Environment-specific elasticity and sensitivity analysis of the stochastic growth rate

Per Åberg [a], Carl Johan Svensson [a,*], Hal Caswell [b], Henrik Pavia [c]

[a] Department of Marine Ecology-Göteborg, University of Gothenburg, Box 461, SE-405 30 Göteborg, Sweden
[b] Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA
[c] Department of Marine Ecology-Tjärnö,, Göteborg University, Tjärnö, SE-452 96 Strömstad, Sweden

A B S T R A C T

For matrix population models, analyses of how sensitive the population growth rate is to changes in vital rates (i.e. perturbations) are important for studies of life history evolution as well as for management and conservation of threatened species. There are two types of sensitivity analyses corresponding to absolute (sensitivity) or relative (elasticity) changes in the vital rates and both types can be applied to both deterministic and stochastic matrix population models. To date, most empirical studies of elasticity and sensitivity of the stochastic growth rate have examined the response to perturbations in the vital rates in a complete set of possible environments. However, it is often of interest to examine the response to perturbations occurring in only a subset of the possible environments. This has been done for periodic time-varying models elsewhere, but here we describe a recently published method for calculating the environment-specific sensitivity and elasticity of the stochastic growth rate and apply this method to data. These environment-specific perturbation analyses provide a logical way of dividing the sensitivity and elasticity among the environments. They give important insight into the selection regime in different environments and can provide valuable information for making management decisions and management evaluations in stochastic environments.

© 2008 Elsevier B.V. All rights reserved.

1. Introduction

Matrix population models are important tools for analyzing the demography of age-, size- or stage-structured populations and they have been extensively applied to a large number of animal and plant species (see Caswell, 2001 for a general review). Among matrix model applications, perturbation analyses, such as sensitivity (Caswell, 1978) and elasticity (proportional sensitivity) (Caswell et al., 1984; de Kroon et al., 1986) of the asymptotic population growth rate λ_1 to changes in survival, growth and reproduction at different life cycle stages, are important analyses for descriptive demography, life history evolution, and management of species and conservation of threatened species. While sensitivity is the rate of change of the population growth rate in response to changes in a demographic parameter, elasticity can be interpreted as the relative contribution of different life cycle stages to population growth (de Kroon et al., 1986; Mesterton-Gibbons, 1993; Caswell, 2001).

Sensitivity and elasticity analyses play an equally important role in stochastic demographic models. In this paper we apply and evaluate a recently developed method (Caswell, 2005) that permits

evaluation of the effects of perturbations within a single environment, or a specified set of environments, within the range of random environmental variability. There are several other methods for calculating the sensitivity and elasticity of the population growth rate in stochastic environments (Tuljapurkar, 1990; Åberg, 1992; Caswell, 1996; Dixon et al., 1996; Tuljapurkar et al., 2003; Caswell, 2001) with the basic perturbation analysis developed by Tuljapurkar (1990). These methods (or equivalent numerical simulations) have now been applied to empirical data numerous times (e.g. Åberg, 1992; Benton and Grant, 1996; Dixon et al., 1996; Caswell and Kaye, 2001; Pavia et al., 2002; Tuljapurkar et al., 2003; Horvits et al., 2005; Smith et al., 2005; Ripley and Caswell, 2006; see also examples calculated from previously published results in Section 14.5 of Caswell, 2001). The sensitivities and elasticities of the stochastic growth rate are sometimes similar to the sensitivity and elasticity of the deterministic population growth rate, calculated from the mean matrix of all environments (Åberg, 1992; Benton and Grant, 1996; Dixon et al., 1996; Caswell, 2001; Tuljapurkar et al., 2003).

A stochastic demographic model describes a population living in an environment in which conditions may change at each projection interval. The sensitivity of the stochastic growth rate (the calculations are described below) gives the change in that rate caused by an incremental change in a demographic parameter applied at

* Corresponding author. Tel.: +46 31 786 2627; fax: +46 31 786 2727.
E-mail address: carl-johan.svensson@marecol.gu.se (C.J. Svensson).

each time, regardless of the state of the environment. Åberg (1992) posed the problem of calculating the effects of changes applied in only a subset of the possible environments. Darwin and Williams (1964) had addressed this problem by simulation in an early periodic matrix population model (for control of rabbit populations by seasonal hunting strategies), and Caswell and Trevisan (1994) derived the analytical sensitivity and elasticity calculations for periodic models.

