Chapter 10
Sensitivity Analysis of Nonlinear Demographic Models

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10.1 Introduction

Nonlinearities in demographic models arise due to density dependence, frequency dependence (in 2-sex models), feedback through the environment or the economy, recruitment subsidy due to immigration, and from the scaling inherent in calculations of proportional population structure. This chapter presents a series of analyses particular to nonlinear models: 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.

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 given by

$$\mathbf{x}(t+1) = f[\mathbf{x}(t)], \tag{10.1}$$

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

$$f(a\mathbf{x}_1 + b\mathbf{x}_2) = af(\mathbf{x}_1) + bf(\mathbf{x}_2) \tag{10.2}$$

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

If a model is not linear, it is nonlinear. Not surprisingly, this covers a lot of territory, but nonlinearity in demographic models can be classified into four main sources: density dependence, environmental feedback, interactions between the sexes, and models that arise in calculation of proportional structure.

Density dependence: arises when one or more of the per-capita vital rates are functions of the numbers or density of the population. Such effects have been incorporated into demographic studies of plants (e.g., Solbrig et al. 1988; Gillman et al. 1993; Silva Matos et al. 1999; Pardini et al. 2009; Shyu et al. 2013) and animals (e.g., Pennycuick 1969; Clutton-Brock et al. 1997; Cushing et al. 2003; Bonenfant et al. 2009). 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[1]. Weiss and Smouse (1976) proposed a density-dependent matrix model, and Wood and Smouse (1982) applied it to the Gainj people of Papua New Guinea. Density dependence is included in epidemiological feedback models applied to a rural English population in the sixteenth and seventeenth centuries by Scott and Duncan (1998).

  The Easterlin effect (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. Models in which the feedback operates through resource consumption are the basis for the food chain and food web models that underlie models of global biogeochemistry (e.g.,. Hsu et al. 1977; Tilman 1982; Murdoch et al. 2003; Fennel and Neumann 2004). These models are typically unstructured, but there is a rich literature on structured models, written as partial differential equations, to incorporate physiological structure and resource feedback (de Roos and Persson 2013).

  Feedback models are also 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

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[1]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 human demography (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).

economic feedback appears in the food ratio model recently proposed by Lee and Tuljapurkar (2008).

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 (10.2). Nonlinear two-sex models have a long tradition in human demography (see reviews in Keyfitz 1972; 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; Jenouvrier et al. 2010, 2012). Their mathematical properties have been investigated by e.g, Caswell and Weeks (1986), Chung (1994) and Iannelli 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 their analysis 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.

This chapter analyzes the sensitivity and elasticity of equilibria and cycles. Because the dynamic models considered here are discrete, solutions always exist and are unique. The nature and the 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.

10.2   Density-Dependent Models

We begin with the basic discrete-time[2] density-dependent model, written as

$$\mathbf{n}(t + 1) = \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t)]\, \mathbf{n}(t) \tag{10.3}$$

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[2]It is possible to generalize to continuous-time models, that would be written

$$\frac{d\mathbf{n}}{dt} = \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t)]\, \mathbf{n}(t)$$

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]

10.2.1   Linearizations Around Equilibria

An equilibrium of (10.3) satisfies

$$\hat{\mathbf{n}} = \mathbf{A}\left[\boldsymbol{\theta}, \hat{\mathbf{n}}\right]\hat{\mathbf{n}}. \tag{10.4}$$

Such an equilibrium may be stable (small perturbations from $\hat{\mathbf{n}}$ eventually return to the equilibrium) or unstable.[4] That stability is determine by the linearization of the nonlinear system (10.3) near $\hat{\mathbf{x}}$. That is, define the deviation from $\hat{\mathbf{x}}$ as $\mathbf{z}(t) = \mathbf{x}(t) - \hat{\mathbf{x}}$. Then $\mathbf{z}(t)$ follows

$$\mathbf{z}(t+1)\mathbf{M}[\boldsymbol{\theta}, \hat{\mathbf{x}}]\mathbf{z}(t) \tag{10.5}$$

The matrix $\mathbf{M}$ is the Jacobian matrix,

$$\mathbf{M} = \left.\frac{\partial \mathbf{x}(t+1)}{\partial \mathbf{x}^{\mathsf{T}}(t)}\right|_{\hat{\mathbf{x}}} \tag{10.6}$$

