Takada–Nakajima theorem holds and density dependence is non-positive, successful invasion will increase the effective density at equilibrium, and an evolutionary stable strategy (ESS) will maximize it. The relative selective pressures on the a_{ij} are given by $\partial\lambda/\partial a_{ij}$.

This theorem provides an important connection between the sensitivity of λ and the sensitivity of equilibrium density to changes in the matrix entries. It is applicable to both evolutionary questions (showing the consequences for equilibrium density of successful invasion) and management problems (providing conditions that guarantee that increasing λ will also increase equilibrium density).

These results apply to the effective density (eqn 2), not to the total density $N_{\text{tot}}=\sum_i n_i$. Other than satisfying a natural human inclination to count things, N_{tot} has little to recommend it, because it ignores important ecological differences among stages. In a tree model, for example, it would be calculated by adding together the density of tiny seedlings and huge trees. In a fish model, it would add the densities of larval fish and of adult fish weighing a million times more. In a model for *Tribolium*, it would add the number of cannibalistic larvae and quiescent pupae. The effective density, in contrast, measures density in the same units in which it affects the vital rates of the population.

The Takada–Nakajima theorem has two important limitations: $\mathbf{A}_N$ must be a function of a linear combination of stage densities, and density dependence must operate through only one such linear combination. Although most density-dependent models use only a single measure of density*, this probably reflects convenience rather than biology. In reality, different vital rates are doubtless affected by different measures of effective density, so these are serious limitations.

A GENERAL THEOREM ON DENSITY-DEPENDENT SENSITIVITY

Here we present a more general theorem that removes both these limitations. In what follows, we present the derivation of the theorem step-by-step, because these steps make it clear how to actually apply the result. If you are more interested in the destination than the journey, you may skip directly to Theorem 1 at the end of this section. To simplify the notation, we write $\mathbf{A}$ explicitly as a function of a parameter θ and of two measures of density, $f_1(\mathbf{n})$ and $f_2(\mathbf{n})$

$$\mathbf{A} = \mathbf{A}[\theta, f_1(\mathbf{n}), f_2(\mathbf{n})] \tag{5}$$

where $f_1(\mathbf{n})$ and $f_2(\mathbf{n})$ are arbitrary differentiable functions of $\mathbf{n}$. We will extend the results to more than two measures of density below.

The equilibrium $\hat{\mathbf{n}}$ at a parameter value θ_0 satisfies

$$\hat{\mathbf{n}} = \mathbf{A}[\theta_0, f_1(\hat{\mathbf{n}}), f_2(\hat{\mathbf{n}})]\hat{\mathbf{n}}. \tag{6}$$

Thus $\hat{\mathbf{n}}$ is a right eigenvector of $\mathbf{A}[\theta_0, f_1(\hat{\mathbf{n}}), f_2(\hat{\mathbf{n}})]$ corresponding to the dominant eigenvalue $\lambda = 1$. Let $\mathbf{v}$ be the corresponding left eigenvector, scaled so that $\mathbf{v}^{\mathsf{T}}\hat{\mathbf{n}} = 1$; we assume that $\mathbf{A}[\theta_0, f_1(\hat{\mathbf{n}}), f_2(\hat{\mathbf{n}})]$ is non-negative and irreducible, so that $\hat{\mathbf{n}}$ and $\mathbf{v}$ are both non-negative.

We impose a small perturbation on θ, so that

$$\theta_0 \longrightarrow \theta_0 + \mathrm{d}\theta \tag{7}$$

leading to a new equilibrium $\hat{\mathbf{n}} + \mathrm{d}\hat{\mathbf{n}}$ that satisfies

*We know of only three exceptions: a model for *Tribolium* in which cannibalism of eggs and of pupae depend on two different linear combinations of densities (Costantino *et al.* 1997), a model for the spotted owl in which pair formation and juvenile survival depend on different combinations of densities (Lamberson *et al.* 1992), and a model for the cormorant in which fecundity and survival depend on different combinations of densities (Frederiksen *et al.* 2001).

