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Research Article

Perturbation analysis of nonlinear matrix population models

Hal Caswell

Table of Contents

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research article

Perturbation analysis of nonlinear matrix population models

Hal Caswell [1,2]

Abstract

Perturbation analysis examines the response of a model to changes in its parameters. It is commonly applied to population growth rates calculated from linear models, but there has been no general approach to the analysis of nonlinear models. Nonlinearities in demographic models may arise due to density-dependence, frequency-dependence (in 2-sex models), feedback through the environment or the economy, and recruitment subsidy due to immigration, or from the scaling inherent in calculations of proportional population structure. This paper uses matrix calculus to derive the sensitivity and elasticity of equilibria, cycles, ratios (e.g., dependency ratios), age averages and variances, temporal averages and variances, life expectancies, and population growth rates, for both age-classified and stage-classified models. Examples are presented, applying the results to both human and non-human populations.

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1. Introduction

The goal of this paper is to present a new approach to the perturbation analysis of nonlinear population models, providing the sensitivity and elasticity of a wide range of demographic quantities.

1.1 Perturbation analysis

The output of any model depends on the values of its parameters. Perturbation analysis asks how changes in one or more parameters will affect the output. Widely used by demographers of all types, perturbation analysis is important in evolutionary biology (where the perturbations are produced by mutation or recombination), conservation, pest control, and and population policy (where the concern is with management manipulations), and sampling theory (the parameters to which a quantity is most sensitive are those that must be estimated most precisely). The results of perturbation analysis are often expressed as sensitivities (the sensitivity of y to x is the derivative dy/dx) and elasticities (the elasticity of y to x is $(x/y)dy/dx$).

The perturbation analysis of linear demographic models has focused on the sensitivity of λ or r (e.g., Keyfitz 1971, Hamilton 1966, Caswell 1978, Baudisch 2005), of the stable age or stage distribution (Coale 1957, 1972, Caswell 1982), and of life expectancy (Keyfitz 1977, Pollard 1982, Vaupel 1986, Vaupel and Romo 2003, Caswell 2006). The perturbation analysis of short-term transient dynamics has recently been presented (Caswell 2007a).

This paper presents new methods for perturbation analysis of nonlinear models, using matrix calculus. It uses those methods to analyze the sensitivity of a selection of important *nonlinear* models: density-dependent, environment-dependent, subsidized, two-sex, and proportional structure models.

Plant and animal demographers have recognized the need for sensitivity analysis of nonlinear models (e.g., Grant and Benton 2000, 2003), but until now there has been no general perturbation analysis for such models. Instead, most studies have relied on numerical calculations using difference quotients. This is a notoriously unstable method for computing derivatives, requires lots of computation, and provides no analytical insight into the structure of the sensitivities.

Yearsley et al. (2003) used an analytical approach, analyzing a model with a known characteristic equation, in which the vital rates depend only on total density. They derived the sensitivity of the equilibrium density by implicit differentiation of the characteristic equation. There exists a related but distinct set of results in evolutionary biodemography that analyze the sensitivity of the invasion exponent in density-dependent models. The sensitivity of this exponent to a parameter is the selection gradient on that parameter;

together with a measure of genetic variation it determines the rate of phenotypic change under selection. The sensitivity of the invasion exponent to parameter changes has been shown to be equal to the sensitivity of a kind of weighted average population density to those parameter changes (Takada and Nakajima 1992, 1998, Caswell et al. 2004, Caswell 2007b).

1.2 Organization of this paper

Because this paper relies on techniques from matrix calculus, I begin in Section 2. with a brief review of those techniques. Section 3. analyzes density-dependent models, introduces methods for analyzing various dependent variables, and shows how to calculate elasticities as well as sensitivities. Sections 2. and 3. are essential to the rest of the paper. The subsequent sections can, to an extent, be read independently. Section 4. analyzes environmental feedback models, Section 5. analyzes subsidized models and Section 6. considers the equilibria of proportional structures, such as arise in calculating the stable stage distribution, the dependency ratio, and means and variances of age at reproduction. Section 7. analyzes frequency-dependent two-sex models, including the sensitivity of both population structure (Section 7.1) and growth rate (Section 7.2). Finally, Section 8.1 analyzes the sensitivity of cycles in density-dependent models. For a preview of the results that will be in hand by the end of the paper, skip ahead to Table 3.

This paper contains examples from animal, plant, and human populations, because I assume at the outset that demographic studies on different species have the potential to inform each other, especially if the species differ in interesting biological properties. This perspective has a long history (e.g., Pearl et al. 1927) and enough recent examples (e.g., Wachter and Finch 1997, Carey 2003, Wachter and Bulatao 2003, Keyfitz and Caswell 2005) that it is now referred to as biodemography (Carey and Vaupel 2005).

1.3 Nonlinear models and their dynamics

Nonlinearity is defined in contrast to linearity. If $\mathbf{x}$ is an age or stage distribution vector, and if the dynamics of $\mathbf{x}$ are

$$\mathbf{x}(t+1) = f[\mathbf{x}(t)], \tag{1}$$

then the model is linear if $f(\cdot)$ is a linear function, i.e., if

$$f\left(a\mathbf{x}_1 + b\mathbf{x}_2\right) = af\left(\mathbf{x}_1\right) + bf\left(\mathbf{x}_2\right) \tag{2}$$

for any constants a and b and any vectors $\mathbf{x}_1$ and $\mathbf{x}_2$.

A nonlinear model is simply any model that is not linear. Nonlinearity in demographic models arises from four main sources: density-dependence, environmental feedback, 2-sex models, and calculation of proportional structure.

Density-dependence: arises when the per-capita vital rates are functions of the numbers or density of the population. Such effects are well documented in plants (e.g., Solbrig et al. 1988, Gillman et al. 1993, Silva Matos et al. 1999) and animals (e.g., Pennycuick 1969, Longstaff 1977, Clutton-Brock et al. 1997, Tanner 1999, Cushing et al. 2003). Density-dependence has been intensively studied in the laboratory (e.g., Pearl et al. 1927, Frank et al. 1957, Costantino and Desharnais 1991, Carey et al. 1995, Mueller and Joshi 2000, Cushing et al. 2003). It can arise from competition for food, space, or other resources, or from interactions (e.g., cannibalism) among individuals.

Simple density-dependence is less often invoked by human demographers.[3] Weiss and Smouse (1976) proposed a density-dependent matrix model, and Wood and Smouse (1982) applied it to a population of the Gainj people of Papua New Guinea. Density-dependence is included in epidemiological feedback models applied to a rural English population in the 16th and 17th centuries by Scott and Duncan (1998). The Easterlin effect (e.g., Easterlin 1961) produces density-dependence in which fertility is a function of cohort size. Analysis of the Easterlin effect has focused mostly on the possibility that it could generate cycles in births (e.g., Lee 1974, 1976, Frauenthal and Swick 1983, Wachter and Lee 1989, Chu 1998).

Environmental (or economic) feedback. Density-dependent models are often an attempt to sneak in, by the back door as it were, a feedback through the environment. A change in population size changes some aspect of the environment, which affects the vital rates, which in turn affect future population size. MacArthur (1972) showed that simple density-dependent models in ecology could be derived from to models including the feedback between the dynamics of consumers and their resources. Consumer-resource models (e.g., Hsu et al. 1977, Tilman 1982, Murdoch et al. 2003) are the basis for the models of food chains and food webs that underlie models of global biogeochemistry (Fennel and Neumann 2004).

Feedback models are often invoked in human demography, with the feedback operating through the economy (Lee 1986, 1987, Chu 1998). An interesting aspect of these approaches is the possibility that, if larger populations support more robust economies, the feedback could be positive instead of negative (Lee 1986, Cohen 1995, Appendix 6). An exciting combination of ecological and economic feedback appears in the food ratio model recently proposed by Lee and Tuljapurkar (2007).

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[3] Lee (1987) reviewed the situation and said "…we might say that human demography is all about Leslie matrices and the determinants of unconstrained growth in linear models, whereas animal population studies are all about Malthusian equilibrium through density dependence in nonlinear models …". He admits that this is an exaggeration, and there clearly are nonlinear concerns in the field (Bonneuil 1994), but a non-exhaustive survey finds no mention of density-dependence in several contemporary human demography texts (e.g., Hinde 1998, Preston et al. 2001, Keyfitz and Caswell 2005).

Two-sex models. To the extent that both males and females are required for reproduction (and, in the bigger scheme of things, this is not always so), demography is nonlinear because the marriage function or mating function cannot satisfy (2). Nonlinear two-sex models have a long tradition in human demography (see reviews in Keyfitz 1972b, Pollard 1977) and have been applied in ecology (e.g., Lindström and Kokko 1998, Legendre et al. 1999, Kokko and Rankin 2006, Lenz et al. 2007). Their mathematical properties have been investigated by e.g, Caswell and Weeks (1986), Chung (1994), Ianelli et al. (2005), and in a very abstract setting by Nussbaum (1988, 1989).

In their most basic form, two-sex models differ from density-dependent models in that the vital rates depend only on the relative, not the absolute, abundances of stages in the population (they are sometimes called frequency-dependent for this reason). This has important implications for their dynamics.

Models for proportional population structure. Even when the dynamics of abundance are linear, the dynamics of *proportional* population structure are nonlinear (e.g., Tuljapurkar 1997). This leads to some useful results on the sensitivity of the stable age or stage distribution and the reproductive value.

Linear models lead to exponential growth and convergence to a stable structure. Much of the analysis of linear models focuses on the population growth rate λ or $r = \log \lambda$. Nonlinear models do not usually lead to exponential growth (frequency-dependent two-sex models are an exception). Instead, their trajectories converge to an attractor. The attractor may be an equilibrium point, a cycle, an invariant loop (yielding quasiperiodic dynamics), or a strange attractor (yielding chaotic dynamics); see Cushing (1998) or Caswell (2001, Chapter 16) for a detailed discussion.

In this paper, I will analyze the sensitivity and elasticity of equilibria and cycles. Because the dynamic models considered here are discrete, solutions always exist and are unique. The nature of number of the attractors depends on the specific model. Perturbation analysis always considers perturbations of *something*, so the equilibria or cycles must be found before their perturbation properties can be analyzed.

A note on notation. Matrices are denoted by upper case bold symbols (e.g., $\mathbf{A}$), vectors (usually) by lower case bold symbols ($\mathbf{n}$); a_{ij} is the (i, j) entry of the matrix $\mathbf{A}$, n_i is the ith entry of the vector $\mathbf{n}$, and $\mathbf{n}^{\mathsf{T}}$ is the transpose of $\mathbf{n}$. The exceptions to these conventions are noted when they occur. Logarithms are natural. The vector norm $\|\mathbf{x}\|$ is, unless noted otherwise, the 1-norm. In addition to the ordinary matrix product, the Kronecker product $\mathbf{A} \otimes \mathbf{B}$ and the Hadamard product $\mathbf{A} \circ \mathbf{B}$ will appear. The symbol $\operatorname{diag}(\mathbf{x})$ denotes the square matrix with $\mathbf{x}$ on the diagonal and zeros elsewhere. The symbol $\mathbf{e}$ denotes a vector of 1s; the vector $\mathbf{e}_i$ is a vector with 1 in the ith entry and zeros elsewhere. The identity matrix is $\mathbf{I}$; sometimes its dimension will be indicated by a subscript, as in $\mathbf{I}_s$ for the $s \times s$ identity. The end of an example is denoted by the symbol $\diamondsuit$.

2. Matrix calculus

Matrix calculus permits the consistent differentiation of scalar-, vector-, and matrix-valued functions of scalar, vector, or matrix arguments. Because this method is not well-known in either ecology (but see Caswell 2006, 2007a) or demography (but see Willekens 1977, Ekamper and Keilman 1993 for related approaches), the next section presents a brief statement of the essential results. More detail can be found in Caswell (2007a). There exist several conventions for matrix calculus, differing in their arrangements of the matrix and vector entries. The best is that of Magnus and Neudecker (1985, 1988); it is called the vector-rearrangement method in the review paper of Nel (1980).

If x and y are scalars, the derivative of y with respect to x is the familiar derivative dy/dx. If $\mathbf{y}$ is a $n \times 1$ vector and x a scalar, the derivative of $\mathbf{y}$ with respect to x is the $n \times 1$ vector

$$\frac{d\mathbf{y}}{dx} = \left(\begin{array}{c} \dfrac{dy_1}{dx} \\ \vdots \\ \dfrac{dy_n}{dx} \end{array} \right). \tag{3}$$

If y is a scalar and $\mathbf{x}$ is a $m \times 1$ vector, the derivative of y with respect to $\mathbf{x}$ is the $1 \times m$ gradient vector

$$\frac{dy}{d\mathbf{x}^{\mathsf{T}}} = \left(\begin{array}{ccc} \dfrac{\partial y}{\partial x_1} & \cdots & \dfrac{\partial y}{\partial x_m} \end{array} \right) \tag{4}$$

Note the orientation of $d\mathbf{y}/dx$ as a column vector and $dy/d\mathbf{x}^{\mathsf{T}}$ as a row vector.

If $\mathbf{y}$ is a $n \times 1$ vector and $\mathbf{x}$ a $m \times 1$ vector, the derivative of $\mathbf{y}$ with respect to $\mathbf{x}$ is the $n \times m$ Jacobian matrix

$$\frac{d\mathbf{y}}{d\mathbf{x}^{\mathsf{T}}} = \left(\frac{dy_i}{dx_j} \right). \tag{5}$$

Derivatives involving matrices are written by transforming the matrices into vectors using the vec operator (which stacks the columns of the matrix into a column vector), and then applying the rules for vector differentiation. Thus, the derivative of the $m \times n$ matrix $\mathbf{Y}$ with respect to the $p \times q$ matrix $\mathbf{X}$ is the $mn \times pq$ matrix

$$\frac{d\mathrm{vec}\,\mathbf{Y}}{d\mathrm{vec}^{\mathsf{T}}\mathbf{X}}. \tag{6}$$

For notational convenience, I will write $\text{vec}^{\mathsf{T}}\mathbf{X}$ for $(\text{vec}\,\mathbf{X})^{\mathsf{T}}$.

These definitions (unlike some alternatives; see Magnus and Neudecker 1985) lead to the familiar chain rule. If $\mathbf{Y}$ is a function of $\mathbf{X}$ and $\mathbf{X}$ is a function of $\mathbf{Z}$, then

$$\frac{d\text{vec}\,\mathbf{Y}}{d\text{vec}^{\mathsf{T}}\mathbf{Z}} = \frac{d\text{vec}\,\mathbf{Y}}{d\text{vec}^{\mathsf{T}}\mathbf{X}}\,\frac{d\text{vec}\,\mathbf{X}}{d\text{vec}^{\mathsf{T}}\mathbf{Z}}. \tag{7}$$

The derivatives of matrices are constructed by forming the differentials of the expressions involving the matrices. The differential of a matrix (or vector) is the matrix (or vector) of differentials of the elements; i.e.,

$$d\mathbf{X} = \left(\; dx_{ij} \;\right). \tag{8}$$

If, for vectors $\mathbf{x}$ and $\mathbf{y}$ and some matrix $\mathbf{Q}$, it can be shown that

$$d\mathbf{y} = \mathbf{Q}d\mathbf{x} \tag{9}$$

then

$$\frac{d\mathbf{y}}{d\mathbf{x}^{\mathsf{T}}} = \mathbf{Q}. \tag{10}$$

(the "first identification theorem" of Magnus and Neudecker (1985); see also Neudecker 1969).

The combination of the chain rule and the identification theorem permits more complicated expressions involving differentials to be turned into derivatives with respect to an arbitrary vector, say $\mathbf{u}$. If

$$d\mathbf{y} = \mathbf{Q}d\mathbf{x} + \mathbf{R}d\mathbf{z} \tag{11}$$

then

$$\frac{d\mathbf{y}}{d\mathbf{u}^{\mathsf{T}}} = \mathbf{Q}\frac{d\mathbf{x}}{d\mathbf{u}^{\mathsf{T}}} + \mathbf{R}\frac{d\mathbf{z}}{d\mathbf{u}^{\mathsf{T}}} \tag{12}$$

for any $\mathbf{u}$.

We will make extensive use the Kronecker product, defined as

$$\mathbf{A} \otimes \mathbf{B} = \begin{pmatrix} a_{11}\mathbf{B} & a_{12}\mathbf{B} & \cdots \\ a_{21}\mathbf{B} & a_{22}\mathbf{B} & \cdots \\ \vdots & \vdots & \ddots \end{pmatrix}. \tag{13}$$

The vec operator and the Kronecker product are related (Roth 1934); if

$$\mathbf{Y} = \mathbf{ABC} \tag{14}$$

then

$$\text{vec}\,\mathbf{Y} = (\mathbf{C}^{\mathsf{T}} \otimes \mathbf{A})\,\text{vec}\,\mathbf{B}. \tag{15}$$

3. Density-dependent models

We begin with the basic density-dependent model, written as

$$\mathbf{n}(t+1) = \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t)]\ \mathbf{n}(t) \tag{16}$$

where $\mathbf{n}(t)$ is a population vector of dimension $s \times 1$ and $\mathbf{A}$ is a population projection matrix of dimension $s \times s$. The matrix $\mathbf{A}$ depends on a $p \times 1$ vector $\boldsymbol{\theta}$ of parameters as well as on the current population vector $\mathbf{n}(t)$.