From an evolutionary perspective, it may be of interest to know which environments (e.g. cold years, hot years, years with fires, etc.) favour, and which do not favour, selection for certain life history traits. A division of the sensitivity of the stochastic growth rate into environment-specific components could be used to compare the selection gradient in rare environments to that in more common environments and thus provide a deeper insight into the selection regime. Similarly, partitioning the elasticity of the stochastic growth rate into environment-specific components might suggest different management strategies in different environmental states.

Having raised the issue, Åberg (1992) presented a few simulation-based calculations of the elasticity of the stochastic growth rate to changes in single environments for a seaweed population. Caswell (2005) recently showed how to calculate environment-specific sensitivities and elasticities of the stochastic population growth rate. Here we apply the method to data for two species; our goal is to show how the sensitivity and elasticity of the stochastic population growth rate, when divided among environments, produces a better description of the selection regime for a species. We used data for the savanna grass *Andropogon semiberbis* (Silva et al., 1991; stochastic elasticity in Dixon et al., 1996) as an example where the stochastic process is changed, and data for the shrub *Fumana procumbens* (Bengtsson, 1993; K. Bengtsson and P. Åberg, unpublished data) as an example of large variation due to a catastrophic event. The usefulness of these alternative sensitivity analyses will be discussed in the context of species management and life history evolution.

2. Sensitivity and elasticity of the stochastic population growth rate

Tuljapurkar (1990) introduced the sensitivity and elasticity of the stochastic growth rate. Caswell (2005) extended Tuljapurkar's formula in several directions, including environment-specific sensitivities and elasticities. We summarize the formulae here. A stochastic matrix population model can be written

$$\mathbf{n}(t+1) = \mathbf{A}_t \mathbf{n}(t) \tag{1}$$

where $\mathbf{n}(t)$ is a population vector and $\mathbf{A}_t$ is the population projection matrix generated by a stochastic environmental process at time step t. The stochastic growth rate is

$$\log \lambda_s = \lim_{T \to \infty} \frac{1}{T} \log \left\| \mathbf{A}_{T-1} \cdots \mathbf{A}_0 \mathbf{n}_0 \right\| \tag{2}$$

To write down the sensitivity of $\log \lambda_s$, assume that $\mathbf{A}_t$ is perturbed to $\mathbf{A}_t + \varepsilon \mathbf{C}_t$. The entries of $\mathbf{C}_t$ determine which elements of $\mathbf{A}_t$ are perturbed, and ε is the relative magnitude of those perturbations.

We use a stochastic model for the environments to generate a sequence of matrices $\mathbf{A}_0, \ldots, \mathbf{A}_{T-1}$, where T is a large number. Starting from an arbitrary non-negative initial vector $\mathbf{w}(0)$, with $\left\| \mathbf{w}(0) \right\| = 1$, we then use the sequence of matrices to generate a sequence of stage distribution vectors

$$\mathbf{w}(t+1) = \frac{\mathbf{A}_t \mathbf{w}(t)}{\left\| \mathbf{A}_t \mathbf{w}(t) \right\|} \quad t = 0, \ldots, T-1 \tag{3}$$

and one-step growth rates

$$R(t) = \frac{\left\| \mathbf{A}_t \mathbf{w}(t) \right\|}{\left\| \mathbf{w}(t) \right\|} \quad t = 0, \ldots, T-1 \tag{4}$$

Similarly, starting with an arbitrary non-negative terminal vector $\mathbf{v}(T)$ with $\left\| \mathbf{v}(T) \right\| = 1$, we use the same set of matrices to generate a backwards sequence of reproductive value vectors

$$\mathbf{v}^\mathrm{T}(t-1) = \frac{\mathbf{v}^\mathrm{T}(t)\mathbf{A}_{t-1}}{\left\| \mathbf{v}^\mathrm{T}(t)\mathbf{A}_{t-1} \right\|} \quad t = T, \ldots, 1 \tag{5}$$