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$$\mathbf{A}[\theta_0 + \mathrm{d}\theta, f_1(\hat{\mathbf{n}} + \mathrm{d}\hat{\mathbf{n}}), f_2(\hat{\mathbf{n}} + \mathrm{d}\hat{\mathbf{n}})](\hat{\mathbf{n}} + \mathrm{d}\hat{\mathbf{n}}) = \hat{\mathbf{n}} + \mathrm{d}\hat{\mathbf{n}}. \tag{8}$$

Expanding f_1 and f_2 to first order around $\hat{\mathbf{n}}$ gives

$$\mathbf{A}\left[\theta_0 + \mathrm{d}\theta, f_1(\hat{\mathbf{n}}) + \nabla f_1^{\mathsf{T}}\, \mathrm{d}\hat{\mathbf{n}}, f_2(\hat{\mathbf{n}}) + \nabla f_2^{\mathsf{T}}\, \mathrm{d}\hat{\mathbf{n}}\right] \times (\hat{\mathbf{n}} + \mathrm{d}\hat{\mathbf{n}}) = \hat{\mathbf{n}} + \mathrm{d}\hat{\mathbf{n}}, \tag{9}$$

where the gradient $\nabla f_i = \left(\frac{\partial f_i}{\partial n_1} \quad \frac{\partial f_i}{\partial n_2} \quad \cdots\right)^{\mathsf{T}}$, and all partial derivatives are evaluated at $(\theta_0, \hat{\mathbf{n}})$.

Next, expand $\mathbf{A}$ to first order around $(\theta_0, \hat{\mathbf{n}})$ to obtain

$$\left(\mathbf{A}[\theta_0, f_1(\hat{\mathbf{n}}), f_2(\hat{\mathbf{n}})] + \mathrm{d}\theta \left.\frac{\partial \mathbf{A}}{\partial \theta}\right|_{\theta_0,\hat{\mathbf{n}}} + \nabla f_1^{\mathsf{T}}\, \mathrm{d}\hat{\mathbf{n}} \left.\frac{\partial \mathbf{A}}{\partial f_1}\right|_{\theta_0,\hat{\mathbf{n}}} + \nabla f_2^{\mathsf{T}}\, \mathrm{d}\hat{\mathbf{n}} \left.\frac{\partial \mathbf{A}}{\partial f_2}\right|_{\theta_0,\hat{\mathbf{n}}}\right)(\hat{\mathbf{n}} + \mathrm{d}\hat{\mathbf{n}}) = \hat{\mathbf{n}} + \mathrm{d}\hat{\mathbf{n}} \tag{10}$$

Multiplying and keeping only first-order terms gives

$$\mathbf{A}[\theta_0, f_1(\hat{\mathbf{n}}), f_2(\hat{\mathbf{n}})]\mathrm{d}\hat{\mathbf{n}} + \mathrm{d}\theta \left.\frac{\partial \mathbf{A}}{\partial \theta}\right|_{\theta_0,\hat{\mathbf{n}}} \hat{\mathbf{n}} + \nabla f_1^{\mathsf{T}}\, \mathrm{d}\hat{\mathbf{n}} \left.\frac{\partial \mathbf{A}}{\partial f_1}\right|_{\theta_0,\hat{\mathbf{n}}} \hat{\mathbf{n}} + \nabla f_2^{\mathsf{T}}\, \mathrm{d}\hat{\mathbf{n}} \left.\frac{\partial \mathbf{A}}{\partial f_2}\right|_{\theta_0,\hat{\mathbf{n}}} \hat{\mathbf{n}} = \mathrm{d}\hat{\mathbf{n}}. \tag{11}$$

Multiplying on the left by $\mathbf{v}^{\mathsf{T}}$, dividing by $\mathrm{d}\theta$, and rearranging terms yields

$$\left(\mathbf{v}^{\mathsf{T}} \left.\frac{\partial \mathbf{A}}{\partial \theta}\right|_{\theta_0,\hat{\mathbf{n}}} \hat{\mathbf{n}}\right) = \left\{-\left(\mathbf{v}^{\mathsf{T}} \left.\frac{\partial \mathbf{A}}{\partial f_1}\right|_{\theta_0,\hat{\mathbf{n}}} \hat{\mathbf{n}}\right)\nabla f_1^{\mathsf{T}} - \left(\mathbf{v}^{\mathsf{T}} \left.\frac{\partial \mathbf{A}}{\partial f_2}\right|_{\theta_0,\hat{\mathbf{n}}} \hat{\mathbf{n}}\right)\nabla f_2^{\mathsf{T}}\right\} \frac{\partial \hat{\mathbf{n}}}{\partial \theta}. \tag{12}$$