To obtain $\mathbf{M}$, differentiate both sides of (10.3),

$$d\mathbf{x}(t+1) = (d\mathbf{A})\,\mathbf{x} + \mathbf{A}\,(d\mathbf{x}) \tag{10.7}$$

Applying the vec operator to both sides gives

$$d\mathbf{x}(t+1) = \left(\mathbf{x}^{\mathsf{T}} \otimes \mathbf{I}_s\right) d\text{vec}\,\mathbf{A} + \mathbf{A}d\mathbf{x} \tag{10.8}$$

from which

$$\mathbf{M} = \left(\mathbf{x}^{\mathsf{T}} \otimes \mathbf{I}_s\right) \frac{d\text{vec}\,\mathbf{A}}{d\mathbf{x}^{\mathsf{T}}} + \mathbf{A} \tag{10.9}$$

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for some appropriately defined matrix function $\mathbf{A}$; see Verdy and Caswell (2008). Such models are less often used, but see Shyu and Caswell (2016a, 2018) for a two-sex model example.

[3]The explicit dependence on $\boldsymbol{\theta}$ and $\mathbf{n}(t)$ will be neglected when it is obvious from the context.

[4]A careful consideration of stability requires more care with the definition of these terms, but will not concern us here. See Caswell (2001) and Cushing (1998) for more details.

where $\mathbf{I}_s$ is an identity matrix of order s. The linearization at the equilibrium is obtained by evaluating $\mathbf{M}$ at $\mathbf{x} = \hat{\mathbf{x}}$:

$$\mathbf{M}\left[\boldsymbol{\theta}, \hat{\mathbf{x}}\right] = \left(\hat{\mathbf{x}}^\mathsf{T} \otimes \mathbf{I}_s\right) \frac{\partial \operatorname{vec} \mathbf{A}\left[\boldsymbol{\theta}, \hat{\mathbf{x}}\right]}{\partial \mathbf{x}^\mathsf{T}} + \mathbf{A}\left[\boldsymbol{\theta}, \hat{\mathbf{x}}\right] \qquad (10.10)$$

If all the eigenvalues of $\mathbf{M}$ are less than one in magnitude, the equilibrium $\hat{\mathbf{x}}$ is locally asymptotically stable. The linearization also provides valuable information about short-term transient responses to perturbation; see Sect. 10.2.4.

10.2.2 Sensitivity of Equilibrium

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 (10.4):

$$d\hat{\mathbf{n}} = (d\mathbf{A})\hat{\mathbf{n}} + \mathbf{A}(d\hat{\mathbf{n}}). \qquad (10.11)$$

Rewrite this as

$$d\hat{\mathbf{n}} = \mathbf{I}_s(d\mathbf{A})\hat{\mathbf{n}} + \mathbf{A}(d\hat{\mathbf{n}}), \qquad (10.12)$$

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, $\operatorname{vec} \hat{\mathbf{n}} = \hat{\mathbf{n}}$, and apply Roth's theorem, to obtain

$$d\hat{\mathbf{n}} = \left(\hat{\mathbf{n}}^\mathsf{T} \otimes \mathbf{I}_s\right) d\operatorname{vec} \mathbf{A} + \mathbf{A}d\hat{\mathbf{n}}. \qquad (10.13)$$

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

$$d\operatorname{vec} \mathbf{A} = \frac{\partial \operatorname{vec} \mathbf{A}}{\partial \boldsymbol{\theta}^\mathsf{T}} d\boldsymbol{\theta} + \frac{\partial \operatorname{vec} \mathbf{A}}{\partial \mathbf{n}^\mathsf{T}} d\hat{\mathbf{n}}. \qquad (10.14)$$

Substituting (10.14) into (10.13) and applying the chain rule leads to[5]

$$\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^\mathsf{T}} = \left(\hat{\mathbf{n}}^\mathsf{T} \otimes \mathbf{I}_s\right) \left(\frac{\partial \operatorname{vec} \mathbf{A}}{\partial \boldsymbol{\theta}^\mathsf{T}} + \frac{\partial \operatorname{vec} \mathbf{A}}{\partial \mathbf{n}^\mathsf{T}} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^\mathsf{T}}\right) + \mathbf{A}\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^\mathsf{T}}. \qquad (10.15)$$