3.1 Sensitivity of equilibrium

An equilibrium of (16) satisfies

$$\hat{\mathbf{n}} = \mathbf{A}\left[\boldsymbol{\theta}, \hat{\mathbf{n}}\right] \hat{\mathbf{n}}. \tag{17}$$

Our goal is to find the derivatives of all the entries of $\hat{\mathbf{n}}$ with respect to all of the parameters in $\boldsymbol{\theta}$; these are the entries of the $s \times p$ matrix

$$\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}}.$$

We begin by taking the differential of both sides of (17):

$$d\hat{\mathbf{n}} = (d\mathbf{A})\hat{\mathbf{n}} + \mathbf{A}(d\hat{\mathbf{n}}). \tag{18}$$

Rewrite this as

$$d\hat{\mathbf{n}} = \mathbf{I}_s(d\mathbf{A})\hat{\mathbf{n}} + \mathbf{A}(d\hat{\mathbf{n}}), \tag{19}$$

where $\mathbf{I}_s$ is an identity matrix of dimension s. Next apply the vec operator to both sides, remembering that since $\hat{\mathbf{n}}$ is a column vector, $\text{vec}\,\hat{\mathbf{n}} = \hat{\mathbf{n}}$, and apply Roth's theorem, to obtain

$$d\hat{\mathbf{n}} = \left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right) d\text{vec}\,\mathbf{A} + \mathbf{A}d\hat{\mathbf{n}}. \tag{20}$$

However, $\mathbf{A}$ is a function of both $\boldsymbol{\theta}$ and $\hat{\mathbf{n}}$, so

$$d\text{vec}\,\mathbf{A} = \frac{\partial \text{vec}\,\mathbf{A}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} d\boldsymbol{\theta} + \frac{\partial \text{vec}\,\mathbf{A}}{\partial \mathbf{n}^{\mathsf{T}}} d\hat{\mathbf{n}}. \tag{21}$$

Substituting (21) into (20) and applying the chain rule leads to[4]

$$\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right) \left(\frac{\partial \mathrm{vec}\, \mathbf{A}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} + \frac{\partial \mathrm{vec}\, \mathbf{A}}{\partial \mathbf{n}^{\mathsf{T}}} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} \right) + \mathbf{A} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}}. \tag{22}$$

Finally, solve (22) for $d\hat{\mathbf{n}}/d\boldsymbol{\theta}^{\mathsf{T}}$ to obtain

$$\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\mathbf{I}_s - \mathbf{A} - \left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right) \frac{\partial \mathrm{vec}\, \mathbf{A}}{\partial \mathbf{n}^{\mathsf{T}}} \right)^{-1} \left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right) \frac{\partial \mathrm{vec}\, \mathbf{A}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} \tag{23}$$

where $\mathbf{A}$, $\partial \mathrm{vec}\, \mathbf{A}/\partial \boldsymbol{\theta}^{\mathsf{T}}$, and $\partial \mathrm{vec}\, \mathbf{A}/\partial \hat{\mathbf{n}}^{\mathsf{T}}$ are evaluated at $\hat{\mathbf{n}}$.

The following example, applying (23) to a simple model, shows the basic steps and output of the analysis.

Example 1 (A simple two-stage model) The most basic distinction in the life cycle of many organisms is between non-reproducing juveniles and reproducing adults. A model based on these stages (Neubert and Caswell 2000) is parameterized by the juvenile survival σ_1, the adult survival σ_2, the growth or maturation probability γ (the expected time to maturity is $1/\gamma$), and the adult fertility f. The projection matrix is

$$\mathbf{A} = \begin{pmatrix} \sigma_1(1-\gamma) & f \\ \sigma_1\gamma & \sigma_2 \end{pmatrix}. \tag{24}$$

Any of the vital rates could be density-dependent; here we suppose that juvenile survival σ_1 depends on total density:

$$\sigma_1(\mathbf{n}) = \tilde{\sigma} \exp(-\mathbf{e}^{\mathsf{T}}\mathbf{n}); \tag{25}$$

where $\mathbf{e}$ is a vector of ones.

Define the parameter vector as $\boldsymbol{\theta} = \begin{pmatrix} f & \gamma & \tilde{\sigma} & \sigma_2 \end{pmatrix}^{\mathsf{T}}$. To apply (23) requires the derivatives of $\mathbf{A}[\boldsymbol{\theta}, \mathbf{n}]$ with respect to $\boldsymbol{\theta}$ and with respect to $\mathbf{n}$. These are

$$\frac{d\mathrm{vec}\, \mathbf{A}}{df} = \mathrm{vec} \begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix} \tag{26}$$

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[4] It is reassuring to check that the dimensions of all these quantities are compatible:

$$\underbrace{\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}}}_{s\times p} = \underbrace{\left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right)}_{s\times s^2} \left(\underbrace{\frac{\partial \mathrm{vec}\, \mathbf{A}}{\partial \boldsymbol{\theta}^{\mathsf{T}}}}_{s^2\times p} + \underbrace{\frac{\partial \mathrm{vec}\, \mathbf{A}}{\partial \mathbf{n}^{\mathsf{T}}}}_{s^2\times s} \underbrace{\frac{\partial\hat{\mathbf{n}}}{\partial \boldsymbol{\theta}^{\mathsf{T}}}}_{s\times p} \right) + \underbrace{\mathbf{A}}_{s\times s} \underbrace{\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}}}_{s\times p}.$$

$$\frac{d\text{vec}\,\mathbf{A}}{d\gamma} = \text{vec}\begin{pmatrix} -\sigma_1(\mathbf{n}) & 0 \\ \sigma_1(\mathbf{n}) & 0 \end{pmatrix} \tag{27}$$

$$\frac{d\text{vec}\,\mathbf{A}}{d\tilde{\sigma}} = \text{vec}\begin{pmatrix} (1-\gamma)\exp(-\mathbf{e}^{\mathsf{T}}\mathbf{n}) & 0 \\ \gamma\exp(-\mathbf{e}^{\mathsf{T}}\mathbf{n}) & 0 \end{pmatrix} \tag{28}$$

$$\frac{d\text{vec}\,\mathbf{A}}{d\sigma_2} = \text{vec}\begin{pmatrix} 0 & 0 \\ 0 & 1 \end{pmatrix} \tag{29}$$

$$\frac{d\text{vec}\,\mathbf{A}}{dn_1} = \frac{d\text{vec}\,\mathbf{A}}{dn_2} = \text{vec}\begin{pmatrix} -\sigma_1(\mathbf{n})(1-\gamma) & 0 \\ -\sigma_1(\mathbf{n})\gamma & 0 \end{pmatrix}. \tag{30}$$

The derivative of $\mathbf{A}$ with respect to the $\boldsymbol{\theta}$ is the 4×4 matrix

$$\frac{\partial\text{vec}\,\mathbf{A}}{\partial\boldsymbol{\theta}^{\mathsf{T}}} = \begin{pmatrix} 0 & -\sigma_1(\mathbf{n}) & (1-\gamma)\exp(-\mathbf{e}^{\mathsf{T}}\mathbf{n}) & 0 \\ 0 & \sigma_1(\mathbf{n}) & \gamma\exp(-\mathbf{e}^{\mathsf{T}}\mathbf{n}) & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}, \tag{31}$$

where each column corresponds to an entry of $\boldsymbol{\theta}$ and each row to an element of vec $\mathbf{A}$. The derivative of $\mathbf{A}$ with respect to $\mathbf{n}$ is

$$\frac{\partial\text{vec}\,\mathbf{A}}{\partial\mathbf{n}^{\mathsf{T}}} = \begin{pmatrix} -\sigma_1(\mathbf{n})(1-\gamma) & -\sigma_1(\mathbf{n})(1-\gamma) \\ -\sigma_1(\mathbf{n})\gamma & -\sigma_1(\mathbf{n})\gamma \\ 0 & 0 \\ 0 & 0 \end{pmatrix}. \tag{32}$$

Each column corresponds to an entry of $\mathbf{n}$ and each row to an element of vec $\mathbf{A}$.

Using some arbitrary parameter values (not unreasonable for humans or other large mammals)

$$\begin{aligned} f &= 0.25 \\ \gamma &= 1/15 \\ \tilde{\sigma} &= 0.98 \\ \sigma_2 &= 0.95 \end{aligned}$$

leads to an equilibrium population

$$\hat{\mathbf{n}} = \begin{pmatrix} 0.1053 \\ 0.1109 \end{pmatrix}, \tag{33}$$

obtained by iterating the model to convergence.

Evaluating (31) and (32) at $\hat{\mathbf{n}}$ and substituting into (23) gives the sensitivity of $\hat{\mathbf{n}}$ to $\boldsymbol{\theta}$,

$$\begin{aligned} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}} &= \left(\begin{array}{cccc} \frac{d\hat{\mathbf{n}}}{df} & \frac{d\hat{\mathbf{n}}}{d\gamma} & \frac{d\hat{\mathbf{n}}}{d\tilde{\sigma}} & \frac{d\hat{\mathbf{n}}}{d\sigma_2} \end{array} \right) \\ &= \left(\begin{array}{cccc} 0.57 & 0.90 & 0.50 & 1.77 \\ 0.48 & 2.26 & 0.52 & 3.49 \end{array} \right) \end{aligned} \tag{34}$$

Each column is the derivative of the vector $\hat{\mathbf{n}}$ to one of the parameters. With these parameters, the equilibrium population is very sensitive to changes in adult survival. Increases in the maturation rate increase adult density much more than juvenile density. Changes in fertility or in juvenile survival have about equal effects on juvenile and adult density.

These patterns reflect the life history, although comparative study of this dependence has scarcely begun. For example, if the demographic parameters were more appropriate for an insect, say with high fertility ($f = 70$), rapid maturation ($\gamma = 0.9$), and low juvenile survival ($\tilde{\sigma} = 0.1$), and in which most adults die after reproducing once ($\sigma_2 = 0.01$), then the equilibrium would become

$$\hat{\mathbf{n}} = \left(\begin{array}{c} 1.826 \\ 0.026 \end{array} \right) \tag{35}$$

with sensitivities

$$\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\begin{array}{cccc} 0.01 & 1.08 & 9.86 & 0.99 \\ -0.0002 & 0.02 & 0.14 & 0.01 \end{array} \right). \tag{36}$$

In this life history, increases in fertility have very small effects on the equilibrium population, and the effect of increased fertility on adult density is slightly negative. Changes in the maturation rate or in juvenile or adult survival have much larger impacts on juvenile density than on adult density. $\diamondsuit$

3.2 Dependent variables: beyond $\hat{\mathbf{n}}$

The equilibrium vector $\hat{\mathbf{n}}$ is usually not the only dependent variable of interest. If we write $\mathbf{m} = \mathbf{m}(\mathbf{n})$ for any vector- or scalar-valued transformation of $\mathbf{n}$, then the sensitivity of $\mathbf{m}$ is just

$$\frac{d\hat{\mathbf{m}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \frac{d\hat{\mathbf{m}}}{d\mathbf{n}^{\mathsf{T}}} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}}. \tag{37}$$

The possibilities for dependent variables are, roughly speaking, limited only by one's imagination. The following is a list of examples.

1. Weighted population density. Let $\mathbf{c} \geq 0$ be a vector of weights. Weighted population density is then $N(t) = \mathbf{c}^{\mathsf{T}}\mathbf{n}(t)$. Examples include total density ($\mathbf{c} = \mathbf{e}$), the density of a subset of stages ($c_i = 1$ for stages to be counted; $c_i = 0$ otherwise), biomass (c_i is the biomass of stage i), basal area, metabolic rate, etc. The sensitivity of $\hat{N}$ is
$$\frac{d\hat{N}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \mathbf{c}^{\mathsf{T}} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}}. \tag{38}$$
2. Ratios, measuring the relative abundances of different stages. Let
$$R(t) = \frac{\mathbf{a}^{\mathsf{T}}\mathbf{n}(t)}{\mathbf{b}^{\mathsf{T}}\mathbf{n}(t)} \tag{39}$$
where $\mathbf{a} \geq 0$ and $\mathbf{b} \geq 0$ are weight vectors. Examples include the dependency ratio (in human populations, the ratio of the individuals below 15 or above 65 to those between 15 and 65; see Section 6.2), the sex ratio, and the ratio of juveniles to adults (used in wildlife management; see Skalski et al. 2005). Differentiating (39) gives
$$\frac{d\hat{R}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\frac{\mathbf{b}^{\mathsf{T}}\hat{\mathbf{n}}\mathbf{a}^{\mathsf{T}} - \mathbf{a}^{\mathsf{T}}\hat{\mathbf{n}}\mathbf{b}^{\mathsf{T}}}{\left(\mathbf{b}^{\mathsf{T}}\hat{\mathbf{n}}\right)^2} \right) \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}}. \tag{40}$$
3. Age or stage averages. These include quantities such as the mean age or size in the stable population or at equilibrium and the mean age at reproduction in the stable population. Their perturbation analysis is presented in Section 6.3.
4. Properties of cycles. Nonlinear models may produce population cycles. Attention may focus on the mean, the variance, or higher moments of the population vector or of some scalar measure of density, over such cycles. The sensitivity of these moments is explored in Section 8.1.

3.3 Elasticity analysis

The derivatives in the matrix $d\hat{\mathbf{n}}/d\boldsymbol{\theta}^{\mathsf{T}}$ give the results of small additive perturbations of the parameters. It is often useful to study the elasticities, which give the proportional result of small proportional perturbations. The elasticity of $\hat{n}_i$ to θ_j is
$$\frac{\theta_j}{\hat{n}_i} \frac{d\hat{n}_i}{d\theta_j}. \tag{41}$$

Creating a matrix of these elasticities requires multiplying column j of $d\hat{\mathbf{n}}/d\boldsymbol{\theta}^{\mathsf{T}}$ by θ_j and dividing row i by $\hat{n}_i$. This is just
$$\text{diag}\ (\hat{\mathbf{n}})^{-1}\ \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}}\ \text{diag}\,(\boldsymbol{\theta}), \tag{42}$$

The elasticity of any other (scalar- or vector-valued) dependent variable $f(\hat{\mathbf{n}})$ is given by

$$\operatorname{diag}\left(f(\hat{\mathbf{n}})\right)^{-1}\frac{df(\hat{\mathbf{n}})}{d\boldsymbol{\theta}^{\mathsf{T}}}\operatorname{diag}(\boldsymbol{\theta}). \tag{43}$$

Example 2 (Metabolic population size in *Tribolium*) Flour beetles of the genus *Tribolium* have been the subject of a long series of experiments on nonlinear population dynamics (reviewed by Cushing et al. 2003). *Tribolium* lives in stored flour. In addition to feeding on the flour, adults and larvae cannibalize eggs, and adults cannibalize pupae. These interactions are the source of nonlinearity in the demography, and are captured in a three-stage (larvae, pupae, and adults) model. The projection matrix is

$$\mathbf{A}[\boldsymbol{\theta},\mathbf{n}] = \begin{pmatrix} 0 & 0 & b\exp(-c_{el}n_1 - c_{ea}n_3) \\ 1-\mu_l & 0 & 0 \\ 0 & \exp(-c_{pa}n_3) & 1-\mu_a \end{pmatrix} \tag{44}$$

where b is the clutch size, c_{ea}, c_{el}, and c_{pa} are rates of cannibalism (of eggs by adults, eggs by larvae, and pupae by adults, respectively), and μ_l and μ_a are larval and adult mortalities (the mortality of pupae, in these laboratory conditions, is effectively zero). Parameter values from an experiment reported by Costantino et al. (1997)

$$\begin{aligned} b &= 6.598 \\ c_{ea} &= 1.155\times 10^{-2} \\ c_{el} &= 1.209\times 10^{-2} \\ c_{pa} &= 4.7\times 10^{-3} \\ \mu_a &= 7.729\times 10^{-3} \\ \mu_l &= 2.055\times 10^{-1} \end{aligned}$$

produce a stable equilibrium

$$\hat{\mathbf{n}} = \begin{pmatrix} 22.6 \\ 18.0 \\ 385.2 \end{pmatrix}. \tag{45}$$ ◇

The sensitivity of $\hat{\mathbf{n}}$ is calculated using (23). However, the damage caused by *Tribolium* as a pest of stored grain products might well depend more on metabolism than on numbers. Emekci et al. (2001) estimated the metabolic rates of larvae, pupae, and adults as 9, 1, and 4.5 μl CO$_2$ h^{-1}, respectively. We define the metabolic population size as $N_m(t) = \mathbf{c}^{\mathsf{T}}\mathbf{n}(t)$ where $\mathbf{c}^{\mathsf{T}} = \begin{pmatrix} 9 & 1 & 4.5 \end{pmatrix}$, and calculate the sensitivity and elasticity of $\hat{N}_m$ using (42) and (38).

Figure 1 shows the elasticity of $\hat{\mathbf{n}}$ and $\hat{N}_m$ to each of the parameters. The elasticities are diverse and perhaps counterintuitive. Increases in fecundity increase the equilibrium density of all stages; increases in the cannibalism of eggs by adults reduces the density of all stages. But increased cannibalism of pupae by adults increases the density of larvae and pupae, as does an increase in the mortality of adults.

When the stages are weighted by their metabolic rate, the elasticity of $\hat{N}_m$ to fecundity is positive, but the elasticities to all the other paramters (cannibalism rates and mortalities) are negative. The positive effects of c_{pa} and μ_a on $\hat{\mathbf{n}}$ disappear when the stages are weighted according to metabolism.

4. Environmental feedback models

Environmental (or economic) feedback models write the vital rates as functions of some environmental variable, which in turn depends on population density. Feedback models may be static or dynamic. In static feedback models, the environment depends only on current conditions, with no inherent dynamics of its own. In dynamic feedback models, the environment can have dynamics as complicated as those of the population (e.g., if the environmental variable was the abundance of a prey species, affecting the dynamics of a predator species). The sensitivity analysis of dynamic feedback models is given in Section 8.4.

A static feedback model can be written

$$\mathbf{n}(t+1) = \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t), \mathbf{g}(t)]\ \mathbf{n}(t) \tag{46}$$

$$\mathbf{g}(t) = \mathbf{g}[\boldsymbol{\theta}, \mathbf{n}(t)] \tag{47}$$

where $\mathbf{g}(t)$ is a vector (of dimension $q \times 1$) describing the ecological or economic aspects of the environment on which the vital rates depend. As written here, the model admits the possibility that the vital rates in $\mathbf{A}$ might depend directly on $\mathbf{n}$ as well as on the environment.