Because $\hat{\mathbf{n}}$ is the right eigenvector of $\mathbf{A}[\theta_0, f_1(\hat{\mathbf{n}}), f_2(\hat{\mathbf{n}})]$, it follows that

$$\left(\mathbf{v}^{\mathsf{T}} \left.\frac{\partial \mathbf{A}}{\partial \theta}\right|_{\theta_0,\hat{\mathbf{n}}} \hat{\mathbf{n}}\right) = \left.\frac{\partial \lambda}{\partial \theta}\right|_{\theta_0,\hat{\mathbf{n}}}, \tag{13}$$

$$\left(\mathbf{v}^{\mathsf{T}} \left.\frac{\partial \mathbf{A}}{\partial f_i}\right|_{\theta_0,\hat{\mathbf{n}}} \hat{\mathbf{n}}\right) = \left.\frac{\partial \lambda}{\partial f_i}\right|_{\theta_0,\hat{\mathbf{n}}}, \qquad i = 1, 2. \tag{14}$$

Thus eqn 12 can be written as

$$\left.\frac{\partial \lambda}{\partial \theta}\right|_{\theta_0,\hat{\mathbf{n}}} = -\left(\nabla f_1^{\mathsf{T}} \left.\frac{\partial \lambda}{\partial f_1}\right|_{\theta_0,\hat{\mathbf{n}}} + \nabla f_2^{\mathsf{T}} \left.\frac{\partial \lambda}{\partial f_2}\right|_{\theta_0,\hat{\mathbf{n}}}\right) \frac{\partial \hat{\mathbf{n}}}{\partial \theta} \tag{15}$$

$$= \sum_i \left[-\left(\frac{\partial \lambda}{\partial f_1}\frac{\partial f_1}{\partial n_i}\right)\Big|_{\theta_0,\hat{\mathbf{n}}} - \left(\frac{\partial \lambda}{\partial f_2}\frac{\partial f_2}{\partial n_i}\right)\Big|_{\theta_0,\hat{\mathbf{n}}}\right] \frac{\partial \hat{n}_i}{\partial \theta} \tag{16}$$

$$= \frac{\partial \tilde{N}}{\partial \theta}, \tag{17}$$

where $\tilde{N}$ is a weighted linear combination of the stage densities

$$\tilde{N} = \mathbf{g}^{\mathsf{T}}\hat{\mathbf{n}} \tag{18}$$

with the weights in the vector $\mathbf{g}$ given by

$$g_i = \left(-\frac{\partial \lambda}{\partial f_1}\frac{\partial f_1}{\partial n_i} - \frac{\partial \lambda}{\partial f_2}\frac{\partial f_2}{\partial n_i}\right)\Big|_{\theta_0,\hat{\mathbf{n}}}. \tag{19}$$

We call $\tilde{N}$ the biologically effective equilibrium density. The sensitivity of λ to any parameter θ, calculated at equilibrium, is equal to the sensitivity of $\tilde{N}$ to that parameter.

The derivation of eqn 19 shows that the result generalizes directly to any number of densities $f_j(\mathbf{n})$, $j = 1, 2, \ldots$, in which case

$$g_i = \left(-\sum_j \frac{\partial \lambda}{\partial f_j}\frac{\partial f_j}{\partial n_i}\right)\Big|_{\theta_0,\hat{\mathbf{n}}} \tag{20}$$

This proves the following theorem.