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

Finally, solve (10.15) for $d\hat{\mathbf{n}}/d\boldsymbol{\theta}^\mathsf{T}$ to obtain

$$\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^\mathsf{T}} = \left(\mathbf{I}_s - \mathbf{A} - \left(\hat{\mathbf{n}}^\mathsf{T} \otimes \mathbf{I}_s\right) \frac{\partial \operatorname{vec} \mathbf{A}}{\partial \mathbf{n}^\mathsf{T}}\right)^{-1} \left(\hat{\mathbf{n}}^\mathsf{T} \otimes \mathbf{I}_s\right) \frac{\partial \operatorname{vec} \mathbf{A}}{\partial \boldsymbol{\theta}^\mathsf{T}} \qquad (10.16)$$

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

Comparing (10.16) and Eq. (10.10) for the linearization, we see that the sensitivity of equilibrium can be written

$$\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^\mathsf{T}} = (\mathbf{I}_s - \mathbf{M})^{-1} \left(\hat{\mathbf{n}}^\mathsf{T} \otimes \mathbf{I}_s\right) \frac{\partial \operatorname{vec} \mathbf{A}}{\partial \boldsymbol{\theta}^\mathsf{T}}. \qquad (10.17)$$

The matrix $(\mathbf{I}_s - \mathbf{M})$ is singular if 1 is an eigenvalue of $\mathbf{M}$; i.e., at a bifurcation point when the equilibrium $\hat{\mathbf{n}}$ becomes unstable. At that point, quite appropriately, the sensitivity is not defined because the change in the equilibrium is not continuous.

The following example, applying (10.16) 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

$$\mathbf{A} = \begin{pmatrix} \sigma_1(1 - \gamma) & f \\ \sigma_1 \gamma & \sigma_2 \end{pmatrix}. \qquad (10.18)$$

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

$$\sigma_1(\mathbf{n}) = \tilde{\sigma} \exp(-\mathbf{1}^\mathsf{T}\mathbf{n}); \qquad (10.19)$$

where $\mathbf{1}$ is a vector of ones.

Define the parameter vector as $\boldsymbol{\theta} = \left(f \ \gamma \ \tilde{\sigma} \ \sigma_2 \right)^\mathsf{T}$. To apply (10.16) requires the derivatives of $\mathbf{A}[\boldsymbol{\theta}, \mathbf{n}]$ with respect to $\boldsymbol{\theta}$ and with respect to $\mathbf{n}$. These are

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

$$\frac{d\text{vec }\mathbf{A}}{df} = \text{vec}\begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix} \tag{10.20}$$

$$\frac{d\text{vec }\mathbf{A}}{d\gamma} = \text{vec}\begin{pmatrix} -\sigma_1(\mathbf{n}) & 0 \\ \sigma_1(\mathbf{n}) & 0 \end{pmatrix} \tag{10.21}$$

$$\frac{d\text{vec }\mathbf{A}}{d\tilde{\sigma}} = \text{vec}\begin{pmatrix} (1-\gamma)\exp(-\mathbf{1}^\mathsf{T}\mathbf{n}) & 0 \\ \gamma\exp(-\mathbf{1}^\mathsf{T}\mathbf{n}) & 0 \end{pmatrix} \tag{10.22}$$

$$\frac{d\text{vec }\mathbf{A}}{d\sigma_2} = \text{vec}\begin{pmatrix} 0 & 0 \\ 0 & 1 \end{pmatrix} \tag{10.23}$$

$$\frac{d\text{vec }\mathbf{A}}{dn_1} = \frac{d\text{vec }\mathbf{A}}{dn_2} = \text{vec}\begin{pmatrix} -\sigma_1(\mathbf{n})(1-\gamma) & 0 \\ -\sigma_1(\mathbf{n})\gamma & 0 \end{pmatrix}. \tag{10.24}$$

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

$$\frac{\partial\text{vec }\mathbf{A}}{\partial\boldsymbol{\theta}^\mathsf{T}} = \begin{pmatrix} 0 & -\sigma_1(\mathbf{n}) & (1-\gamma)\exp(-\mathbf{1}^\mathsf{T}\mathbf{n}) & 0 \\ 0 & \sigma_1(\mathbf{n}) & \gamma\exp(-\mathbf{1}^\mathsf{T}\mathbf{n}) & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}, \tag{10.25}$$