At equilibrium

$$\hat{\mathbf{n}} = \mathbf{A}[\boldsymbol{\theta}, \hat{\mathbf{n}}, \hat{\mathbf{g}}]\hat{\mathbf{n}} \tag{48}$$

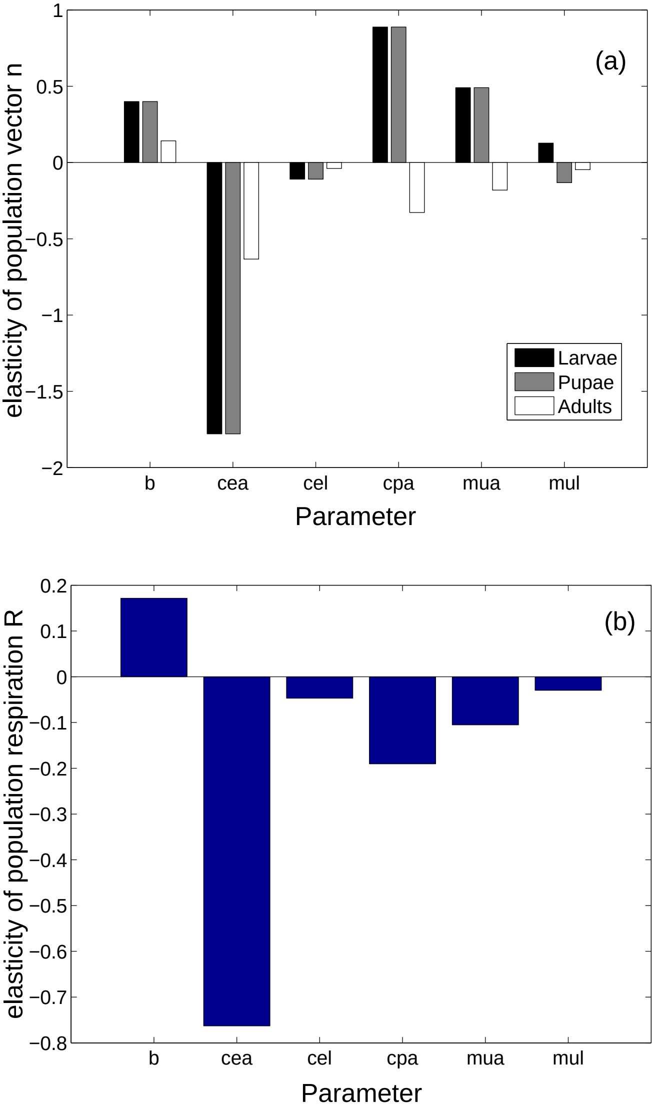
$$\hat{\mathbf{g}} = \mathbf{g}[\boldsymbol{\theta}, \hat{\mathbf{g}}]. \tag{49}$$

Differentiating these expressions gives

$$d\hat{\mathbf{n}} = \mathbf{A}(d\hat{\mathbf{n}}) + (d\mathbf{A})\hat{\mathbf{n}} \tag{50}$$

$$d\hat{\mathbf{g}} = \frac{\partial \hat{\mathbf{g}}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} d\boldsymbol{\theta} + \frac{\partial \hat{\mathbf{g}}}{\partial \mathbf{n}} d\hat{\mathbf{n}}. \tag{51}$$

Figure 1: Sensitivity analysis of equilibrium for the flour beetle *Tribolium* in Example 2. (a) The elasticity of the equilibrium $\hat{\mathrm{n}}$ to the parameters (see Example 2 for definitions). (b) The elasticity of the equilibrium population respiration rate $\hat{N}_m$ to the parameters



Applying the vec operator to (50) and expanding $d\text{vec}\,\mathbf{A}$ bives

$$d\hat{\mathbf{n}} = \left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right) \left[\frac{\partial \text{vec}\,\mathbf{A}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} d\boldsymbol{\theta} + \frac{\partial \mathbf{A}}{\partial \mathbf{g}^{\mathsf{T}}} d\hat{\mathbf{g}} \right] + \mathbf{A} d\hat{\mathbf{n}}. \tag{52}$$

Substituting (51) for $d\hat{\mathbf{g}}$ and rearranging gives

$$\begin{aligned} d\hat{\mathbf{n}} \quad = \quad & \left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right) \left[\frac{\partial \text{vec}\,\mathbf{A}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} + \frac{\partial \text{vec}\,\mathbf{A}}{\partial \mathbf{g}^{\mathsf{T}}} \frac{\partial \hat{\mathbf{g}}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} \right] d\boldsymbol{\theta} \\ & + \left[\mathbf{A} + \left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right) \frac{\partial \text{vec}\,\mathbf{A}}{\partial \mathbf{g}^{\mathsf{T}}} \frac{\partial \hat{\mathbf{g}}}{\partial \mathbf{n}^{\mathsf{T}}} \right] d\hat{\mathbf{n}}. \end{aligned} \tag{53}$$

Solving for $d\hat{\mathbf{n}}$ and applying the identification theorem yields

$$\begin{aligned} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} \quad = \quad & \left[\mathbf{I}_s - \mathbf{A} - \left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right) \frac{\partial \text{vec}\,\mathbf{A}}{\partial \mathbf{g}^{\mathsf{T}}} \frac{\partial \hat{\mathbf{g}}}{\partial \mathbf{n}^{\mathsf{T}}} \right]^{-1} \\ & \times \left(\hat{\mathbf{n}} \otimes \mathbf{I}_s\right) \left[\frac{\partial \text{vec}\,\mathbf{A}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} + \frac{\partial \text{vec}\,\mathbf{A}}{\partial \mathbf{g}^{\mathsf{T}}} \frac{\partial \hat{\mathbf{g}}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} \right]. \end{aligned} \tag{54}$$

$\mathbf{A}$, $\mathbf{g}$, and all derivatives are evaluated at $(\hat{\mathbf{n}}, \hat{\mathbf{g}})$. A comparison of (54) with (23) shows that including the feedback mechanism has simply written $d\text{vec}\,\mathbf{A}/d\mathbf{n}^{\mathsf{T}}$ and $d\text{vec}\,\mathbf{A}/d\boldsymbol{\theta}^{\mathsf{T}}$ in terms of $\mathbf{g}$ using the chain rule.

The environmental variable $\mathbf{g}$ may be of interest in its own right (e.g., in the food ratio model of Lee and Tuljapurkar (2007), in which it is a measure of well-being, measured in terms of food per individual). The sensitivity of $\hat{\mathbf{g}}$ at equilibrium is

$$\frac{d\hat{\mathbf{g}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \frac{\partial \hat{\mathbf{g}}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} + \frac{\partial \hat{\mathbf{g}}}{\partial \mathbf{n}} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} \tag{55}$$

where $d\hat{\mathbf{g}}/d\boldsymbol{\theta}^{\mathsf{T}}$ is given by (51) and $(d\hat{\mathbf{n}}/d\boldsymbol{\theta}^{\mathsf{T}})$ by (54).

5. Subsidized populations and competition for space

A subsidized population is one in which new individuals are recruited from elsewhere rather than (or in addition to) being generated by local reproduction. Subsidy is important in many plant and animal populations, especially of benthic marine invertebrates and fish. Many of these species produce planktonic larvae that may disperse very long distances (Scheltema 1971) before they settle and become sessile for the rest of their lives. Thus a significant part—maybe even all—of the recruitment at any location is independent of local fertility (e.g., Almany et al. 2007). Subsidized models have been used to analyze conservation programs in which captive-reared animals are released into a wild or re-established population (Sarrazin and Legendre 2000). They have been applied to the demography of human organizations (e.g., schools, businesses, learned societies; Gani 1963, Pollard 1968, Bartholomew 1982). Wilson (2004) reported that, as of 2004, more than half of humans lived in countries or regions in which fertility was below replacement level. Immigration into such countries is form of subsidy that can be explored with these models.

In the simplest subsidized models, both local demography and recruitment are density-independent. Alternatively, recruitment may depend on some resource (e.g., space) whose availability depends on the local population, or the local demography after settlement is density-dependent. All three cases can lead to equilibrium populations.

5.1 Density-independent subsidized populations

The model,

$$\mathbf{n}(t+1) = \mathbf{A}[\boldsymbol{\theta}]\mathbf{n}(t) + \mathbf{b}[\boldsymbol{\theta}], \tag{56}$$

includes a subsidy vector $\mathbf{b}$ giving the input of individuals to the population.[5] The parameters $\boldsymbol{\theta}$ may affect $\mathbf{A}$ or $\mathbf{b}$, or both. If the fertility appearing in $\mathbf{A}$ is below replacement, so that $\lambda < 1$, then a stable equilibrium $\hat{\mathbf{n}}$ exists.[6] This equilibrium satisfies

$$\begin{aligned} \hat{\mathbf{n}} &= \mathbf{A}\hat{\mathbf{n}} + \mathbf{b} && (57) \\ &= (\mathbf{I}_s - \mathbf{A})^{-1}\,\mathbf{b}. && (58) \end{aligned}$$

Differentiating (57) and applying the vec operator yields

$$d\hat{\mathbf{n}} = \left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right) d\text{vec}\,\mathbf{A} + \mathbf{A}\left(d\hat{\mathbf{n}}\right) + d\mathbf{b} \tag{59}$$

Solving for $d\hat{\mathbf{n}}$ and applying the chain rule gives the sensitivity of the equilibrium,

$$\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = (\mathbf{I}_s - \mathbf{A})^{-1}\left\{\left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right)\frac{d\text{vec}\,\mathbf{A}}{d\boldsymbol{\theta}^{\mathsf{T}}} + \frac{d\mathbf{b}}{d\boldsymbol{\theta}^{\mathsf{T}}}\right\}. \tag{60}$$

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[5] The same model could describe harvest if $\mathbf{b} \leq 0$ (e.g, Hauser et al. 2006). This form of harvest produces unstable equilibria, and is not considered further here.

[6] If $\lambda > 1$, the population grows exponentially and the subsidy eventually becomes negligible. The equilibrium in this case is non-positive (and hence biologically irrelevant) and unstable. If $\lambda = 1$ then the population would remain constant in the absence of subsidy; any non-zero subsidy will then lead to unbounded population growth.

Example 3 (The Australian Academy of Sciences) Most human organizations are subsidized; recruits (new students in a school, new employees in a company) come from outside, not from local reproduction. In an early example of a subsidized population model, Pollard (1968) analyzed the age structure of the Australian Academy of Sciences, recruitment to which takes place by election.[7] The Academy had been founded in 1954, and between 1955 and 1963 had elected about 6 new Fellows each year, with an age distribution (Pollard 1968, Table 2) given by

Age	Percent
30–34	0.0
35–39	12.2
40–44	24.5
45–49	26.5
50–54	20.4
55–59	4.1
60–64	10.2
65–69	2.0

$\diamondsuit$

Pollard interpolated this distribution to 1-year age classes, and combined it with a 1954 life table for Australian males[8] to construct a model of the form (56) and calculated the equilibrium size and age composition of the Academy. Here, I have used the male life table for Australia 1953–1955 in Keyfitz and Flieger (1968, p. 558) to construct an age-classified matrix $\mathbf{A}$ with age-specific probabilities of survival P_i on its subdiagonal and zeros elsewhere. Were these vital rates and the age distribution of the subsidy vector to remain constant, the Academy would reach an equilibrium size of $\hat{N} = 149.5$ with an age distribution $\hat{\mathbf{n}}$ shown in Figure 2a.

As parameters, consider the age-specific mortality rates $\mu_i = -\log P_i$, and define the parameter vector $\boldsymbol{\theta} = \begin{pmatrix} \mu_1 & \mu_2 & \ldots \end{pmatrix}^{\mathsf{T}}$. Equation (60) then gives the sensitivity of the equilibrium population to changes in age-specific mortality. The sensitivity of the total size of the Academy, $\hat{N} = \mathbf{e}^{\mathsf{T}}\hat{\mathbf{n}}$, calculated using (38), is shown in Figure 2b. It shows that increases in mortality reduce $\hat{N}$ (not surprising), with the greatest effect coming from changes in mortality at ages 48–58.

Because learned societies are often concerned with their age distributions, Pollard (1968) examined the proportion of members over age 70. At equilibrium, this proportion is $\hat{R} = 0.26$. The sensitivity $d\hat{R}/d\boldsymbol{\theta}^{\mathsf{T}}$, calculated using (40), is shown in Figure 2c.

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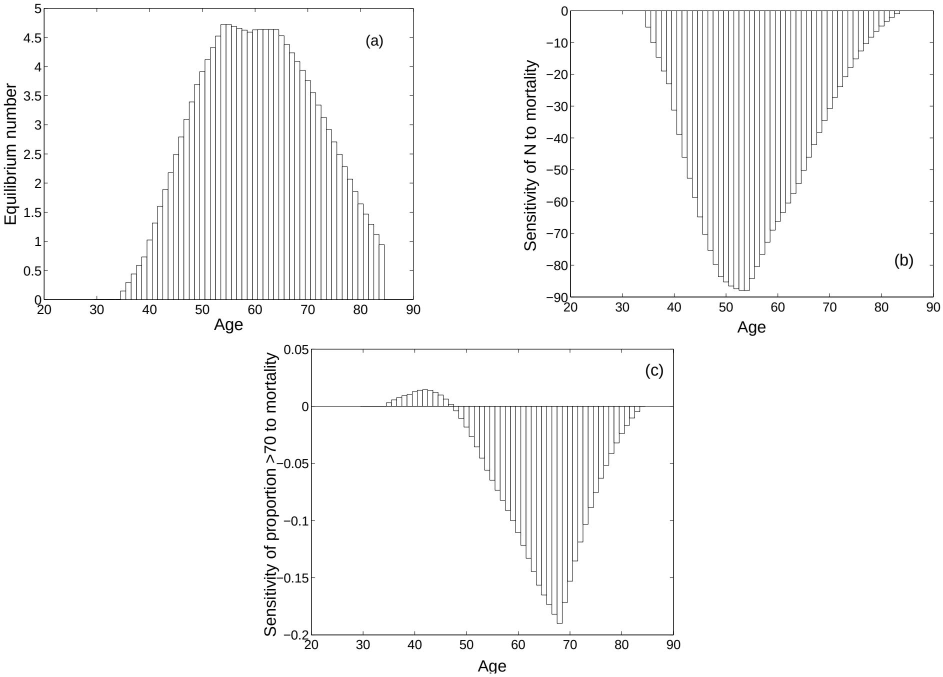
[7] Pollard's paper is remarkable for its treatment of both deterministic and stochastic models, but here I consider only the deterministic case.

[8] Only one woman, the redoubtable geologist Dorothy Hill in 1956, was elected to the Academy prior to 1969.

Figure 2: **Analysis of the equilibrium of a linear subsidized model for the Australian Academy of Science, based on Pollard (1968). (a) The equilibrium age structure of the Academy, assuming recruitment of 6 members per year. (b) The sensitivity, to changes in age-specific mortality, of the number of members. (c) The sensitivity, to changes in age-specific mortality, of the proportion of members over 70 years old**



Increases in mortality before age 48 would increase the proportion of members over 70, while increases in mortality after age 48 would decrease it.[9]

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[9] It is possible to calculate the average age of the Academy, and its sensitivity, using results to be introduced in Section 6.3. The response is very similar to that of the proportion over age 70.

5.2 Linear subsidized models with competition for space

Recruitment in subsidized populations may be limited by the availability of a resource. Roughgarden et al. (1985; see also Pascual and Caswell 1991) presented a model for a population of sessile organisms, such as barnacles, in which recruitment is limited by available space. Barnacles[10] produce larvae that disperse in the plankton for several weeks before settling onto a rock surface or other suitable substrate, after which they no longer move.

Roughgarden's model supposes that settlement is proportional to the free space $F(t)$. Thus the subsidy vector is

$$\mathbf{b}(t) = \begin{pmatrix} \phi F(t) & 0 & \cdots & 0 \end{pmatrix}^{\mathsf{T}}, \tag{61}$$

where ϕ is the settlement rate per unit of free space, and is determined by the pool of available larvae. The free space is the difference between the total area A and the space occupied by the population,

$$F(t) = A - \mathbf{g}^{\mathsf{T}}\mathbf{n}(t) \tag{62}$$

where $\mathbf{g}$ is a vector of stage-specific basal areas. Suppose that all locally-produced larvae are advected away, so that the first row of $\mathbf{A}$ is zero. Then, substituting (62) into (61) and rearranging gives

$$\mathbf{n}(t+1) = \mathbf{B}\mathbf{n}(t) + \begin{pmatrix} \phi A & 0 & \cdots & 0 \end{pmatrix}^{\mathsf{T}} \tag{63}$$

where

$$\mathbf{B} = \begin{pmatrix} -\phi g_1 & -\phi g_2 & \cdots & -\phi g_s \\ a_{21} & a_{22} & \cdots & a_{2s} \\ \vdots & \vdots & \ddots & \vdots \\ a_{s1} & a_{s2} & \cdots & a_{ss} \end{pmatrix}. \tag{64}$$

Although it includes competition for space, the model is linear. The equilibrium $\hat{\mathbf{n}}$ of (63) is stable if the spectral radius of $\mathbf{B}$ is less than one.[11] The formula (60) gives the sensitivity of this equilibrium to changes in the vital rates, the settlement rate, or the individual growth rate. This model might apply to any situation where the recruitment of new individuals depends on the availability of a resource (space, jobs, housing) that can be monopolized by residents.

Example 4 (Intertidal barnacles) Gaines and Roughgarden (1985) modelled a population of the barnacle *Balanus glandula* in central California. In one site (denoted KLM

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[10] The temptation to draw analogies between barnacles and the members of learned academies is almost irresistible.

[11] Because $\mathbf{B}$ contains negative elements, its dominant eigenvalue may be complex or negative, leading to oscillatory approach to the equilibrium.

in their paper), they reported age-independent survival with a probability of $P_i = 0.985$ per week, $i = 1, \ldots, 52$. The growth in basal area of an individual barnacle could be described by $g_x = \pi(\rho x)^2$, where x is age in weeks and ρ is the radial growth rate ($\rho = 0.0041$ cm/wk). The mean settlement rate was $\phi = 0.107$. The matrix $\mathbf{B}$ contains survival probabilities P_i on the subdiagonal, terms of the form $-\phi g_i$ in the first row, and zeros elsewhere.