Theorem 1 Let $\mathbf{A}[\theta, f_1(\mathbf{n}), \ldots, f_m(\mathbf{n})]$ be a density-dependent population projection matrix depending on a parameter θ and on m functions of population density $f_1, \ldots, f_m$. Let $\hat{\mathbf{n}}$ be an equilibrium satisfying eqn 6 and suppose that the functions $f_i(\mathbf{n})$ have Taylor series expansions in the neighbourhood of $\hat{\mathbf{n}}$. Let λ be the dominant eigenvalue of $\mathbf{A}$ evaluated at θ_0 and $\hat{\mathbf{n}}$. Then

$$\left.\frac{\partial \lambda}{\partial \theta}\right|_{\theta_0,\hat{\mathbf{n}}} = \frac{\partial \mathbf{g}^{\mathsf{T}}\hat{\mathbf{n}}}{\partial \theta}, \tag{21}$$

where

$$g_i = \left(-\sum_{j=1}^{m} \frac{\partial \lambda}{\partial f_j}\frac{\partial f_j}{\partial n_i}\right)\Big|_{\theta_0,\hat{\mathbf{n}}}. \tag{22}$$

Interpretations and implications

Some important implications follow directly from Theorem 1:

(1) Rather than simply adding individuals together regardless of their biological properties, the effective equilibrium density $\tilde{N}$ weights each stage by two properties: its contribution to density dependence (measured by $\partial f_j/\partial n_i$) and its effect on λ (measured by $\partial\lambda/\partial f_j$). Thus $\tilde{N}$ combines the two parts of a density-dependent

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model – the impact of density on the vital rates and the impact of the vital rates on population growth – in a precise quantitative way.

(2) It follows immediately from eqn 17 that the elasticity of λ to θ is proportional to the elasticity of $\tilde{N}$ to θ:

$$\left.\frac{\theta}{\lambda}\frac{\partial\lambda}{\partial\theta}\right|_{\theta_0,\hat{\mathbf{n}}} = \frac{\theta}{\lambda}\frac{\partial\tilde{N}}{\partial\theta} = \tilde{N}\frac{\theta}{\tilde{N}}\frac{\partial\tilde{N}}{\partial\theta} \tag{23}$$

with a proportionality constant equal to $\tilde{N}$ (remember that, at equilibrium, $\lambda = 1$).

(3) Any management tactic aimed at increasing λ in a population at equilibrium (e.g. one designed by looking at the sensitivities or elasticities of λ) will also increase the effective equilibrium density. It might not increase the total density $\hat{N}_{\text{tot}}$, but the density weighted according to resource use and demographic effects will increase.

(4) Eigenvalue sensitivities have been used to study the effects of pollutants on population growth rate (e.g., Caswell 1996, 2000; Levin *et al.* 1996). Extending these analyses to include effects on the equilibrium of density-dependent populations is an important problem (Grant 1998; Linke-Gamenick *et al.* 1999; Forbes *et al.* 2001). Our results provide a link between life table response experiments for λ and for $\tilde{N}$.

(5) The quantity

$$\left.\frac{1}{\lambda}\frac{\partial\lambda}{\partial\theta}\right|_{\theta_0,\hat{\mathbf{n}}} \tag{24}$$

is the sensitivity of the invasion exponent to a change in the parameter θ. Successful invasion by a new phenotype will increase the effective equilibrium density $\tilde{N}$, and an ESS will maximize $\tilde{N}$.

(6) The theorems of Takada & Nakajima (1992, 1998) follow immediately as special cases in which **A** depends on a single linear combination of the densities.

EXAMPLES

In this section, we analyse two examples, neither of which satisfy the conditions of Takada & Nakajima (1992, 1998). One is the *Tribolium* model, in which population growth depends on two different linear combinations of stage densities. The other is a model of a territory-limited population, in which population growth depends on a measure of density that is not a linear combination of stage densities.

In each case, we compute the response of $\tilde{N}$ by a sensitivity analysis of the matrix $\mathbf{A}[\theta_0, \hat{\mathbf{n}}]$ using Theorem 1 and compare this predicted response with the actual response of $\tilde{N}$ computed numerically.

Example 1: the *Tribolium* model

The *Tribolium* model (Costantino *et al.* 1997; Cushing *et al.* 2003) has three stages: larvae, pupae and adults. Density dependence operates through cannibalism of eggs by larvae and adults, and through cannibalism of pupae by adults. The population projection matrix is

$$\mathbf{A}_{\mathbf{n}} = \begin{pmatrix} 0 & 0 & b\exp(-c_{\text{el}}n_1 - c_{\text{ea}}n_3) \\ 1-\mu_{\text{l}} & 0 & 0 \\ 0 & \exp(-c_{\text{pa}}n_3) & 1-\mu_{\text{a}} \end{pmatrix} \tag{25}$$