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

$$\frac{\partial\text{vec }\mathbf{A}}{\partial\mathbf{n}^\mathsf{T}} = \begin{pmatrix} -\sigma_1(\mathbf{n})(1-\gamma) & -\sigma_1(\mathbf{n})(1-\gamma) \\ -\sigma_1(\mathbf{n})\gamma & -\sigma_1(\mathbf{n})\gamma \\ 0 & 0 \\ 0 & 0 \end{pmatrix}. \tag{10.26}$$

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)

$$f = 0.25$$

$$\gamma = 1/15$$

$$\tilde{\sigma} = 0.98$$

$$\sigma_2 = 0.95$$

leads to an equilibrium population

$$\hat{\mathbf{n}} = \begin{pmatrix} 0.1053 \\ 0.1109 \end{pmatrix}, \qquad (10.27)$$

obtained by iterating the model to convergence.

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

$$\hat{\mathbf{n}} = \begin{pmatrix} 1.826 \\ 0.026 \end{pmatrix} \qquad (10.28)$$

with sensitivities

$$\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^\mathsf{T}} = \begin{pmatrix} 0.01 & 1.08\ 9.86\ 0.99 \\ -0.0002 & 0.02\ 0.14\ 0.01 \end{pmatrix}. \qquad (10.29)$$

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.   ∎

10.2.3 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

$$\frac{d\hat{\mathbf{m}}}{d\boldsymbol{\theta}^\mathsf{T}} = \frac{d\hat{\mathbf{m}}}{d\mathbf{n}^\mathsf{T}} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^\mathsf{T}}. \qquad (10.30)$$

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 ($\mathbf{c} = \mathbf{1}$), 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

$$\frac{d\hat{N}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \mathbf{c}^{\mathsf{T}} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}}. \tag{10.31}$$

2. Ratios, measuring the relative abundances of different stages. Let

$$R(t) = \frac{\mathbf{a}^{\mathsf{T}} \mathbf{n}(t)}{\mathbf{b}^{\mathsf{T}} \mathbf{n}(t)} \tag{10.32}$$

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 Sect. 10.5.3), the sex ratio, and the ratio of juveniles to adults, which is used in wildlife management; see Skalski et al. (2005). Differentiating (10.32) gives

$$\frac{d\hat{R}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\frac{\mathbf{b}^{\mathsf{T}} \hat{\mathbf{n}} \mathbf{a}^{\mathsf{T}} - \mathbf{a}^{\mathsf{T}} \hat{\mathbf{n}} \mathbf{b}^{\mathsf{T}}}{(\mathbf{b}^{\mathsf{T}} \hat{\mathbf{n}})^2} \right) \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}}. \tag{10.33}$$

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 Sect. 10.5.4.
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 Sect. 10.7.

10.2.4 Reactivity and Transient Dynamics

The asymptotic stability of an equilibrium is determined by the eigenvalues of the Jacobian matrix $\mathbf{M}$ in (10.9), evaluated at that equilibrium. In the short term, however, perturbations of the population away from the equilibrium can exhibit transient dynamics that differ from their asymptotic behavior. In particular, perturbations of stable equilibria, that are destined to eventually return to the equilibrium, may move (much) farther away before that return. Neubert and Caswell (1997) introduced three indices, each calculated from $\mathbf{M}$, to quantify these transient responses.[6] The *reactivity* of an asymptotically stable equilibrium is the maximum, over all perturbations, of the rate at which the trajectory departs from the equilibrium. At any time following a perturbation, there is a maximum (over all perturbations) deviation

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[6]Because these indices are calculated from $\mathbf{M}$, they are properly considered properties of the system and its dynamics. Stott et al. (2011) and Stott (2016) have also considered indices of transient response that reflect the particular initial condition rather than the inherent dynamics of the system.

from the equilibrium. This maximum is the *amplification envelope*. It gives an upper bound on the extent of transient amplification as a function of time. The phrase "over all perturbations" in these definitions signals that the transient amplification depends on the direction of the perturbation. The perturbation that produces the maximum amplification at any specified time is the *optimal perturbation* (Verdy and Caswell 2008).[7]