The equilibrium population $\hat{\mathbf{n}}$ has an exponential age distribution (Figure 3a). It is scaled here relative to total area, so $A = 1$. The equilibrium proportion of free space is $\hat{F} = 0.865$.

To calculate sensitivities, let $\boldsymbol{\theta} = \begin{pmatrix} P_1 & \cdots & P_{52} \end{pmatrix}$. Some of the possible sensitivities are shown in Figure 3. Increasing survival at age j (ages $j = 10, 20, 40$ are shown) reduces the abundance of ages younger than j and increases the abundance of ages older than j (Figure 3b). A perturbation to a parameter, call it ξ, that affects survival at all ages has the effect

$$\frac{d\hat{\mathbf{n}}}{d\xi} = \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} \frac{d\boldsymbol{\theta}}{d\xi} = \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}} \mathbf{e} \tag{65}$$

where $\mathbf{e}$ is a vector of ones. An increase in overall survival would reduce the abundance of age classes 1–6 and increase the abundance of older age classes (Figure 3c).

The sensitivity of $\hat{\mathbf{n}}$ to the larval settlement rate ϕ is obtained from (60) by setting $d\text{vec}\,\mathbf{B}/d\boldsymbol{\phi} = \mathbf{0}_{s^2 \times 1}$, and

$$\frac{d\mathbf{b}}{d\phi} = \begin{pmatrix} \hat{F} & 0 & \cdots & 0 \end{pmatrix}^{\mathsf{T}}$$

Not surprisingly, increases in ϕ increase $\hat{\mathbf{n}}$, with the largest effect on the young age classes (Figure 3d). The sensitivity of $\hat{\mathbf{n}}$ to the radial growth rate ρ is obtained by writing

$$\frac{d\text{vec}\,\mathbf{B}}{d\rho} = \frac{d\text{vec}\,\mathbf{B}}{d\mathbf{g}^{\mathsf{T}}} \frac{d\mathbf{g}}{d\rho} \tag{66}$$

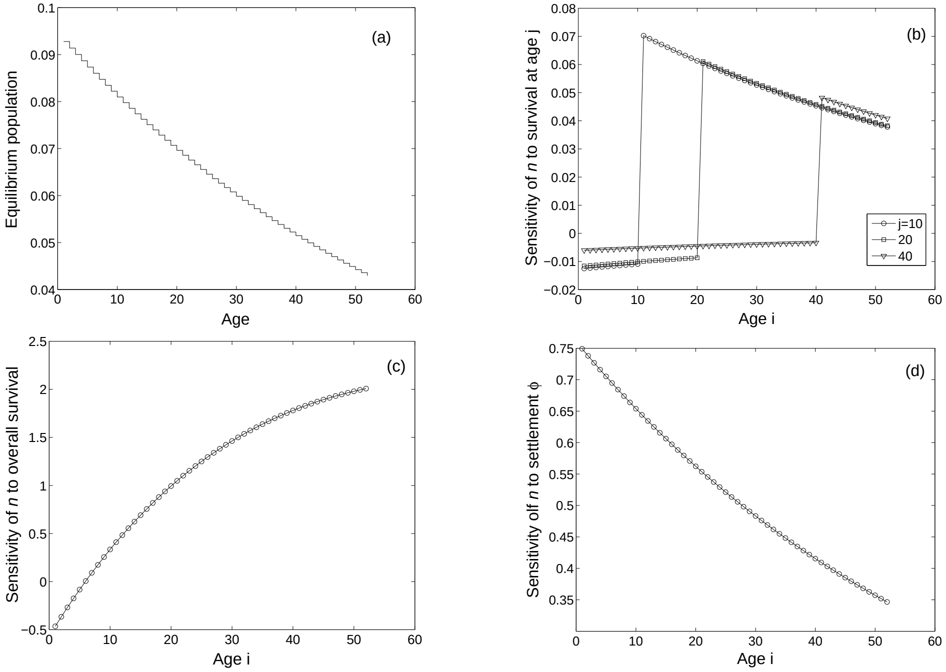
This sensitivity is negative, with the greatest impact on young age classes (Figure 3e).

Finally, the sensitivity of the equilibrium free space is given by

$$\frac{d\hat{F}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \frac{d\hat{F}}{d\mathbf{n}^{\mathsf{T}}} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = -\mathbf{g}^{\mathsf{T}} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} \tag{67}$$ ♢

Increases in survival reduce the amount of free space at equilibrium; the effect is largest for changes in survival of young age classes (Figure 3f). Figure 3g compares the effect on $\hat{F}$ of changes in overall survival, settlement, and radial growth rate. It is not surprising that increases in survival or settlement will reduce free space, but perhaps surprising that increases in the radial growth rate actually increase $\hat{F}$.

Figure 3: A sensitivity analysis of a subsidized population of the intertidal barnacle *Balanus glandula*. (a) The equilibrium population $\hat{\mathrm{n}}$ (scaled relative to a unit of area $A = 1$). (b) The sensitivity of $\hat{\mathrm{n}}$ to a change in survival at ages $j = 10, 20, 40$. (c) The sensitivity of $\hat{\mathrm{n}}$ to changes in overall survival at all ages. (d) The sensitivity of $\hat{\mathrm{n}}$ to the settlement rate ϕ per unit area. *Continued on next figure.*

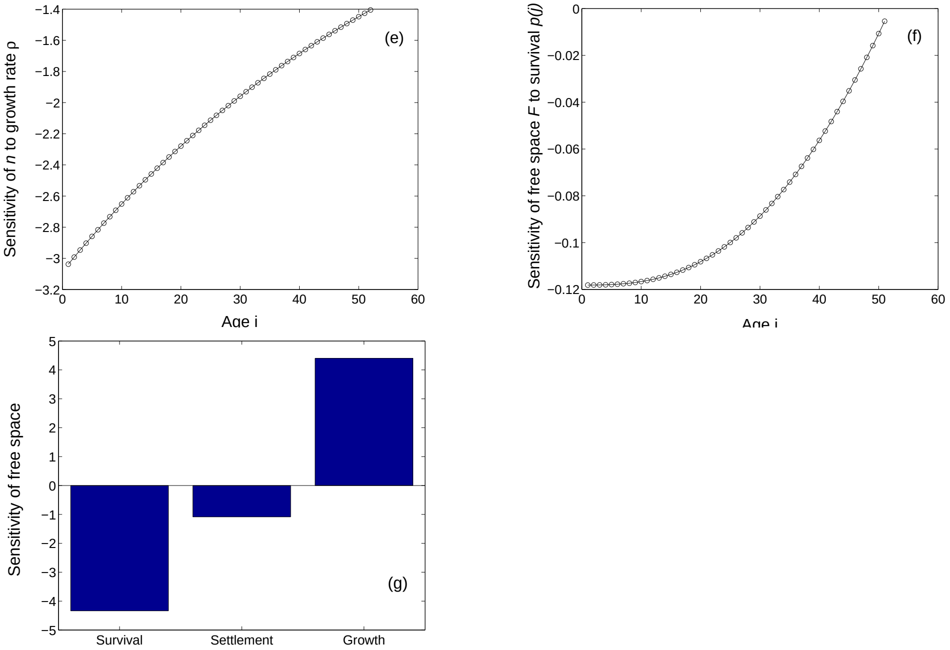


5.3 Density-dependent subsidized models

Once individuals to the population, they may experience a variety of density-dependent effects. For example, Gaines and Roughgarden (1985) found that increased barnacle density led to increased mortality due to attack by the starfish *Pisaster ochraceus*. A model incorporating such effects would be written

$$\mathbf{n}(t+1) = \mathbf{A}\left[\boldsymbol{\theta}, \mathbf{n}(t)\right]\mathbf{n}(t) + \mathbf{b}. \tag{68}$$

Figure 3: (cont'd.) A sensitivity analysis of a subsidized population of the intertidal barnacle *Balanus glandula*. (e) The sensitivity of $\hat{\mathrm{n}}$ to the radial growth rate ρ. (f) The sensitivity of the equilibrium free space $\hat{F}$ to age-specific survival. (g) The sensitivity of $\hat{F}$ to changes in overall survival, settlement rate, and radial growth rate. Based on data of Gaines and Roughgarden (1985)



The sensitivity result (60) extends to this model by substituting

$$d\mathrm{vec}\,\mathbf{A} = \frac{\partial \mathrm{vec}\,\mathbf{A}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} d\boldsymbol{\theta} + \frac{\partial \mathrm{vec}\,\mathbf{A}}{\partial \mathbf{n}^{\mathsf{T}}} d\hat{\mathbf{n}} \tag{69}$$

into (59) and solving for $d\hat{\mathbf{n}}$, to obtain

$$\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\mathbf{I}_s - \mathbf{A} - \left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right) \frac{\partial \mathrm{vec}\,\mathbf{A}}{\partial \mathbf{n}^{\mathsf{T}}} \right)^{-1} \left\{ \left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right) \frac{\partial \mathrm{vec}\,\mathbf{A}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} + \frac{d\mathbf{b}}{d\boldsymbol{\theta}^{\mathsf{T}}} \right\}. \tag{70}$$

where $\mathbf{A}$, $\mathbf{b}$, and all derivatives of $\mathbf{A}$ and $\mathbf{b}$ are evaluated at $\hat{\mathbf{n}}$.

6. Sensitivity of proportional age and stage distributions

The linear model $\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$ will, if $\mathbf{A}$ is primitive, converge to a stable age or stage distribution. But while the dynamics of the population vector $\mathbf{n}(t)$ are linear, but the dynamics of the *proportional* population structure are nonlinear (e.g., Tuljapurkar 1997). We can take advantage of this to analyze the sensitivity of proportional structures by writing them as equilibria of nonlinear maps.

Let $\mathbf{p}$ denote the proportional stage structure vector ($\mathbf{p} \geq 0$, $\mathbf{e}^{\mathsf{T}}\mathbf{p} = 1$). The dynamics of $\mathbf{p}(t)$ satisfy

$$\mathbf{p}(t+1) = \frac{\mathbf{A}\mathbf{p}(t)}{\|\mathbf{A}\mathbf{p}(t)\|}. \tag{71}$$

The stable stage distribution is an equilibrium of (71).

6.1 The stable stage distribution and reproductive value

The sensitivity of the stable stage distribution has been approached as an eigenvector perturbation problem (e.g., Caswell 1982, 2001, Section 9.4, Kirkland and Neumann 1994), but those calculations are complicated. Analysis of the equilibrium of the nonlinear model (71) is much easier.

The stable stage distribution satisfies

$$\hat{\mathbf{p}} = \frac{\mathbf{A}\hat{\mathbf{p}}}{\mathbf{e}^{\mathsf{T}}\mathbf{A}\hat{\mathbf{p}}} \tag{72}$$

where the 1-norm can be replaced by $\mathbf{e}^{\mathsf{T}}\mathbf{A}\hat{\mathbf{p}}$ because $\hat{\mathbf{p}}$ is non-negative. Differentiating both sides gives

$$d\hat{\mathbf{p}} = \frac{1}{\left(\mathbf{e}^{\mathsf{T}}\mathbf{A}\hat{\mathbf{p}}\right)^2} \left[\mathbf{e}^{\mathsf{T}}\mathbf{A}\hat{\mathbf{p}}(d\mathbf{A})\hat{\mathbf{p}} + \mathbf{e}^{\mathsf{T}}\mathbf{A}\hat{\mathbf{p}}\mathbf{A}(d\hat{\mathbf{p}}) - \mathbf{A}\hat{\mathbf{p}}\mathbf{e}^{\mathsf{T}}(d\mathbf{A})\hat{\mathbf{p}} - \mathbf{A}\hat{\mathbf{p}}\mathbf{e}^{\mathsf{T}}\mathbf{A}(d\hat{\mathbf{p}}) \right] \tag{73}$$

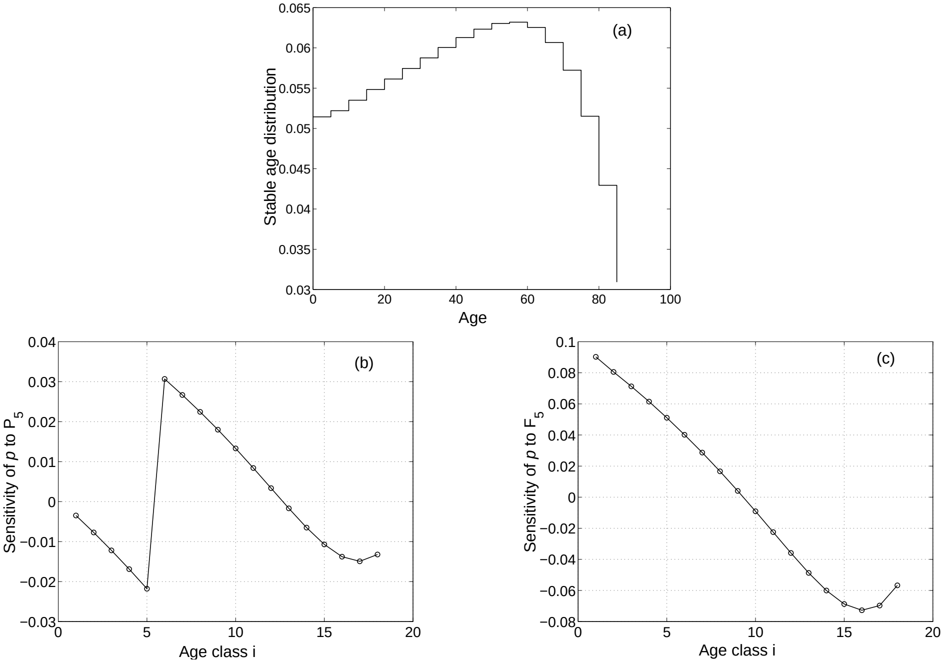
Note that $\mathbf{A}\hat{\mathbf{p}} = \lambda\hat{\mathbf{p}}$ and $\mathbf{e}^{\mathsf{T}}\mathbf{A}\hat{\mathbf{p}} = \lambda$, where λ is the dominant eigenvalue of $\mathbf{A}$. Making these substitutions and applying the vec operator to both sides gives

$$\lambda\, d\hat{\mathbf{p}} = \left[\left(\hat{\mathbf{p}}^{\mathsf{T}} \otimes \mathbf{I}_s\right) - \left(\hat{\mathbf{p}}^{\mathsf{T}} \otimes \hat{\mathbf{p}}\mathbf{e}^{\mathsf{T}}\right) \right] d\mathrm{vec}\,\mathbf{A} + \left[\mathbf{A} - \hat{\mathbf{p}}\mathbf{e}^{\mathsf{T}}\mathbf{A}\right] d\hat{\mathbf{p}} \tag{74}$$

Solving for $d\hat{\mathbf{p}}$ and applying the chain rule gives

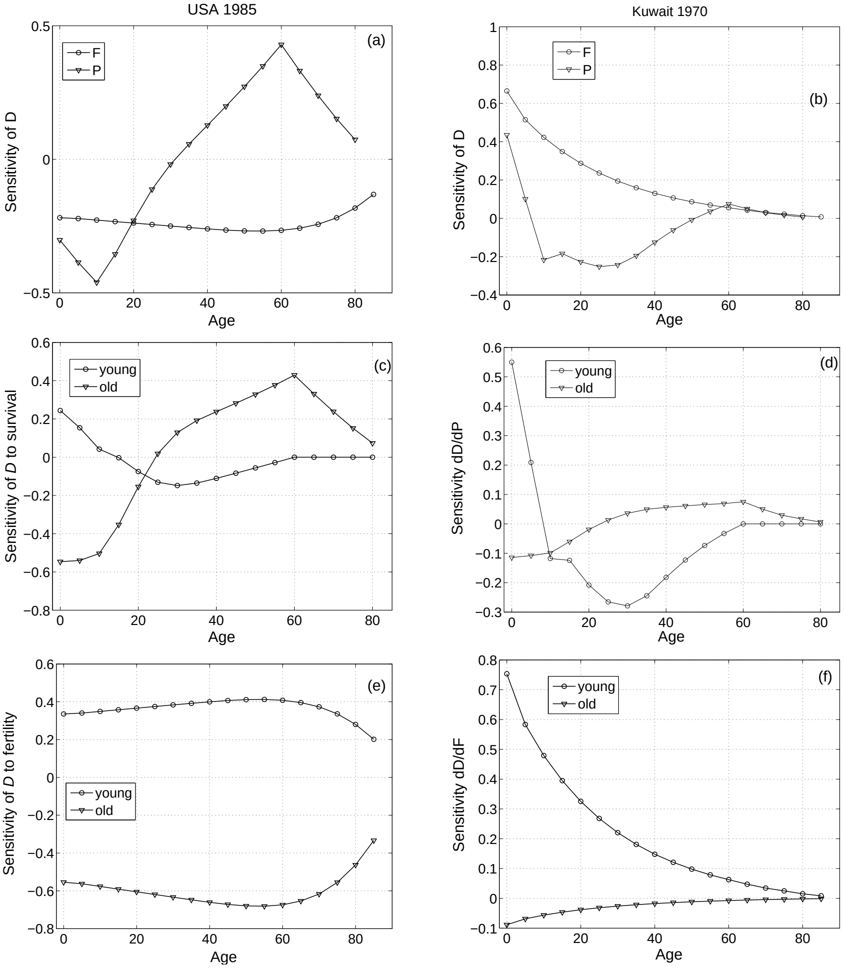
$$\frac{d\hat{\mathbf{p}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\lambda\mathbf{I}_s - \mathbf{A} + \hat{\mathbf{p}}\mathbf{e}^{\mathsf{T}}\mathbf{A}\right)^{-1} \left(\hat{\mathbf{p}}^{\mathsf{T}} \otimes \mathbf{I}_s - \hat{\mathbf{p}}^{\mathsf{T}} \otimes \hat{\mathbf{p}}\mathbf{e}^{\mathsf{T}}\right) \frac{d\mathrm{vec}\,\mathbf{A}}{d\boldsymbol{\theta}^{\mathsf{T}}} \tag{75}$$

Figure 4: **Stable age distribution and sensitivity of stable age distribution to age-specific survival and fertility. (a) The stable age distribution. (b) The sensitivity of the stable age distribution to changes in survival (P_5) in age class 5. (c) Sensitivity of the stable age distribution to changes in fertility (F_5) in age class 5. Based on life table data for the United States in 1985 (Keyfitz and Flieger 1990)**



Example 5 (A human age distribution) As an example, consider the age distribution of the population of the United States in 1985 (data from Keyfitz and Flieger 1990). These vital rates yield a declining population ($\lambda = 0.975$) and an age distribution skewed towards older ages (Figure 4). Applying (75) yields the sensitivity of $\hat{\mathbf{p}}$ to age-specific survival probabilities P_i and fertilities F_i, where age classes $i = 1, \ldots, 18$ correspond to ages $0 - 5, \ldots, 85 - 90$. The overall patterns are familiar from previous sensitivity analyses of stable age distributions (e.g., Caswell 2001, Figure 9.22). Increasing survival probability at a given age increases the relative abundance of the next several age

Figure 5: **Sensitivity of the dependency ratio D, and of its old and young components, to age-specific survival and fertility. Left: calculated from the stable age distribution of the United States in 1985. Right: calculated from the stable age distribution of Kuwait in 1970. (a) and (b): Sensitivity of D to survival (P_i) and fertility (F_i). (c) and (d): Sensitivity of the components of D to survival. (e) and (f): Sensitivity of the components of D to fertility. Life table data from Keyfitz and Flieger (1990)**



classes, at the expense of younger and older age classes. Increasing fertility at a given age increases the abundance of young age classes at the expense of older age classes.