where b is the fertility, c_{ea}, c_{el} and c_{pa} are cannibalism coefficients (of eggs by adults, of eggs by larvae, and of pupae by adults, respectively), and μ_{a} and μ_{l} are adult and larval mortality rates, respectively. Thus two functions of density appear in the model, one describing the cannibalism of eggs and the other the cannibalism of larvae:

$$f_1(\mathbf{n}) = \exp(-c_{\text{el}}n_1 - c_{\text{ea}}n_3), \tag{26}$$

$$f_2(\mathbf{n}) = \exp(-c_{\text{pa}}n_3). \tag{27}$$

Under control conditions, Costantino *et al.* (1997) reported parameter values of

$$b = 6.598$$
$$c_{\text{ea}} = 1.155 \times 10^{-2}$$
$$c_{\text{el}} = 1.209 \times 10^{-2}$$
$$c_{\text{pa}} = 4.7 \times 10^{-3}$$
$$\mu_{\text{a}} = 7.729 \times 10^{-3}$$
$$\mu_{\text{l}} = 2.055 \times 10^{-1}$$

which produce a stable equilibrium

$$\hat{\mathbf{n}} = \begin{pmatrix} 22.61 \\ 17.96 \\ 385.18 \end{pmatrix}. \tag{28}$$

The sensitivities of λ to each of the parameters, calculated from the matrix $\mathbf{A}[\theta, \hat{\mathbf{n}}]$ are:

Parameter	b	c_{ea}	c_{el}	c_{pa}	μ_{a}	μ_{l}
$\left.\frac{\partial\lambda}{\partial\theta}\right\|_{\hat{\mathbf{n}}}$	0.001	−2.894	−0.170	−2.894	−0.985	−0.010

(29)

As expected, λ increases with increased birth rate and decreases with increased cannibalism or mortality.

To calculate the sensitivities of $\tilde{N}$ we need the sensitivities of λ to f_1 and f_2 at equilibrium:

$$\frac{\partial\lambda}{\partial f_1} = b\frac{\partial\lambda}{\partial a_{13}} = 0.8447 \tag{30}$$

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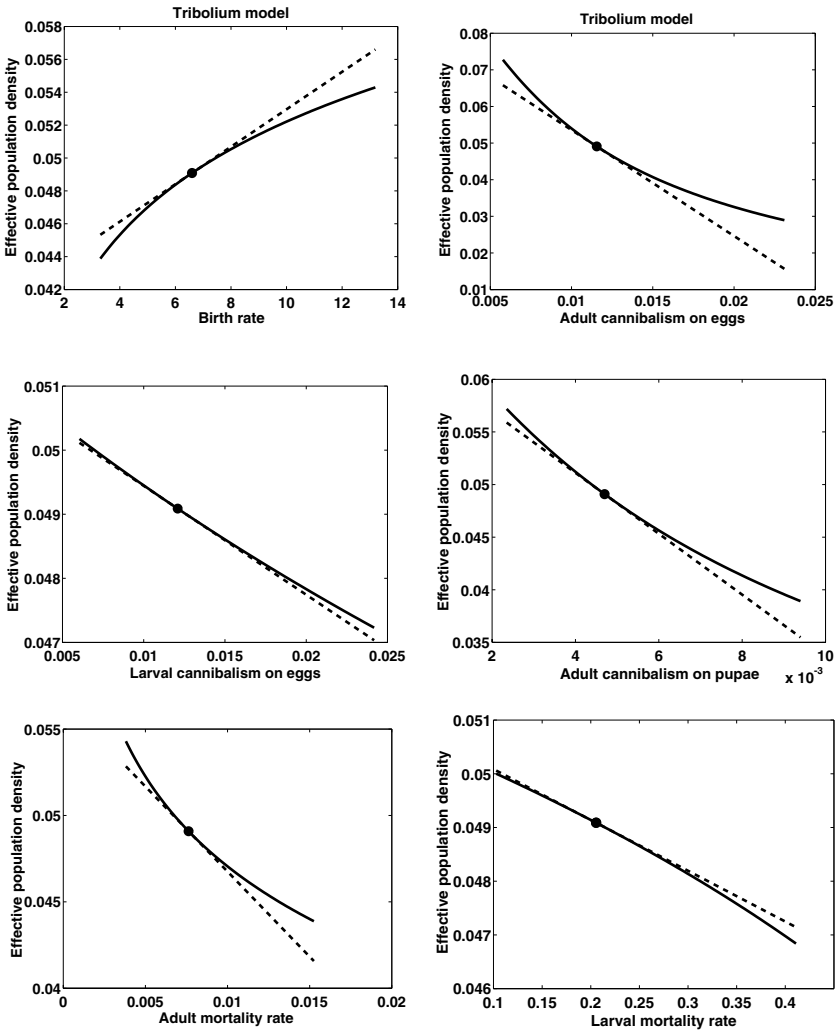