The stochastic growth rate after the perturbation, $\log \lambda_s (\varepsilon)$, is (Tuljapurkar, 1990)

$$\log \lambda_s(\varepsilon) = \log \lambda_s + \varepsilon \lim_{T \to \infty} \frac{1}{T} \sum_{t=0}^{T-1} \frac{\mathbf{v}^\mathrm{T}(t+1)\mathbf{C}_t\mathbf{w}(t)}{R_t \mathbf{v}^\mathrm{T}(t+1)\mathbf{w}(t+1)} \tag{6}$$

The limit that appears as the coefficient of ε on the right-hand side of (6) is the sensitivity of the stochastic growth rate, w.r.t. a series, $\mathbf{C}_t$, of perturbations. If only the (i, j) entry of $\mathbf{A}_t$ is perturbed, and the perturbation is the same at each time, then $\mathbf{C}_t$ is a constant matrix with a 1 in the (i, j) position and zeros elsewhere; i.e.

$$\mathbf{C}_t = \mathbf{e}_i \mathbf{e}_j^\mathrm{T} \tag{7}$$

where $i = 1, 2, \ldots, D$, and $j = 1, 2, \ldots, D$ if the matrix size is $D \times D$. Substituting (7) into (6) leads to Tuljapurkar's formula for the sensitivity of $\log \lambda_s$ to changes in a_{ij}:

$$\frac{\partial \log \lambda_s}{\partial a_{ij}} = \lim_{T \to \infty} \frac{1}{T} \sum_{t=0}^{T-1} \frac{v_i(t+1)w_j(t)}{R_t \mathbf{v}^\mathrm{T}(t+1)\mathbf{w}(t+1)} \tag{8}$$

The elasticity of λ_s to a_{ij} is calculated by assuming that the perturbation $c_{ij}(t)$ is proportional to $a_{ij}(t)$, so that $\mathbf{C}_t$ is now a matrix with $a_{ij}(t)$ in the (i, j) position and zeros elsewhere:

$$\mathbf{C}_t = \mathbf{e}_i \mathbf{e}_i^\mathrm{T} \mathbf{A}_t \mathbf{e}_j \mathbf{e}_j^\mathrm{T} \tag{9}$$

Substituting (9) into (6) gives the elasticity of λ_s to changes in a_{ij}:

$$\frac{\partial \log \lambda_s}{\partial \log a_{ij}} = \lim_{T \to \infty} \frac{1}{T} \sum_{t=0}^{T-1} \frac{v_i(t+1)a_{ij}(t)w_j(t)}{R_t \mathbf{v}^\mathrm{T}(t+1)\mathbf{w}(t+1)} \tag{10}$$

Instead of perturbing $\mathbf{A}_t$ for every time t, we are interested in the sensitivity of $\log \lambda_s$ or the elasticity of λ_s to changes imposed only in a specific environment or a set of environments. To express the results of environment-specific perturbations it is helpful to introduce an explicit notation for the environment. Let u_t denote the state of the environment at time t; a model behind stochasticity provides a rule specifying $\mathbf{A}_t$ as a function of u_t. Let U be the set of possible values of u_t. Let U^* be the subset of U in which perturbations occur. This could be a single environment (e.g. the year of a fire in a grassland) or a set of environments (e.g. years with minimum temperatures less than some critical value). Define the indicator variable J_t as

$$J_t = \begin{cases} 1 & u_t \in U^* \\ 0 & \text{otherwise} \end{cases}$$

The environment-specific perturbation matrix is then

$$\mathbf{C}_t = J_t \mathbf{e}_i \mathbf{e}_j^\mathrm{T} \tag{11}$$

Substituting the perturbation matrix (11) into (6) gives the environment-specific sensitivity of $\log \lambda_s$ to changes in a_{ij}

$$\frac{\partial \log \lambda_s}{\partial a_{ij}} \Big|_{U^*} = \lim_{T \to \infty} \frac{1}{T} \sum_{t=0}^{T-1} \frac{J_t v_i(t+1)w_j(t)}{R_t \mathbf{v}^\mathrm{T}(t+1)\mathbf{w}(t+1)} \tag{12}$$