A similar approach gives the sensitivity of the reproductive value vector $\mathbf{v}$, given by the left eigenvector of $\mathbf{A}$ corresponding to λ. Reproductive value is customarily scaled so that $v_1 = 1$. Scaled in this way, $\mathbf{v}$ satisfies

$$\hat{\mathbf{v}}^{\mathsf{T}} = \frac{\hat{\mathbf{v}}^{\mathsf{T}}\mathbf{A}}{\hat{\mathbf{v}}^{\mathsf{T}}\mathbf{A}\mathbf{e}_1} \tag{76}$$

where $\mathbf{e}_1$ is a vector with 1 in the first entry and zeros elsewhere. Differentiating both sides gives

$$d\hat{\mathbf{v}}^{\mathsf{T}} = \frac{1}{\left(\hat{\mathbf{v}}^{\mathsf{T}}\mathbf{A}\mathbf{e}_1\right)^2}\left[\hat{\mathbf{v}}^{\mathsf{T}}\mathbf{A}\mathbf{e}_1(d\hat{\mathbf{v}}^{\mathsf{T}})\mathbf{A} + \hat{\mathbf{v}}^{\mathsf{T}}\mathbf{A}\mathbf{e}_1\hat{\mathbf{v}}^{\mathsf{T}}(d\mathbf{A}) - (d\hat{\mathbf{v}}^{\mathsf{T}})\mathbf{A}\mathbf{e}_1\hat{\mathbf{v}}^{\mathsf{T}}\mathbf{A} - \hat{\mathbf{v}}^{\mathsf{T}}(d\mathbf{A})\mathbf{e}_1\hat{\mathbf{v}}^{\mathsf{T}}\mathbf{A}\right] \tag{77}$$

But $\hat{\mathbf{v}}^{\mathsf{T}}\mathbf{A} = \lambda\hat{\mathbf{v}}^{\mathsf{T}}$ and $\hat{\mathbf{v}}^{\mathsf{T}}\mathbf{A}\mathbf{e}_1 = \lambda$. Making these substitutions and applying the vec operator (remembering that $\operatorname{vec}\mathbf{v}^{\mathsf{T}} = \mathbf{v}$) gives

$$\lambda d\mathbf{v} = \left[\left(\mathbf{I}_s \otimes \hat{\mathbf{v}}^{\mathsf{T}}\right) - \left(\hat{\mathbf{v}}\mathbf{e}_1^{\mathsf{T}} \otimes \hat{\mathbf{v}}^{\mathsf{T}}\right)\right] d\operatorname{vec}\mathbf{A} + \left(\mathbf{A}^{\mathsf{T}} - \hat{\mathbf{v}}\mathbf{e}_1^{\mathsf{T}}\mathbf{A}^{\mathsf{T}}\right) d\mathbf{v}. \tag{78}$$

Solving for $d\mathbf{v}$ and using the chain rule gives

$$\frac{d\hat{\mathbf{v}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\lambda\mathbf{I}_s - \mathbf{A}^{\mathsf{T}} + \hat{\mathbf{v}}\mathbf{e}_1^{\mathsf{T}}\mathbf{A}^{\mathsf{T}}\right)^{-1}\left[\left(\mathbf{I}_s \otimes \hat{\mathbf{v}}^{\mathsf{T}}\right) - \left(\hat{\mathbf{v}}\mathbf{e}_1^{\mathsf{T}} \otimes \hat{\mathbf{v}}^{\mathsf{T}}\right)\right]\frac{d\operatorname{vec}\mathbf{A}}{d\boldsymbol{\theta}^{\mathsf{T}}} \tag{79}$$

6.2 Sensitivity of the dependency ratio

The dependency ratio characterizes an age distribution by the relative abundance of two groups, one assumed to be dependent and the other productive (e.g., Keyfitz and Flieger 1990, p. 32; Li and Tuljapurkar, unpublished). It is often assumed that persons younger than 15 or older than 65 are dependent on productive individuals between 15 and 65. The dependency ratio is defined as

$$D = \frac{\mathbf{a}^{\mathsf{T}}\hat{\mathbf{p}}}{\mathbf{b}^{\mathsf{T}}\hat{\mathbf{p}}} \tag{80}$$

where $\mathbf{a}$ is a vector with ones for the dependent ages and zeros otherwise, and $\mathbf{b}$ is its complement. Applying equation (40) for the sensitivity of a ratio gives

$$\frac{dD}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\frac{\mathbf{b}^{\mathsf{T}}\hat{\mathbf{p}}\mathbf{a}^{\mathsf{T}} - \mathbf{a}^{\mathsf{T}}\hat{\mathbf{p}}\mathbf{b}^{\mathsf{T}}}{\left(\mathbf{b}^{\mathsf{T}}\hat{\mathbf{p}}\right)^2}\right)\frac{d\hat{\mathbf{p}}}{d\boldsymbol{\theta}^{\mathsf{T}}}. \tag{81}$$

where $d\hat{\mathbf{p}}/\boldsymbol{\theta}^{\mathsf{T}}$ is given by (75).

This result can be generalized in several ways. The analysis may be performed separately for the dependent young and the dependent old, by suitable modification of $\mathbf{a}$ and $\mathbf{b}$. These two components are likely to be influenced by different demographic factors and can respond to perturbations in opposite directions. The $0-1$ vectors $\mathbf{a}$ and $\mathbf{b}$ may be replaced by vectors of weights; e.g., age-specific consumption and age-specific income (Li and Tuljapurkar, unpublished). The analysis applies to stage-classified models, provided that dependent and independent stages can be identified. It also applies to nonlinear models, with the stable stage distribution $\hat{\mathbf{p}}$ replaced by the equilibrium population $\hat{\mathbf{n}}$ in (81). It can be extended to transient dynamics, where the age distribution, and thus the dependency ratio, varies over time (Caswell 2007a). Finally, the sensitivity (81) makes it possible to carry out LTRE analyses (Caswell 2001, Chapter 10) to decompose differences in dependency ratios into components due to differences in each of the vital rates.

Example 5 ((cont'd) Dependency ratios in human populations.) The United States in 1985 had a set of vital rates leading to a low growth rate ($\lambda = 0.975$), and a relatively low dependency ratio, dominated by the old. Kuwait in 1970, in contrast, had a high growth rate ($\lambda = 1.210$) and one of the highest dependency ratios listed in the compilation of Keyfitz and Flieger (1990), dominated by the young:

	U.S.A. 1985	Kuwait 1970
D	0.668	1.025
D_y	0.260	0.956
D_o	0.406	0.069

◇

where D_y and D_o are the dependency ratios calculated for the young and old separately. The sensitivities of D, D_y, and D_o to changes in age-specific survival and fertility are shown in Figure 5. The responses of D to changes in the vital rates differ between the two countries. In the U.S., increases in fertility would reduce D. In Kuwait, increases in fertility (especially at young ages) would increase D. In the U.S., increases in survival[12] before age 30 reduce D; increases after age 30 increase D. In Kuwait, increases in survival, except at very young and very old ages, reduce D.

Breaking D into its young and old components helps to explain these differences. In both countries, there is a crossover in survival effects. Increases in survival at early ages increase D_y and reduce D_o. At later ages, increases in survival reduce D_y and increase D_o. Increases in fertility increase D_y and reduce D_o. In the U.S. population, both these effects are large, with the negative effect on D_o larger than the positive effect on D_y. In the Kuwaiti population, the positive effect on D_y is much greater than the negative effect on D_o.

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[12] Or, equivalently, reductions in mortality. For these parameter values, the sensitivity to mortality is approximately the sensitivity to survival with the opposite sign.

6.3 Sensitivity of mean age and related quantities

From an age distribution $\hat{\mathbf{p}}$, it is possible to compute the mean age of any age-specific property (e.g., production of children, collection of retirement benefits, exposure to toxic chemicals; see Chu 1998, p. 26 for general discussions). The most familiar of these is the mean age of reproduction, which is one measure of generation time (Coale 1972).

Let $\mathbf{f}$ be a vector of age-specific per-capita fertilities. The age distribution of offspring production is then $\mathbf{f} \circ \hat{\mathbf{p}}$, where $\circ$ is the Hadamard, or element-by-element product. The mean age of the mothers of these offspring is obtained by normalizing $\mathbf{f} \circ \hat{\mathbf{p}}$ to sum to 1 and taking the mean over the resulting distribution,

$$\bar{a}_{\mathbf{f}} = \frac{\mathbf{c}^{\mathsf{T}} \left(\mathbf{f} \circ \hat{\mathbf{p}} \right)}{\mathbf{e}^{\mathsf{T}} \left(\mathbf{f} \circ \hat{\mathbf{p}} \right)} \tag{82}$$

where

$$\mathbf{c}^{\mathsf{T}} = \begin{pmatrix} 1 & 2 & \cdots & s \end{pmatrix},$$

with s as the last age class.

Now differentiate $\bar{a}_{\mathbf{f}}$, following the now-familiar rules for ratios. The differential of the Hadamard product of two vectors is $d(\mathbf{a} \circ \mathbf{b}) = \text{diag}\,(\mathbf{a}) d\mathbf{b} + \text{diag}\,(\mathbf{b}) d\mathbf{a}$. The result is

$$\frac{d\bar{a}_{\mathbf{f}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\frac{\mathbf{e}^{\mathsf{T}} \left(\mathbf{f} \circ \hat{\mathbf{p}} \right) \mathbf{c}^{\mathsf{T}} - \mathbf{c}^{\mathsf{T}} \left(\mathbf{f} \circ \hat{\mathbf{p}} \right) \mathbf{e}^{\mathsf{T}}}{\left(\mathbf{f}^{\mathsf{T}} \hat{\mathbf{p}} \right)^2} \right) \left(\text{diag}\,(\mathbf{f}) \frac{d\hat{\mathbf{p}}}{d\boldsymbol{\theta}^{\mathsf{T}}} + \text{diag}\,(\hat{\mathbf{p}}) \frac{d\mathbf{f}}{d\boldsymbol{\theta}^{\mathsf{T}}} \right) \tag{83}$$

where $d\hat{\mathbf{p}}/d\boldsymbol{\theta}^{\mathsf{T}}$ is given by (75).

This result can be generalized in several ways. Setting $\mathbf{f} = \mathbf{e}$ makes the age-specific property that of simply being alive, and $\bar{a}_{\mathbf{e}} = \mathbf{c}^{\mathsf{T}} \mathbf{e}$ is then the mean age of the stable population, the sensitivity of which is

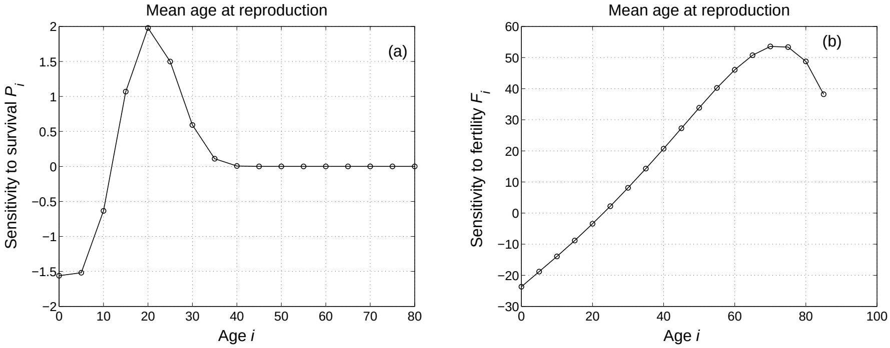
$$\frac{d\bar{a}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \mathbf{c}^{\mathsf{T}} \frac{d\hat{\mathbf{p}}}{d\boldsymbol{\theta}^{\mathsf{T}}} \tag{84}$$

The calculations can also be applied to the equilibrium population in a nonlinear model by substituting $\hat{\mathbf{n}}$ for $\hat{\mathbf{p}}$. They apply directly to stage-classified models with stages defined on an interval scale (e.g., size classes), in which case they give, e.g., the mean size at reproduction. If the stages are not evenly spaced, then $\mathbf{c}$ would be replaced by

$$\mathbf{c}^{\mathsf{T}} = \begin{pmatrix} x_1 & x_2 & \cdots & x_s \end{pmatrix} \tag{85}$$

where x_i is the value associated with stage i.

Figure 6: **Sensitivity of the mean age at reproduction to changes in age-specific survival and fertility, for the life table of the population of the United States, 1985 (data from Keyfitz and Flieger 1990)**



◇

Example 5 ((cont'd.) Mean age of reproduction.) The mean age of reproduction in the stable age distribution of the United States in 1985 was $\bar{a}_{\mathbf{f}} = 24.02$ years (using the mid-points of the 5-year age intervals as the measure of age). The sensitivities of $\bar{a}_{\mathbf{f}}$ to changes in age-specific survival and fertility are shown in Figure 6. Increases in survival prior to age 15 reduce $\bar{a}_{\mathbf{f}}$. Increases in survival after age 45 have almost no effect on $\bar{a}_{\mathbf{f}}$, because fertility is essentially zero after this age. Between age 15 and age 45, increases in survival increase the mean age of reproduction.

Increases in fertility reduce $\bar{a}_{\mathbf{f}}$ if they happen before age 25 and increase $\bar{a}_{\mathbf{f}}$ if they happen after age 25. These sensitivities are quite large, although this is somewhat irrelevant since the largest sensitivities are for ages at which fertility is zero and unlikely to be modified.

6.4 Sensitivity of variance in age

We can also calculate the sensitivity of the higher moments. For example, the variance in the age at reproduction is

$$V_{\mathbf{f}} = \overline{a_{\mathbf{f}}^2} - \left(\bar{a}_{\mathbf{f}}\right)^2 . \tag{86}$$

This variance might, for example, be useful as a measure of the extent of iteroparity. The sensitivity of $V_{\mathbf{f}}$ to changes in parameters is obtained by writing the first term as

$$\overline{a_{\mathbf{f}}^2} = \frac{(\mathbf{c} \circ \mathbf{c})^{\mathsf{T}} \left(\mathbf{f} \circ \hat{\mathbf{p}}\right)}{\mathbf{e}^{\mathsf{T}} \left(\mathbf{f} \circ \hat{\mathbf{p}}\right)} \tag{87}$$

and then differentiating

$$dV_{\mathbf{f}} = d\left(\overline{a_{\mathbf{f}}^2}\right) - 2\bar{a}_{\mathbf{f}}\ \left(d\bar{a}_{\mathbf{f}}\right). \tag{88}$$

The final result is

$$\begin{aligned} \frac{dV_{\mathbf{f}}}{d\boldsymbol{\theta}^{\mathsf{T}}} &= \left(\frac{\mathbf{e}^{\mathsf{T}}(\mathbf{f}\circ\hat{\mathbf{p}})(\mathbf{c}\circ\mathbf{c})^{\mathsf{T}} - (\mathbf{c}\circ\mathbf{c})^{\mathsf{T}}\left(\mathbf{f}\circ\hat{\mathbf{p}}\right)\mathbf{e}^{\mathsf{T}}}{\left(\mathbf{f}^{\mathsf{T}}\hat{\mathbf{p}}\right)^2}\right) \\ &\quad \times\left(\operatorname{diag}\left(\mathbf{f}\right)\frac{d\hat{\mathbf{p}}}{d\boldsymbol{\theta}^{\mathsf{T}}} + \operatorname{diag}\left(\hat{\mathbf{p}}\right)\frac{d\mathbf{f}}{d\boldsymbol{\theta}^{\mathsf{T}}}\right) - 2\bar{a}_{\mathbf{f}}\frac{d\bar{a}_{\mathbf{f}}}{d\boldsymbol{\theta}^{\mathsf{T}}}. \end{aligned} \tag{89}$$

where $d\hat{\mathbf{p}}/d\boldsymbol{\theta}^{\mathsf{T}}$ is given by (75) and $d\bar{a}_{\mathbf{f}}/d\boldsymbol{\theta}^{\mathsf{T}}$ is given by (83).

7. Frequency-dependent two-sex models

In sexually reproducing species, nonlinearity can arise from the dependence of reproduction on the relative abundance of males and females. This dependence is captured in a marriage function or mating rule (e.g., McFarland 1972, Pollak 1987, 1990). When the vital rates depend only on the relative, rather than the absolute, abundance of males and females, then $\mathbf{A}[\boldsymbol{\theta}, \mathbf{n}]$ is homogeneous of degree 0 in $\mathbf{n}$; i.e.,

$$\mathbf{A}[\boldsymbol{\theta}, c\mathbf{n}] = \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}] \qquad \text{for any } c \neq 0. \tag{90}$$

Such models are called frequency-dependent (Caswell and Weeks 1986, Caswell 2001) to distinguish them from density-dependent nonlinear models that do not have this homogeneity property.