Figure 1 The response of the effective equilibrium density $\tilde{N}$ to changes in each of the six parameters of the *Tribolium* model (solid lines), compared with the slopes predicted from the sensitivity of λ at equilibrium (dashed lines).

$$\frac{\partial\lambda}{\partial f_2} = \frac{\partial\lambda}{\partial a_{32}} = 0.0459 \tag{31}$$

The gradient vectors, calculated by differentiating f_1 and f_2 with respect to the n_i at equilibrium, are

$$\nabla f_1 = \begin{pmatrix} -1.076 \\ 0 \\ -1.027 \end{pmatrix} \times 10^{-4}, \quad \nabla f_2 = \begin{pmatrix} 0 \\ 0 \\ -7.689 \end{pmatrix} \times 10^{-4}. \tag{32}$$

The weights $\mathbf{g}$, calculated from eqn 20, are

$$\mathbf{g}^{\mathsf{T}} = (\,0.908 \quad 0.0 \quad 1.221\,) \times 10^{-4}. \tag{33}$$

Thus, the effective density, $\tilde{N} \approx (0.09 \times 10^{-3})\hat{n}_1 + (0.12 \times 10^{-3})\hat{n}_3$, is roughly proportional to the sum of larvae and adults (to be more precise, adults get 34% more weight than larvae). Pupae, because they make no contribution to density dependence, do not contribute to $\tilde{N}$.

Figure 1 shows the effect of changing each parameter and re-computing $\tilde{N}$. Both λ and $\tilde{N}$ increase with b, and decrease with increases in any of the cannibalism coefficients or mortality rates. The sensitivity of $\tilde{N}$ to the parameters agrees with the sensitivity of λ evaluated at equilibrium (eqn 29).

As the equilibrium (eqn 28) includes very few pupae, the changes in $\tilde{N}$ are very similar to changes in N_{tot}. This explains why changes in N_{tot} and in λ appeared similar in a numerical calculation in Caswell (2001).

Example 2: a territory-limitation model

In some forms of density dependence, the vital rates may depend on functions that cannot be expressed as linear combinations of the n_i. For example, Grant & Benton (2000, 2003) posed the following scenario as one in which the sensitivity of λ at equilibrium would reveal nothing about the sensitivity of equilibrium total population size:

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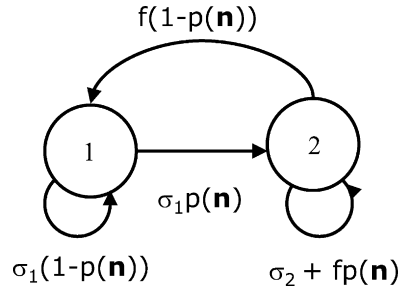

Figure 2 A life cycle graph for a density-dependent model of territory limitation. Stages 1 and 2 are floaters and breeders, respectively. The function $p(\mathbf{n})$ is the probability of a bird without a territory (either a floater or a newborn bird) obtaining a territory; σ_1 and σ_2 are the survival probabilities of floaters and breeders, and f is the per-capita fertility of breeders.

> 'Consider a population that inhabits an environment in which there are a fixed number of territories, each of which can support a single adult individual. At each time step, the adults reproduce, a fixed proportion of the adults die, and their places are taken by randomly chosen offspring of the population … Population size is determined by the number of available territories, so an increase in adult fertility will have no impact on population size. However, invasibility analysis shows that such a change will have an impact on individual fitness'.