Because of the homogeneity of $\mathbf{A}[\boldsymbol{\theta}, \mathbf{n}]$, frequency-dependent models do not converge to an equilibrium density $\hat{\mathbf{n}}$. Instead, there may exist[13] a stable equilibrium proportional structure $\hat{\mathbf{p}}$ to which the population will converge, at which point it grows exponentially at a rate λ given by the dominant eigenvalue of $\mathbf{A}[\boldsymbol{\theta}, \hat{\mathbf{p}}]$. Thus sensitivity analysis of two-sex models must include both the population structure and the population growth rate.

7.1 Sensitivity of the population structure

The equilibrium proportional population structure $\hat{\mathbf{p}}$ satisfies

$$\hat{\mathbf{p}} = \frac{\mathbf{A}[\boldsymbol{\theta}, \hat{\mathbf{p}}]\ \hat{\mathbf{p}}}{\|\mathbf{A}[\boldsymbol{\theta}, \hat{\mathbf{p}}]\ \hat{\mathbf{p}}\|} \tag{91}$$

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[13] A sufficient, but not necessary, condition for the existence of an equilibrium is that $\mathbf{A}$ cannot map a nonzero vector $\mathbf{n}$ directly to zero; necessary conditions are more difficult (Nussbaum 1988, 1989).

where $\hat{p}_i \geq 0$ and $\mathbf{e}^{\mathsf{T}}\hat{\mathbf{p}} = 1$. Differentiating (91) gives

$$d\hat{\mathbf{p}} = \frac{\mathbf{e}^{\mathsf{T}}\mathbf{A}\hat{\mathbf{p}}\left[(d\mathbf{A})\hat{\mathbf{p}} + \mathbf{A}(d\hat{\mathbf{p}})\right] - \mathbf{A}\hat{\mathbf{p}}\left[\mathbf{e}^{\mathsf{T}}(d\mathbf{A})\hat{\mathbf{p}} + \mathbf{e}^{\mathsf{T}}\mathbf{A}(d\hat{\mathbf{p}})\right]}{\left(\mathbf{e}^{\mathsf{T}}\mathbf{A}\hat{\mathbf{p}}\right)^2}. \tag{92}$$

Making the substitutions $\mathbf{A}\hat{\mathbf{p}} = \lambda\hat{\mathbf{p}}$ and $\mathbf{e}^{\mathsf{T}}\mathbf{A}\hat{\mathbf{p}} = \lambda$ and rearranging gives

$$\lambda d\hat{\mathbf{p}} = (d\mathbf{A})\hat{\mathbf{p}} + \mathbf{A}(d\hat{\mathbf{p}}) - \hat{\mathbf{p}}\mathbf{e}^{\mathsf{T}}(d\mathbf{A})\hat{\mathbf{p}} - \hat{\mathbf{p}}\mathbf{e}^{\mathsf{T}}\mathbf{A}(d\hat{\mathbf{p}}). \tag{93}$$

Applying the vec operator to both sides, expanding $d\mathrm{vec}\,\mathbf{A}$, invoking the chain rule, and solving for $d\hat{\mathbf{p}}/d\boldsymbol{\theta}^{\mathsf{T}}$ gives

$$\frac{d\hat{\mathbf{p}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left[\lambda\mathbf{I}_s - \mathbf{A} + \hat{\mathbf{p}}\mathbf{e}^{\mathsf{T}}\mathbf{A} - \left[\hat{\mathbf{p}}^{\mathsf{T}} \otimes \left(\mathbf{I}_s - \hat{\mathbf{p}}\mathbf{e}^{\mathsf{T}}\right)\right]\frac{\partial\mathrm{vec}\,\mathbf{A}}{\partial\mathbf{p}^{\mathsf{T}}}\right]^{-1}\left[\hat{\mathbf{p}}^{\mathsf{T}} \otimes \left(\mathbf{I}_s - \hat{\mathbf{p}}\mathbf{e}^{\mathsf{T}}\right)\right]\frac{\partial\mathrm{vec}\,\mathbf{A}}{\partial\boldsymbol{\theta}^{\mathsf{T}}} \tag{94}$$

where $\mathbf{A}$ and all derivatives are evaluated at $\hat{\mathbf{p}}$. Note that (94) differs from the expression (75) for the stable stage distribution in the linear model only in the term involving $\partial\mathrm{vec}\,\mathbf{A}/\partial\mathbf{p}^{\mathsf{T}}$, which of course is zero in the linear model.

7.2 Sensitivity of population growth rate

Because a population with the equilibrium structure grows exponentially, I once suggested treating $\mathbf{A}[\boldsymbol{\theta}, \hat{\mathbf{p}}]$ as a constant matrix and applying eigenvalue sensitivity analysis to it, in order to examine life history evolution in 2-sex models (Caswell 2001, p. 577). This was incorrect, because it ignored the effect of parameter changes on $\mathbf{A}$ through their effects on the equilibrium $\hat{\mathbf{p}}$. A correct calculation obtains the sensitivity of λ including effects of parameters on both $\mathbf{A}$ and $\hat{\mathbf{p}}$.

Note that $\hat{\mathbf{p}}$ is a right eigenvector of $\mathbf{A}[\boldsymbol{\theta}, \hat{\mathbf{p}}]$ corresponding to λ. Let $\mathbf{v}$ be the corresponding left eigenvector, where $\mathbf{v}^{\mathsf{T}}\mathbf{A}[\boldsymbol{\theta}, \hat{\mathbf{p}}] = \lambda\mathbf{v}^{\mathsf{T}}$ and $\mathbf{v}^{\mathsf{T}}\hat{\mathbf{p}} = 1$. Then

$$d\lambda = \mathbf{v}^{\mathsf{T}}(d\mathbf{A})\hat{\mathbf{p}} \tag{95}$$

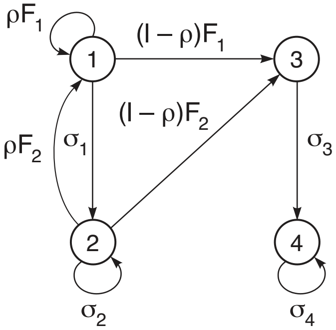
(Caswell 1978). Apply the vec operator and Roth's theorem to get

$$d\lambda = \left(\hat{\mathbf{p}}^{\mathsf{T}} \otimes \mathbf{v}^{\mathsf{T}}\right) d\mathrm{vec}\,\mathbf{A}. \tag{96}$$

Expanding $d\mathrm{vec}\,\mathbf{A}$ gives

$$\frac{d\lambda}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\hat{\mathbf{p}}^{\mathsf{T}} \otimes \mathbf{v}^{\mathsf{T}}\right)\left[\frac{\partial\mathrm{vec}\,\mathbf{A}}{\partial\boldsymbol{\theta}^{\mathsf{T}}} + \frac{\partial\mathrm{vec}\,\mathbf{A}}{\partial\hat{\mathbf{p}}^{\mathsf{T}}}\frac{d\hat{\mathbf{p}}}{d\boldsymbol{\theta}^{\mathsf{T}}}\right] \tag{97}$$

Figure 7: Life cycle graph for the 2-sex model for passerine birds (Legendre et al. 1999). Stages 1 and 2 are juvenile and adult females; stages 3 and 4 are juvenile and adult males. Parameters are stage specific survival probabilities σ_i, stage-specific fertilities F_i, and primary sex ratio (proportion female) ρ



where $\mathbf{A}$, $\mathbf{v}$, and the derivatives of $\mathbf{A}$ are all evaluated at the equilibrium $\hat{\mathbf{p}}$, and $d\hat{\mathbf{p}}/d\boldsymbol{\theta}^{\mathsf{T}}$ is given by (94).

Note that λ is the invasion exponent for this model, and thus the sensitivity of λ to a parameter gives the selection gradient on that parameter. Tuljapurkar et al. (2007) used this fact to explore the effect of male fertility patterns on the evolution of aging; the sensitivity (97) could be used to generalize such results.

Although two-sex models are an important case of homogeneous models, they are not the only case. Keyfitz's (1972a) interpretation of the Easterlin hypothesis describes fertility as dependent on only the relative, not absolute, size of a cohort. A model based on this premise would be frequency-dependent (homogeneous) and would lead to an exponentially growing population to which (97) would be applicable.

Example 6 (A two-sex model for passerine birds) Legendre et al. (1999) used a frequency-dependent two-sex model to study the introductions of passerine birds to New Zealand. The life cycle includes two age classes (first year and older) for females and for males. The life cycle graph is shown in Figure 7. The numbers of females and males are $N_f = n_1 + n_2$ and $N_m = n_3 + n_4$, respectively.

Because passerines are typically monogamous within a breeding season, and assuming that mating is indiscriminate with respect to age, Legendre et al. (1999) used as a mating function

$$B(\mathbf{n}) = \min\left(N_f, N_m\right), \tag{98}$$

giving the number of matings as a function of the number of males and females. The per-capita fertility of a female of age-class i is the number of matings divided by the number of females and multiplied by the number of surviving offspring per mating.

$$\begin{aligned} F(\mathbf{n}) &= \frac{\sigma_0 \phi_i B(\mathbf{n})}{N_f} && (99) \\ &= \begin{cases} \sigma_0 \phi_i \frac{N_m}{N_f} & N_f \geq N_m \\ \sigma_0 \phi & N_f < N_m \end{cases} && (100) \end{aligned}$$

where σ_0 is the probability of survival from fledging to age 1 and ϕ_i is the clutch size of age class i. When males are the scarcer sex (the avian equivalent of a marriage squeeze) fertility is proportional to the ratio of males to females. When females are the scarcer sex, all females are mated and fertility depends only on fecundity and neonatal survival.

Births are allocated to females and males according to a primary sex ratio ρ which gives the proportion female. The resulting two-sex projection matrix is

$$\mathbf{A}[\mathbf{n}] = \left(\begin{array}{cc|cc} \rho F_1(\mathbf{n}) & \rho F_2(\mathbf{n}) & 0 & 0 \\ \sigma_1 & \sigma_2 & 0 & 0 \\ \hline (1-\rho)F_1(\mathbf{n}) & (1-\rho)F_2(\mathbf{n}) & 0 & 0 \\ 0 & 0 & \sigma_3 & \sigma_4 \end{array} \right) \qquad (101)$$

Legendre et al. (1999) considered typical values for passerine birds of $\sigma_0 = 0.2$, $\phi_i = 7$, and $\rho = 0.5$. They set male and female survival equal ($\sigma_1 = \sigma_3 = 0.35$, $\sigma_2 = \sigma_4 = 0.4$), but this is a pathological special case in this model, so instead I consider two cases, one in which male mortality is higher than female mortality, and one in which the difference is reversed.[14] The survival probabilities and equilibrium population structures are

$$\boldsymbol{\sigma} = \left(\begin{array}{c} 0.35 \\ 0.5 \\ \hline 0.25 \\ 0.4 \end{array} \right) \qquad \hat{\mathbf{p}} = \left(\begin{array}{c} 0.320 \\ 0.226 \\ \hline 0.320 \\ 0.134 \end{array} \right) \qquad (102)$$

$$\boldsymbol{\sigma} = \left(\begin{array}{c} 0.25 \\ 0.4 \\ \hline 0.35 \\ 0.5 \end{array} \right) \qquad \hat{\mathbf{p}} = \left(\begin{array}{c} 0.320 \\ 0.134 \\ \hline 0.320 \\ 0.226 \end{array} \right) \qquad (103)$$

$$(104)$$

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[14] In a survey of the literature, adult mortality for female passerines exceeded that for males in 21 out of 28 cases (Promislow et al. 1992). Birds differ from mammals in this respect.

Table 1: Elasticity of $\hat{\mathrm{p}}$ to parameters in two-sex model for passerine birds, under two mortality scenarios. When male mortality is greater than female mortality, males are rarer than females and fertility at equilibrium is limited by the mating function. When male mortality is less than female mortality, females are rare and fertility is not affected by the mating function

Males rare

Stage	σ_0	ρ	σ_1	σ_2	σ_3	σ_4	ϕ_1	ϕ_2
$\hat{p}_1$	0.455	0.453	−0.226	−0.229	0.000	0.000	0.266	0.189
$\hat{p}_2$	−0.890	1.799	0.774	0.783	−0.398	−0.268	−0.521	−0.369
$\hat{p}_3$	0.455	−1.547	−0.226	−0.229	0.000	0.000	0.266	0.189
$\hat{p}_4$	−0.664	−0.428	−0.226	−0.229	0.669	0.450	−0.389	−0.275

Females rare

Stage	σ_0	ρ	σ_1	σ_2	σ_3	σ_4	ϕ_1	ϕ_2
$\hat{p}_1$	0.455	1.547	0.000	0.000	−0.226	−0.229	0.320	0.135
$\hat{p}_2$	−0.664	0.428	0.669	0.450	−0.226	−0.229	−0.467	−0.197
$\hat{p}_3$	0.455	−0.453	0.000	0.000	−0.226	−0.229	0.320	0.135
$\hat{p}_4$	−0.890	−1.799	−0.398	−0.268	0.774	0.783	−0.627	−0.264

The elasticities of $\hat{\mathbf{p}}$ to each of the parameters, calculated from (94), are shown in Table 1. Regardless of which sex is scarcer, increasing neonatal survival increases the proportion of young, at the expense of the proportion of adults, in both sexes. Increasing the sex ratio ρ increases the proportion of females at the expense of males. Increasing female survival (σ_1 or σ_2) increases the proportion of adult females at the expense of all other stages; increasing male survival has the opposite effect. However, when females are rare, increasing female survival has no effect on the proportion of juveniles. When males are rare, increases in male survival have no effect on the proportion of juveniles. Increasing fecundity increases the proportion of juveniles, at the expense of adults, in both sexes and for either mortality pattern.

The elasticity of the population growth rate λ at equilibrium is shown in Table 2, and is compared to the naive calculation that treats $\mathbf{A}[\boldsymbol{\theta}, \hat{\mathbf{p}}]$ as a fixed matrix. When males are rare, so that fertility is limited by the mating function, the naive calculations are dramatically wrong. When calculated correctly, increases in the primary sex ratio ρ reduce λ, because they reduce the availability of males. Increases in female survival have no effect on λ, because the extra females produced have no opportunity to reproduce. Increases in male survival increase λ because they increase female fertility. In each case, the naive calculation leads, incorrectly, to the opposite conclusion.

When females are rare (which renders the model linear and female-dominant at equilibrium), the correct and the naive calculations agree. This is a consequence of using the minimum as a birth function. Some preliminary calculations using the harmonic mean birth function,

$$B(\mathbf{n}) = \frac{2N_f N_m}{N_f + N_m}, \tag{105}$$

in which both males and females influence fertility at all population structures, suggest that the naive elasticity calculations are always wrong.

Table 2: The elasticity of λ to parameters in the two-sex model for passerine birds, under two mortality scenarios. The correct calculation is based on (97). The naive calculation incorrectly treats $\mathbf{A}[\hat{\mathbf{p}}, \boldsymbol{\theta}]$ as a fixed matrix, ignoring the effect of parameters on the equilibrium population structure $\hat{\mathbf{p}}$

	Males rare		Females rare	
	Correct	Naive	Correct	Naive
σ_0	0.669	0.545	0.669	0.669
ρ	-0.669	0.545	0.669	0.669
σ_1	0	0.226	0.198	0.198
σ_2	0	0.229	0.133	0.133
σ_3	0.198	0	0	0
σ_4	0.133	0	0	0
ϕ_1	0.392	0.319	0.471	0.471
ϕ_2	0.277	0.226	0.198	0.198

◇

8. Sensitivity of population cycles

Equilibria are not the only attractors relevant in nature (e.g., Clutton-Brock et al. 1997) or the laboratory (e.g., Cushing et al. 2003). Cycles, invariant loops, and strange attractors also occur, and are sensitive to changes in parameters. This section examines the sensitivity of cycles.