The following model implements such a scenario, in the context of a bird population. Let n_1 denote birds without a territory (floaters) and n_2 denote birds with a territory (breeders). The life cycle graph is shown in Fig. 2. Floaters survive with probability σ_1 and obtain a territory with a probability $p(\mathbf{n})$ that depends on the current population and the number of territories. Breeders survive with probability σ_2 and produce f surviving offspring per individual; those offspring obtain a territory with probability $p(\mathbf{n})$. The model is

$$\mathbf{n}(t+1) = \begin{pmatrix} \sigma_1[1-p(\mathbf{n})] & f[1-p(\mathbf{n})] \\ \sigma_1 p(\mathbf{n}) & \sigma_2 + fp(\mathbf{n}) \end{pmatrix} \mathbf{n}(t). \tag{34}$$

The function $p(\mathbf{n})$ implements the density dependence. Assume a fixed number of territories, and scale $\mathbf{n}$ relative to that number, so n_2 is the fraction of territories occupied and n_1 is the number of floaters per territory. Assuming that any surviving breeder keeps its territory, the probability of a floater obtaining a territory is

$$p(\mathbf{n}) = \frac{\text{number of empty territories}}{\text{number of candidates for territories}}$$

$$= \begin{cases} \frac{1-\sigma_2 n_2}{\sigma_1 n_1 + f n_2} & \text{if } \sigma_1 n_1 + f n_2 \geq 1 - \sigma_2 n_2 \\ 1 & \text{otherwise.} \end{cases} \tag{35}$$

If $n_2(0) \leq 1$, then $n_2(t) \leq 1$ for all t, so we do not consider the impossible scenario where more than 100% of territories are occupied.

The model has equilibria at the origin and at

$$\hat{\mathbf{n}} = \begin{pmatrix} \frac{f+\sigma_2-1}{1-\sigma_1} \\ 1 \end{pmatrix}. \tag{36}$$

The equilibrium at the origin is unstable if $\sigma_2 + f > 1$; that is, if the population is able to grow at low densities when territories are abundant. In this case, the positive equilibrium is stable.

Changes in the parameters σ_1, σ_2, or f change the relative abundance of breeders and floaters, the total population size, and $\tilde{N}$. As an example, set $\sigma_1 = 0.7$, $\sigma_2 = 0.8$ and $f = 1$. For these parameters, a straightforward calculation gives

$$\mathbf{g}^{\mathsf{T}} = \left(\frac{-\partial\lambda}{\partial p}\frac{\partial p}{\partial n_1} \quad \frac{-\partial\lambda}{\partial p}\frac{\partial p}{\partial n_2} \right)\Big|_{\hat{\mathbf{n}}} \tag{37}$$

$$= (\,0.0306 \quad 0.3408\,). \tag{38}$$

The effective equilibrium density $\tilde{N} \approx 0.03\hat{n}_1 + 0.34\hat{n}_2$ gives about 10 times more weight to breeders than to floaters, but includes both. Figure 3 shows the response of $\tilde{N}$ to changes in each of the parameters, compared with the sensitivity of λ to those parameters, evaluated at equilibrium. The sensitivity of λ is positive for each parameter; as λ is the invasion exponent, selection would favour invasion by phenotypes with increased survival or fertility; those invasions would increase $\tilde{N}$ and an ESS would maximize $\tilde{N}$.

DISCUSSION

The search for links between the evolutionary and the population dynamic consequences of parameter changes is an important problem (Grant & Benton 2000, 2003). It is easily resolved in the density-independent case, where λ measures both fitness (an evolutionary consequence) and the asymptotic growth rate (a population dynamic consequence). In density-dependent models, the invasion exponent is an evolutionary consequence, but attention has fixated on N_{tot} as a population dynamic consequence, and the two are linked only in special cases. The difficulty is resolved by shifting attention from $\hat{N}_{\text{tot}}$ to $\tilde{N}$ as the measure of population density. Then, our results provide a general relationship between the evolutionary and population dynamic consequences of parameter changes: the sensitivity of the invasion exponent equals the sensitivity of the effective equilibrium density. Of course, equilibrium density does not exhaust the list of population consequences in density-dependent models any more than population growth rate does in density-independent models.

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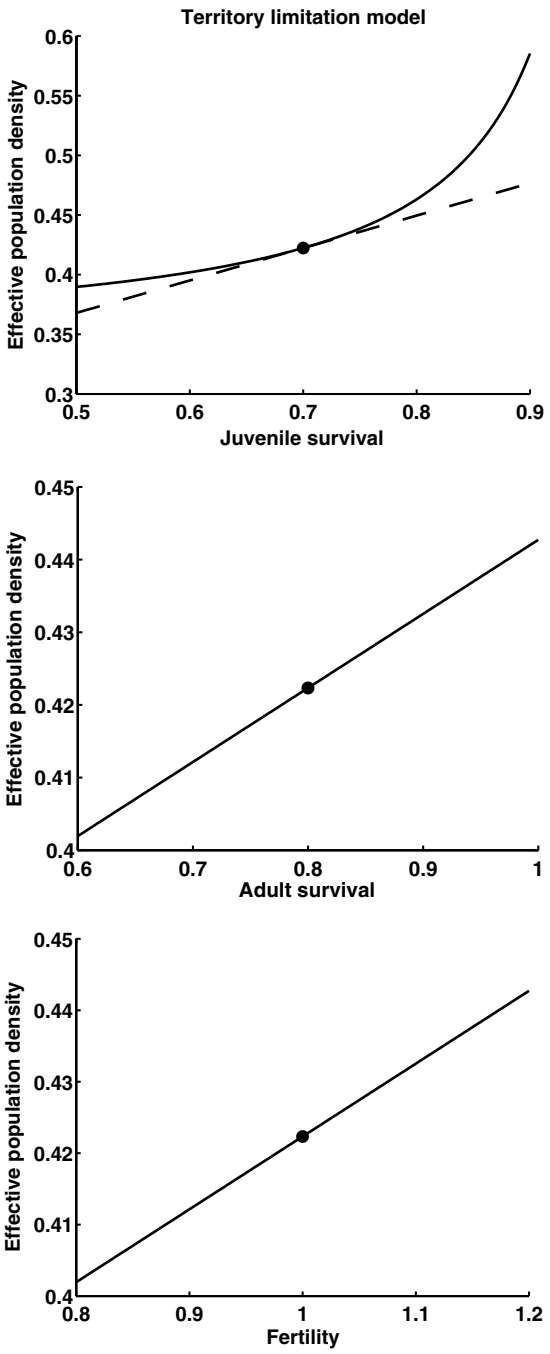

Figure 3 The response of the effective equilibrium density $\tilde{N}$ to changes in each of the three parameters of the territory-limitation model (solid lines), compared with the slopes predicted from the sensitivity of λ at equilibrium (dashed lines). The responses of $\tilde{N}$ to adult survival and fertility are so close to linear that the lines are hard to distinguish.

The effective equilibrium density weights the stages by their impact on demography at equilibrium. A stage has low (or zero) weight in $\tilde{N}$ only if the density of that stage has little (or no) effect on λ at equilibrium. This could happen for two reasons: either that stage has no effect on the vital rates through the functions f_i, or the vital rates that it affects have no effect on population growth. This underscores the importance of identifying the mechanisms by which stage-specific density-dependence actually operates, which is not often done.

$\tilde{N}$ will often be more relevant than N_{tot}, which adds together stages regardless of their effects on the environment or demography. But in some cases, weighted densities other than $\tilde{N}$ might be of interest. Pest control, for example, might focus on specific stages because of their economic impact rather than their demographic importance. However, if economic impact is mediated through resource consumption, then it should be correlated with demographic impact and be reflected in $\tilde{N}$. A weighting by reproductive value might be particularly relevant for conservation applications, but this is most applicable for problems of demographic stochasticity in small populations, not populations at equilibrium. In any event, reproductive value is usually highest for adult stages, which are likely to have the greatest density-dependent and demographic effects. We emphasize that it is of little use to speculate about such subtle effects without developing a density-dependent model that incorporates them, and most such models to date have not.

Population studies often yield only a single estimate of **A**, with no information about density dependence. If that matrix is evaluated at or close to equilibrium (a conjecture that would be supported if $\lambda \approx 1$), then the linear sensitivity analysis of λ provides information on the sensitivity of effective equilibrium density in the unknown nonlinear model. Thus the robustness of linear sensitivity analysis is even greater than previously thought (cf. Caswell 2001, p. 615).

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