8.1 Sensitivity of the population vector

A k-cycle is a sequence of population vectors $\hat{\mathbf{n}}_1, \ldots, \hat{\mathbf{n}}_k$, satisfying

$$\begin{aligned} \hat{\mathbf{n}}_{i+1} &= \mathbf{A}\left[\boldsymbol{\theta}, \hat{\mathbf{n}}_i\right] \hat{\mathbf{n}}_i \qquad i = 1, \ldots, k-1 \\ \hat{\mathbf{n}}_1 &= \mathbf{A}\left[\boldsymbol{\theta}, \hat{\mathbf{n}}_k\right] \hat{\mathbf{n}}_k. \end{aligned} \tag{106}$$

A change in parameters will modify each point in the cycle; the first goal of perturbation analysis is thus to find the sensitivities

$$\frac{d\hat{\mathbf{n}}_1}{d\boldsymbol{\theta}^{\mathsf{T}}}, \ \ldots, \ \frac{d\hat{\mathbf{n}}_k}{d\boldsymbol{\theta}^{\mathsf{T}}}. \tag{107}$$

The following is the derivation of these sensitivities for a 2-cycle. The extension cycles of arbitrary length will follow. To simplify notation, define

$$\mathbf{A}_i \equiv \mathbf{A}\left[\boldsymbol{\theta}, \hat{\mathbf{n}}_i\right]. \tag{108}$$

The 2-cycle satisfies

$$\hat{\mathbf{n}}_1 = \mathbf{A}_2 \hat{\mathbf{n}}_2 \tag{109}$$

$$\hat{\mathbf{n}}_2 = \mathbf{A}_1 \hat{\mathbf{n}}_1 \tag{110}$$

Differentiating both equations, applying the vec operator, and expanding $d\text{vec}\,\mathbf{A}_i/d\boldsymbol{\theta}^{\mathsf{T}}$ yields a system of equations

$$\frac{d\hat{\mathbf{n}}_1}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\hat{\mathbf{n}}_2^{\mathsf{T}} \otimes \mathbf{I}_s\right) \frac{\partial \text{vec}\,\mathbf{A}_2}{\partial \boldsymbol{\theta}^{\mathsf{T}}} + \left(\hat{\mathbf{n}}_2^{\mathsf{T}} \otimes \mathbf{I}_s\right) \frac{\partial \text{vec}\,\mathbf{A}_2}{\partial \mathbf{n}_2^{\mathsf{T}}} \left(\frac{d\hat{\mathbf{n}}_2}{d\boldsymbol{\theta}^{\mathsf{T}}}\right) + \mathbf{A}_2 \left(\frac{d\hat{\mathbf{n}}_2}{d\boldsymbol{\theta}^{\mathsf{T}}}\right) \tag{111}$$

$$\frac{d\hat{\mathbf{n}}_2}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\hat{\mathbf{n}}_1^{\mathsf{T}} \otimes \mathbf{I}_s\right) \frac{\partial \text{vec}\,\mathbf{A}_1}{\partial \boldsymbol{\theta}^{\mathsf{T}}} + \left(\hat{\mathbf{n}}_1^{\mathsf{T}} \otimes \mathbf{I}_s\right) \frac{\partial \text{vec}\,\mathbf{A}_1}{\partial \mathbf{n}_1^{\mathsf{T}}} \left(\frac{d\hat{\mathbf{n}}_1}{d\boldsymbol{\theta}^{\mathsf{T}}}\right) + \mathbf{A}_1 \left(\frac{d\hat{\mathbf{n}}_1}{d\boldsymbol{\theta}^{\mathsf{T}}}\right) \tag{112}$$

This system can be written in block matrix form. Defiine $\mathbf{H}_i \equiv \hat{\mathbf{n}}_i^{\mathsf{T}} \otimes \mathbf{I}_s$. Then

$$
\begin{aligned}
\frac{d}{d\boldsymbol{\theta}^{\mathsf{T}}}\left(\begin{array}{c}\hat{\mathbf{n}}_1\\ \hline \hat{\mathbf{n}}_2\end{array}\right) \quad = \quad & \left(\begin{array}{c|c}0 & \mathbf{H}_2\\ \hline \mathbf{H}_1 & 0\end{array}\right)\left(\begin{array}{c}\dfrac{\partial \text{vec}\,\mathbf{A}_1}{\partial\boldsymbol{\theta}^{\mathsf{T}}}\\ \dfrac{\partial \text{vec}\,\mathbf{A}_2}{\partial\boldsymbol{\theta}^{\mathsf{T}}}\end{array}\right)\\
& + \quad \left[\left(\begin{array}{c|c}0 & \mathbf{H}_2\\ \hline \mathbf{H}_1 & 0\end{array}\right)\left(\begin{array}{c|c}\dfrac{\partial \text{vec}\,\mathbf{A}_1}{\partial\mathbf{n}_1^{\mathsf{T}}} & 0\\ \hline 0 & \dfrac{\partial \text{vec}\,\mathbf{A}_2}{\partial\mathbf{n}_2^{\mathsf{T}}}\end{array}\right) + \left(\begin{array}{c|c}0 & \mathbf{A}_2\\ \hline \mathbf{A}_1 & 0\end{array}\right)\right]\\
& \times\frac{d}{d\boldsymbol{\theta}^{\mathsf{T}}}\left(\begin{array}{c}\hat{\mathbf{n}}_1\\ \hline \hat{\mathbf{n}}_2\end{array}\right)
\end{aligned}
\qquad (113)
$$

Solving for the sensitivities gives

$$
\begin{aligned}
\frac{d}{d\boldsymbol{\theta}^{\mathsf{T}}}\left(\begin{array}{c}\hat{\mathbf{n}}_1\\ \hline \hat{\mathbf{n}}_2\end{array}\right) \quad = \quad & \left[\mathbf{I}_{2s} - \left(\begin{array}{c|c}0 & \mathbf{H}_2\\ \hline \mathbf{H}_1 & 0\end{array}\right)\left(\begin{array}{c|c}\dfrac{\partial \text{vec}\,\mathbf{A}_1}{\partial\mathbf{n}_1^{\mathsf{T}}} & 0\\ \hline 0 & \dfrac{\partial \text{vec}\,\mathbf{A}_2}{\partial\mathbf{n}_2^{\mathsf{T}}}\end{array}\right)\right.\\
& \left. - \left(\begin{array}{c|c}0 & \mathbf{A}_2\\ \hline \mathbf{A}_1 & 0\end{array}\right)\right]^{-1}\left(\begin{array}{c|c}0 & \mathbf{H}_2\\ \hline \mathbf{H}_1 & 0\end{array}\right)\left(\begin{array}{c}\dfrac{\partial \text{vec}\,\mathbf{A}_1}{\partial\boldsymbol{\theta}^{\mathsf{T}}}\\ \dfrac{\partial \text{vec}\,\mathbf{A}_2}{\partial\boldsymbol{\theta}^{\mathsf{T}}}\end{array}\right)
\end{aligned}
\qquad (114)
$$

where the matrices $\mathbf{A}_i$ and the derivatives of $\mathbf{A}_i$ are all evaluated at $\hat{\mathbf{n}}_i$. The analogy with (23) is apparent.

This calculation can be extended to cycles of any period, in terms of block matrices as in (114). The pattern of the block matrices is clear from a 3-cycle. Define the following matrices:

$$
\mathbb{N} \quad = \quad \left(\begin{array}{c}\hat{\mathbf{n}}_1\\ \hat{\mathbf{n}}_2\\ \hat{\mathbf{n}}_3\end{array}\right) \qquad (115)
$$

$$
\mathbb{A} \quad = \quad \left(\begin{array}{ccc}0 & 0 & \mathbf{A}_3\\ \mathbf{A}_1 & 0 & 0\\ 0 & \mathbf{A}_2 & 0\end{array}\right) \qquad (116)
$$

$$\mathbb{H} = \begin{pmatrix} 0 & 0 & \mathbf{H}_3 \\ \mathbf{H}_1 & 0 & 0 \\ 0 & \mathbf{H}_2 & 0 \end{pmatrix} \tag{117}$$

$$\mathbb{C} = \begin{pmatrix} \dfrac{\partial \text{vec}\,\mathbf{A}_1}{\partial \mathbf{n}_1^{\mathsf{T}}} & 0 & 0 \\ 0 & \dfrac{\partial \text{vec}\,\mathbf{A}_2}{\partial \mathbf{n}_2^{\mathsf{T}}} & 0 \\ 0 & 0 & \dfrac{\partial \text{vec}\,\mathbf{A}_3}{\partial \mathbf{n}_3^{\mathsf{T}}} \end{pmatrix} \tag{118}$$

$$\mathbb{D} = \begin{pmatrix} \dfrac{\partial \text{vec}\,\mathbf{A}_1}{\partial \boldsymbol{\theta}^{\mathsf{T}}} \\ \dfrac{\partial \text{vec}\,\mathbf{A}_1}{\partial \boldsymbol{\theta}^{\mathsf{T}}} \\ \dfrac{\partial \text{vec}\,\mathbf{A}_1}{\partial \boldsymbol{\theta}^{\mathsf{T}}} \end{pmatrix}. \tag{119}$$

In terms of these matrices, the sensitivity of each point in the 3-cycle is given by

$$\frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left[\mathbf{I}_{3s} - \mathbb{A} - \mathbb{H}\mathbb{C}\right]^{-1} \mathbb{H}\mathbb{D}. \tag{120}$$

8.2 Sensitivity of weighted densities and time averages

The matrix $d\mathbb{N}/d\boldsymbol{\theta}^{\mathsf{T}}$ contains the sensitivity of every stage to every parameter at every point in the cycle. This potential overload of information can be simplified by calculating the sensitivities of weighted densities and/or time averages over the cycle. To do this, it is convenient to write the points in the cycle as an array (of dimension $s \times k$)

$$\mathbf{G} = \begin{pmatrix} \hat{\mathbf{n}}_1 & \hat{\mathbf{n}}_2 & \cdots & \hat{\mathbf{n}}_k \end{pmatrix}. \tag{121}$$

The block vector $\mathbb{N}$ is

$$\mathbb{N} = \text{vec}\,\mathbf{G}. \tag{122}$$

Weighted densities. Let $\mathbf{c}$ be a vector of weights, and let $\hat{N}_i = \mathbf{c}^{\mathsf{T}}\hat{\mathbf{n}}_i$ be the (scalar) weighted density at the ith point on the cycle. Then write

$$\hat{\mathbf{N}} = \begin{pmatrix} \hat{N}_1 \\ \vdots \\ \hat{N}_k \end{pmatrix} \tag{123}$$

The vector $\hat{\mathbf{N}}$ can be calculated from $\mathbb{N}$ as

$$\begin{aligned} \hat{\mathbf{N}} &= \left(\begin{array}{ccc} \mathbf{c}^{\mathsf{T}}\hat{\mathbf{n}}_1 & \cdots & \mathbf{c}^{\mathsf{T}}\hat{\mathbf{n}}_k \end{array} \right)^{\mathsf{T}} \\ &= \operatorname{vec}\left(\mathbf{c}^{\mathsf{T}}\mathbf{G}\right) \\ &= \left(\mathbf{I}_k \otimes \mathbf{c}^{\mathsf{T}}\right) \operatorname{vec}\mathbf{G} \\ &= \left(\mathbf{I}_k \otimes \mathbf{c}^{\mathsf{T}}\right) \mathbb{N} \qquad \text{dimension} = k \times 1. \end{aligned} \tag{124}$$

Time-averaged population vector. Let $\mathbf{b}$ be a probability vector ($b_i \geq 0$, $\mathbf{e}^{\mathsf{T}}\mathbf{b} = 1$) and define the time-averaged population vector as

$$\bar{\mathbf{n}} = \sum_{i=1}^{k} b_i \hat{\mathbf{n}}_i. \tag{125}$$

Then

$$\begin{aligned} \bar{\mathbf{n}} &= \mathbf{G}\mathbf{b} \\ &= \left(\mathbf{b}^{\mathsf{T}} \otimes \mathbf{I}_s\right) \operatorname{vec}\mathbf{G} \\ &= \left(\mathbf{b}^{\mathsf{T}} \otimes \mathbf{I}_s\right) \mathbb{N} \qquad \text{dimension} = s \times 1 \end{aligned} \tag{126}$$

Time-averaged weighted density. Taking the time average of the $\hat{N}_i$ gives

$$\begin{aligned} \bar{N} &= \sum_i b_i \mathbf{c}^{\mathsf{T}}\hat{\mathbf{n}}_i \\ &= \mathbf{c}^{\mathsf{T}}\mathbf{G}\mathbf{b} \\ &= \left(\mathbf{b}^{\mathsf{T}} \otimes \mathbf{c}^{\mathsf{T}}\right) \mathbb{N} \end{aligned} \tag{127}$$

Thus the sensitivities of the weighted densities, the time-averaged population, and the time-averaged weighted density are obtained by differentiating (124), (126), and (127) as

$$\frac{d\hat{\mathbf{N}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\mathbf{I}_k \otimes \mathbf{c}^{\mathsf{T}}\right) \frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}} \tag{128}$$

$$\frac{d\bar{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\mathbf{b}^{\mathsf{T}} \otimes \mathbf{I}_s\right) \frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}} \tag{129}$$

$$\frac{d\bar{N}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\mathbf{b}^{\mathsf{T}} \otimes \mathbf{c}^{\mathsf{T}}\right) \frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}} \tag{130}$$

where $d\mathbb{N}/\boldsymbol{\theta}^{\mathsf{T}}$ is given by (120).

Example 7 (A 2-cycle in the *Tribolium* model.) A series of experiments on *Tribolium* reported by Dennis et al. (1995) produced stable 2-cycles by experimentally manipulating the adult mortality μ_a. Using the model in Example 2 and the estimated parameters

$$\begin{aligned} b &= 11.677 \\ c_{ea} &= 1.100 \times 10^{-2} \\ c_{el} &= 9.3 \times 10^{-3} \\ c_{pa} &= 1.78 \times 10^{-2} \\ \mu_a &= 1.108 \times 10^{-1} \\ \mu_l &= 5.129 \times 10^{-1} \end{aligned}$$

(Dennis et al. 1995, Table 1) leads to a 2-cycle

$$\hat{\mathbf{n}}_1 = \begin{pmatrix} 325.3 \\ 8.9 \\ 118.5 \end{pmatrix} \qquad \hat{\mathbf{n}}_2 = \begin{pmatrix} 18.2 \\ 158.4 \\ 106.4 \end{pmatrix}, \tag{131}$$

in which the population oscillates between a state dominated by larvae and adults and a state dominated by pupae and adults.

As an example of the rich sensitivity analyses possible for even such a simple model, I examine the elasticity of the population vector $\hat{\mathbf{n}}_i$, of the total population $\hat{N}_i = \mathbf{e}^\mathsf{T}\hat{\mathbf{n}}_i$, of the total population respiration $\hat{R}_i = \mathbf{c}^\mathsf{T}\hat{\mathbf{n}}_i$ (with $\mathbf{c}$ the vector of stage-specific respiration rates from Example 2), and of the time averages $\bar{\mathbf{n}}$, $\bar{N}$, and $\bar{R}$. The results are collected in Figure 8.

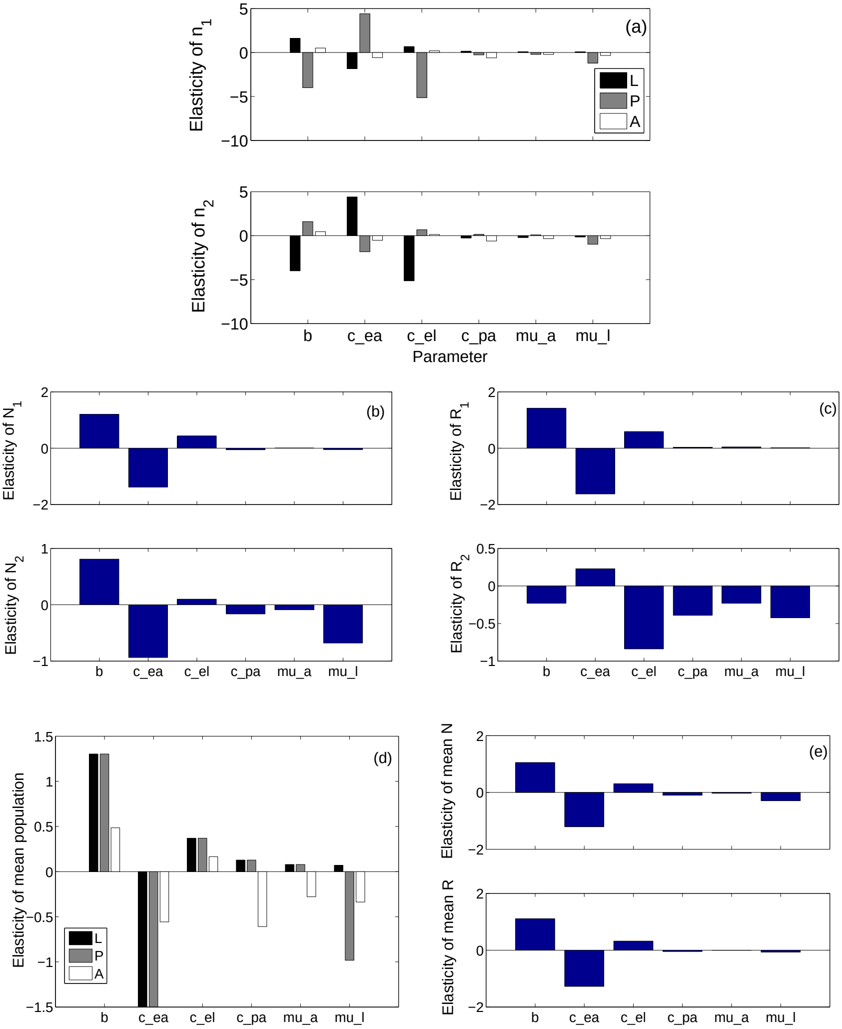
First, the elasticities of the $\hat{\mathbf{n}}_i$ differ from stage to stage and from one point on the cycle to another (Figure 8a). Increases in fecundity, for example, increase the density of larvae and reduce the density of pupae in $\hat{\mathbf{n}}_1$, but have the opposite effects in $\hat{\mathbf{n}}_2$. The elasticities to b, c_{ea}, and c_{el} are much larger than those to the other parameters (cf. the elasticities of the equilibrium $\hat{n}$ in Figure 1).

The elasticities of total population are similar at the two points in the cycle (Figure 8b), except that larval mortality μ_l has a large negative effect on $\hat{N}_2$, but only a small effect on $\hat{N}_1$. The elasticities of total respiration $\hat{R}_i$, however, are different at the two points in the cycle (Figure 8c).

The elasticities of the time-averaged population vector $\bar{\mathbf{n}}$ (Figure 8d) are similar to those of the equilibrium vector in Figure 1 (although they need not be). This pattern is not predictable from the patterns of the elasticities of the population vectors $\hat{\mathbf{n}}_1$ and $\hat{\mathbf{n}}_2$ (Figure 8a).

Finally, the elasticities of the time averages, $\bar{N}$ and $\bar{R}$, of the weighted densities are similar to each other tnd to the elasticities of the time-averaged population $\bar{\mathbf{n}}$.

Figure 8: **Analysis of a 2-cycle in the *Tribolium* model. (a) Elasticity of the density of each stage, with respect to each parameter, at $\hat{\mathrm{n}}_1$ and $\hat{\mathrm{n}}_2$. (b) Elasticity of the total population $\hat{N}$ at each point in the cycle. (c) Elasticity of the total respiration $\hat{R}$ at each point in the cycle. (d) Elasticity of the time-averaged population $\bar{\mathrm{n}}$. (e) Elasticity of the time-averaged total population $\bar{N}$ and the time-averaged total respiration $\bar{R}$**



◇

The sensitivity analysis of cycles thus depends very much on the dependent variables of interest. The matrix $d\mathbb{N}/d\boldsymbol{\theta}^{\mathsf{T}}$ (Figure 8a) contains 36 pieces of information: the effects of 6 parameters on 3 stages at 2 points in the cycle. A focus on weighted density reduces this to 12 (Figures 8b,c), but the results may depend very much on the particular weighting vector chosen. A focus on time averages reduces the information from 36 to 18 numbers (Figure 8d), and the response of the time-averaged weighted densities finally are described by just 6 numbers. The good news is that equations (120), (124), (126), and (127) make it easy to compute all these sensitivities.

8.3 Sensitivity of temporal variance in density

The variance over a cycle in a weighted density $\hat{N}$ can be written

$$V(\hat{N}) = E(\hat{N}^2) - \Big[E(\hat{N})\Big]^2 \tag{132}$$

where $E(\hat{N}) = \bar{N} = \mathbf{c}^{\mathsf{T}}\mathbf{G}\mathbf{b}$ and

$$\begin{aligned} E(\hat{N}^2) &= \sum_{i=1}^{k} b_i \left(\mathbf{c}^{\mathsf{T}}\hat{\mathbf{n}}_i\right)^2 & (133)\\ &= (\mathbf{c}\circ\mathbf{c})^{\mathsf{T}}(\mathbf{G}\circ\mathbf{G})\mathbf{b} & (134)\end{aligned}$$

Taking the differential of $E(\hat{N}^2)$ and applying the vec operator gives

$$dE(\hat{N}^2) = 2\left[\mathbf{b}^{\mathsf{T}}\otimes(\mathbf{c}\circ\mathbf{c})^{\mathsf{T}}\right]\operatorname{diag}(\mathbb{N})\, d\mathbb{N}. \tag{135}$$

Combining this with the differential of $E(\hat{N})^2$ gives the sensitivity of $V(\hat{N})$:

$$\frac{dV(\hat{N})}{d\boldsymbol{\theta}^{\mathsf{T}}} = 2\left\{\left[\mathbf{b}^{\mathsf{T}}\otimes(\mathbf{c}\circ\mathbf{c})^{\mathsf{T}}\right]\operatorname{diag}(\mathbb{N}) - \bar{N}\left(\mathbf{b}^{\mathsf{T}}\otimes\mathbf{c}^{\mathsf{T}}\right)\right\}\frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}} \tag{136}$$

where $d\mathbb{N}/d\boldsymbol{\theta}^{\mathsf{T}}$ is given by (120). The extension to higher moments, should one want to know, say, the sensitivity of the skewness of population size over a cycle, is possible.

8.4 Dynamic environmental feedback models

The static environmental feedback model of Section 4. assumed that the environmental variable $\mathbf{g}(t)$ had no inherent dynamics of its own. A more general, dynamic environmental feedback model can be written

$$\begin{aligned} \mathbf{n}(t+1) &= \mathbf{A}[\boldsymbol{\theta},\mathbf{n}(t),\mathbf{g}(t)]\mathbf{n}(t)\\ \mathbf{g}(t+1) &= \mathbf{B}[\boldsymbol{\theta},\mathbf{n}(t),\mathbf{g}(t)]\mathbf{g}(t) & (137)\end{aligned}$$

allowing for $\mathbf{n}(t)$ to depend on both the environment and on its own density, and likewise for the environmental factor.

The sensitivity of the equilibrium of (137) can be found using an approach similar to that applied above to cycles. At equilibrium,

$$\begin{aligned} \hat{\mathbf{n}} &= \mathbf{A}[\boldsymbol{\theta}, \hat{\mathbf{n}}, \hat{\mathbf{g}}]\hat{\mathbf{n}} \qquad (138) \\ \hat{\mathbf{g}} &= \mathbf{B}[\boldsymbol{\theta}, \hat{\mathbf{n}}, \hat{\mathbf{g}}]\hat{\mathbf{g}} \qquad (139) \end{aligned}$$

Differentiating both sides of each equation, expanding $d\text{vec}\,\mathbf{A}$ and $d\text{vec}\,\mathbf{B}$, and applying the vec operator gives

$$d\hat{\mathbf{n}} = \mathbf{A}\left(d\hat{\mathbf{n}}\right) + \left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right)\left(\frac{\partial \text{vec}\,\mathbf{A}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} d\boldsymbol{\theta} + \frac{\partial \mathbf{A}}{\partial \mathbf{n}^{\mathsf{T}}} d\hat{\mathbf{n}} + \frac{\partial \mathbf{A}}{\partial \mathbf{g}^{\mathsf{T}}} d\hat{\mathbf{g}}\right) \qquad (140)$$

$$d\hat{\mathbf{g}} = \mathbf{B}\left(d\hat{\mathbf{n}}\right) + \left(\hat{\mathbf{g}}^{\mathsf{T}} \otimes \mathbf{I}_q\right)\left(\frac{\partial \text{vec}\,\mathbf{B}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} d\boldsymbol{\theta} + \frac{\partial \mathbf{B}}{\partial \mathbf{n}^{\mathsf{T}}} d\hat{\mathbf{n}} + \frac{\partial \mathbf{B}}{\partial \mathbf{g}^{\mathsf{T}}} d\hat{\mathbf{g}}\right). \qquad (141)$$

Applying the identification theorem and the chain rule gives

$$\begin{aligned} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} &= \mathbf{A}\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} + \left(\hat{\mathbf{n}} \otimes \mathbf{I}_s\right)\frac{\partial \text{vec}\,\mathbf{A}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} + \left(\hat{\mathbf{n}} \otimes \mathbf{I}_s\right)\frac{\partial \text{vec}\,\mathbf{A}}{\partial \mathbf{n}^{\mathsf{T}}}\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} \\ &\quad + \left(\hat{\mathbf{n}} \otimes \mathbf{I}_s\right)\frac{\partial \text{vec}\,\mathbf{A}}{\partial \mathbf{g}^{\mathsf{T}}}\frac{d\hat{\mathbf{g}}}{d\boldsymbol{\theta}^{\mathsf{T}}} \qquad (142) \end{aligned}$$

with a similar expression for $d\hat{\mathbf{g}}/d\boldsymbol{\theta}^{\mathsf{T}}$. All matrices and their derivatives are evaluated at the equilibrium $(\hat{\mathbf{n}}, \hat{\mathbf{g}})$. This system can be written in block matrix form by defining

$$\begin{aligned} \mathbf{H} &\equiv \left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right) \qquad (143) \\ \mathbf{J} &\equiv \left(\hat{\mathbf{g}}^{\mathsf{T}} \otimes \mathbf{I}_q\right) \qquad (144) \end{aligned}$$

Then define

$$\mathbb{A} = \left(\begin{array}{c|c} \mathbf{A} & 0 \\ \hline 0 & \mathbf{B} \end{array}\right) \qquad (145)$$

$$\mathbb{H} = \left(\begin{array}{c|c} 0 & \mathbf{H} \\ \hline \mathbf{J} & 0 \end{array}\right) \qquad (146)$$

$$\mathbb{C} = \left(\begin{array}{c|c} \dfrac{\partial \text{vec}\,\mathbf{B}}{\partial \mathbf{n}^{\mathsf{T}}} & \dfrac{\partial \text{vec}\,\mathbf{B}}{\partial \mathbf{g}^{\mathsf{T}}} \\ \hline \dfrac{\partial \text{vec}\,\mathbf{A}}{\partial \mathbf{n}^{\mathsf{T}}} & \dfrac{\partial \text{vec}\,\mathbf{A}}{\partial \mathbf{g}^{\mathsf{T}}} \end{array}\right) \qquad (147)$$

$$\mathbb{D} = \begin{pmatrix} \dfrac{\partial \text{vec}\,\mathbf{A}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} \\ \dfrac{\partial \text{vec}\,\mathbf{B}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} \end{pmatrix} \tag{148}$$

$$\mathbb{N} = \begin{pmatrix} \hat{\mathbf{n}} \\ \hat{\mathbf{g}} \end{pmatrix} \tag{149}$$

In terms of these matrices,

$$\frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \mathbb{H}\mathbb{D} + (\mathbb{A} + \mathbb{H}\mathbb{C}) \frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}}. \tag{150}$$

Solving for $d\mathbb{N}/d\boldsymbol{\theta}^t r$ gives the sensitivity of both the population and the environmental factor,

$$\frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\mathbf{I}_{s+q} - \mathbb{A} - \mathbb{H}\mathbb{C}\right)^{-1} \mathbb{H}\mathbb{D}. \tag{151}$$

9. Sensitivity of life expectancy

Life expectancy is traditionally calculated from linear age-classified models. It can also be calculated from linear stage-classified models (Caswell 2001, 2006). Here, I extend the caculation to the equilibria of nonlinear age- or stage-classified models. Write the density-dependent projection matrix as

$$\mathbf{A}[\boldsymbol{\theta}, \mathbf{n}] = \mathbf{U}[\boldsymbol{\theta}, \mathbf{n}] + \mathbf{F}[\boldsymbol{\theta}, \mathbf{n}] \tag{152}$$

where $\mathbf{U}$ contains the transition probabilities for individuals already present in the population and $\mathbf{F}$ describes the production of new individuals by reproduction (this decomposition dates back to Feichtinger 1971; see Caswell 2001 Chapter 5, Caswell 2006, Tuljapurkar and Horvitz 2006 for recent developments). The matrix $\mathbf{U}$ is the transient matrix of an absorbing Markov chain, with death as an absorbing state. The fundamental matrix of this chain at equilibrium is

$$\mathbf{N}[\boldsymbol{\theta}, \hat{\mathbf{n}}] = \left(\mathbf{I}_s - \mathbf{U}[\boldsymbol{\theta}, \hat{\mathbf{n}}]\right)^{-1} \tag{153}$$

where the inverse is guaranteed to exist if the spectral radius of $\mathbf{U}$ is less than 1 (Iosifescu 1980). The (i, j) element of $\mathbf{N}$ is the expected time spent in stage i, before death, by an individual in stage j. Suppose that stage 1 represents newborn individuals. Then the life

Table 3: Summary of models and main sensitivity results of the paper. Extending sensitivities to additional dependent variables (ratios, averages, rates, etc.) is described in Section 3.2. The extension from sensitivities to elasticities is given in Section 3.3.

Model	Sensitivity of …		Equation[s]
Density-dependent	… equilibrium	$\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(23)
$\mathbf{n}(t+1) = \mathbf{A}\left[\boldsymbol{\theta}, \mathbf{n}(t)\right] \mathbf{n}(t)$	… cycle	$\frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(120)
	… weighted density, time average		(124) – (127)
	… temporal variance	$\frac{dV(\hat{N})}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(136)
	… life expectancy	$\frac{d\eta_1}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(157)
Environmental feedback			
$\mathbf{n}(t+1) = \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t), \mathbf{g}(t)]\ \mathbf{n}(t)$			
$\mathbf{g}(t) = \mathbf{g}[\boldsymbol{\theta}, \mathbf{n}(t)]$	... equilibrium (static)	$\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}}, \frac{d\hat{\mathbf{g}}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(54), (55)
$\mathbf{g}(t+1) = \mathbf{B}[\boldsymbol{\theta}, \mathbf{n}(t), \mathbf{g}(t)]\ \mathbf{g}(t)$	… equilibrium (dynamic)	$\frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(151)

Table 3: (continued)

Model	Sensitivity of …		Equation[s]
Frequency-dependent (two-sex) $\mathbf{n}(t+1) = \mathbf{A}\left[\boldsymbol{\theta}, \mathbf{n}(t)\right]\mathbf{n}(t)$ $\mathbf{A}[\boldsymbol{\theta}, \mathbf{n}]$ homogeneous of degree zero in $\mathbf{n}$	… equilibrium structure	$\dfrac{d\hat{\mathbf{p}}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(94)
	… population growth rate	$\dfrac{d\lambda}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(97)
Subsidized (linear or nonlinear) $\mathbf{n}(t+1) = \mathbf{A}\left[\boldsymbol{\theta}, \mathbf{n}(t)\right]\mathbf{n}(t) + \mathbf{b}[\boldsymbol{\theta}, \mathbf{n}]$	… equilibrium population	$\dfrac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(60), (70)
Proportional structure $\mathbf{p}(t+1) = \dfrac{\mathbf{A}[\boldsymbol{\theta}]\mathbf{p}(t)}{\mathbf{e}^{\mathsf{T}}\mathbf{A}[\boldsymbol{\theta}]\mathbf{p}(t)}$	… age- or stage distribution	$\dfrac{d\hat{\mathbf{p}}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(75)
	… reproductive value	$\dfrac{d\hat{\mathbf{v}}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(79)
	… dependency ratio	$\dfrac{dD}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(81)
	… mean age of reproduction	$\dfrac{d\bar{a}_{\mathbf{f}}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(83)
	… variance in age of reproduction	$\dfrac{dV_{\mathbf{f}}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(89)

expectancy at birth is the mean time to absorbtion (i.e., death) for an individual in stage 1. This is η_1, the first entry of the vector obtained by summing the columns of $\mathbf{N}$; i.e.,

$$\eta_1 = \mathbf{e}^{\mathsf{T}}\mathbf{N}\mathbf{e}_1 \tag{154}$$

where $\mathbf{e}_1$ has 1 in the first entry and 0 elsewhere.[15] Differentiating η_1 and applying the vec operator gives

$$d\eta_1 = \left(\mathbf{e}_1^{\mathsf{T}} \otimes \mathbf{e}^{\mathsf{T}}\right) d\text{vec}\,\mathbf{N}, \tag{155}$$

but $d\text{vec}\,\mathbf{N} = \left(\mathbf{N}^{\mathsf{T}} \otimes \mathbf{N}\right) d\text{vec}\,\mathbf{U}$ (Caswell 2006), and in the nonlinear model

$$d\text{vec}\,\mathbf{U} = \frac{\partial \text{vec}\,\mathbf{U}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} d\boldsymbol{\theta} + \frac{\partial \text{vec}\,\mathbf{U}}{\partial \mathbf{n}^{\mathsf{T}}} d\hat{\mathbf{n}}. \tag{156}$$

Thus

$$\frac{d\eta_1}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\mathbf{e}_1^{\mathsf{T}} \otimes \mathbf{e}^{\mathsf{T}}\right) \left[\left(\mathbf{N}^{\mathsf{T}} \otimes \mathbf{N}\right) \frac{\partial \text{vec}\,\mathbf{U}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} + \left(\mathbf{N}^{\mathsf{T}} \otimes \mathbf{N}\right) \frac{\partial \text{vec}\,\mathbf{U}}{\partial \mathbf{n}} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}} \right] \tag{157}$$

where $\mathbf{U}$, $\mathbf{N}$, and the derivatives of $\mathbf{U}$ are evaluated at equilibrium and $d\hat{\mathbf{n}}/d\boldsymbol{\theta}^{\mathsf{T}}$ is given by (23). In a linear model, $\mathbf{U}$ is independent of $\mathbf{n}$ and (157) reduces to the sensitivity of life expectancy given in Caswell (2006).

10. Summary and discussion

The results obtained in this paper (Table 3) comprise a fairly complete perturbation analysis of nonlinear demographic models. The nonlinearities may arise from density-dependence, frequency-dependence, environmental feedback, proportional population structure calculations, or recruitment subsidy. The sensitivity calculations accommodate a wide range of dependent variables and the calculation of both sensitivity and elasticity with respect to any kind of demographic parameters.

Most of the results in this paper follow a straightforward method:

1. Write the model, carefully specifying the dependence of the vital rates on $\boldsymbol{\theta}$ and $\mathbf{n}$.
2. Write an expression for the equilibrium.
3. Take the differential of the equilibrium; this usually includes matrix differentials of the form $d\mathbf{A}$.
4. Use the vec operator and Roth's theorem to obtain an expression that involves only the differentials of vectors.
5. If necessary, use the chain rule for total differentials to expand $dvec\mathbf{A}$ as in (21).

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[15] The usual demographic notation for life expectancy at age x is $\overset{o}{e}_x$, but the letter e is already doing heavy lifting in this paper, so I have adopted a notation (Caswell 2006) used in the Markov chain literature (e.g., Iosifescu 1980) for the mean time to absorbtion.

6. Solve for $d\hat{\mathbf{n}}$ and use the first identification theorem (10) to get the derivative $d\hat{\mathbf{n}}/d\boldsymbol{\theta}^{\mathsf{T}}$.
7. If desired, use the chain rule to develop sensitivities of a different dependent variable (call it $\mathbf{m}$), to a different set of parameters (call it ξ):

$$\frac{d\hat{\mathbf{m}}}{d\boldsymbol{\xi}^{\mathsf{T}}} = \frac{d\hat{\mathbf{m}}}{d\hat{\mathbf{n}}^{\mathsf{T}}} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} \frac{d\boldsymbol{\theta}}{d\boldsymbol{\xi}}.$$

   Obtain elasticities using (43).

The extension of perturbation analysis from linear to nonlinear models has many applications. Grant and Benton (2003), for example, emphasized the distinction between applications in evolutionary demography and applications in population policy, management, and conservation. Evolutionary questions depend on the selection gradients on traits. A selection gradient is the sensitivity of the rate of increase of a phenotype, when introduced at low density into a population with some other phenotype. This rate of increase is called an invasion exponent; the sensitivity analysis of these exponents in nonlinear models is now well understood (Caswell 2001, Section 16.11, Caswell et al. 2004, Caswell 2007b). On the other hand, population management (protecting endangered species, controlling invasive pests, or maintaining sustainable harvests) focuses more on equilibrium population size than on growth rates. The methods of this paper solve these problems.

This approach could be applied to many other demographic problems. Of particular interest are stage-classified epidemic models (Klepac et al. 2007), transient amplification of perturbations in reactive ecological systems (Verdy and Caswell 2008), and the decomposition of rates into components due to changes in the vital rates and to changes in population structure (a problem independently investigated by ecologists and human demographers (Vaupel and Romo 2002, Bullock et al. 1996).

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