The transient dynamics of the perturbed system are described by the evolution of the magnitude of $\mathbf{z}$, as measured by the Euclidean norm $\|\mathbf{z}\| = \sqrt{\mathbf{z}^\mathsf{T}\mathbf{z}}$. The reactivity is the maximum, over all perturbations, of the growth rate of $\|\mathbf{z}\|$, as $t \to 0$, and is given by

$$v_0 = \begin{cases} \lambda_1\left[\mathbf{H}(\mathbf{M})\right] \text{ continuous time} \\ \log \sigma_1\left(\mathbf{M}\right) \text{ discrete time} \end{cases} \tag{10.34}$$

The matrix $\mathbf{H}(\mathbf{M}) = \left(\mathbf{M} + \mathbf{M}^\mathsf{T}\right)/2$ is the Hermitian part of $\mathbf{M}$ and λ_1 denotes the eigenvalue with largest real part (Neubert and Caswell 1997). In discrete time, reactivity is the log of the largest singular value of $\mathbf{M}$, which we denote $\sigma_1(\mathbf{M})$.

The amplification envelope is

$$\rho(t) = \begin{cases} \sigma_1\left(e^{\mathbf{M}t}\right) \text{ continuous} \\ \sigma_1\left(\mathbf{M}^t\right) \text{ discrete} \end{cases} \tag{10.35}$$

The optimal perturbation, normalized to length 1, is given by the right singular vector corresponding to the singular value that defines $\rho(t)$.

Verdy and Caswell (2008) presented a complete sensitivity analysis of reactivity, the amplification envelope, and the optimal perturbation, in both continuous and discrete time. Suppose the ξ be one of the indices, and suppose that the model depends on a parameter vector $\boldsymbol{\theta}$. Changes in $\boldsymbol{\theta}$ will change the equilibrium vector, which will contribute to changes in the Jacobian matrix, so that the sensitivity of ξ to $\boldsymbol{\theta}$ is

$$\frac{d\xi}{d\boldsymbol{\theta}^\mathsf{T}} = \left(\frac{d\xi}{d\text{vec}^\mathsf{T}\mathbf{M}}\right)\left(\frac{\partial \text{vec}\,\mathbf{M}}{\partial \boldsymbol{\theta}^\mathsf{T}} + \frac{\partial \text{vec}\,\mathbf{M}}{\partial \hat{\mathbf{n}}^\mathsf{T}}\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^\mathsf{T}}\right) \tag{10.36}$$

The sensitivity of ξ in (10.36) requires four pieces: the linearization $\mathbf{M}$ at the equilibrium, which is given by (10.10), the sensitivity of the equilibrium $\hat{\mathbf{n}}$ to the parameters, which is given by (10.16), the sensitivity of the Jacobian matrix $\mathbf{M}$ to the parameters, and the sensitivity of the index ξ to the matrix $\mathbf{M}$. The sensitivity

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[7]It is now known that reactivity is a common property of many ecological systems, including populations described by discrete matrix population models (Neubert and Caswell 1997; Chen and Cohen 2001; Neubert et al. 2004; Marvier et al. 2004; Caswell and Neubert 2005; Verdy and Caswell 2008).

of ξ to $\mathbf{M}$ depends on which index, but the calculations involve perturbations of eigenvalues, singular values, or the matrix exponential, and are given in Verdy and Caswell (2008). The derivative of the linearization $\mathbf{M}$ is obtained by differentiating all the terms in Eq. (10.10); the result, along with several examples, is given in Verdy and Caswell (2008, eq. (37)).

10.2.5 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,

$$\frac{\epsilon \hat{\mathbf{n}}}{\epsilon \boldsymbol{\theta}^\mathsf{T}} = \mathcal{D}\left(\hat{\mathbf{n}}\right)^{-1} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^\mathsf{T}} \mathcal{D}\left(\boldsymbol{\theta}\right), \tag{10.37}$$

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

$$\frac{\epsilon f(\hat{\mathbf{n}})}{\epsilon \boldsymbol{\theta}^\mathsf{T}} = \mathcal{D}\left(f(\hat{\mathbf{n}})\right)^{-1} \frac{df(\hat{\mathbf{n}})}{d\boldsymbol{\theta}^\mathsf{T}} \mathcal{D}\left(\boldsymbol{\theta}\right). \tag{10.38}$$

As usual, elasticities can only be calculated when $\boldsymbol{\theta} \geq 0$ and $f(\hat{\mathbf{n}}) > 0$.

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

$$\mathbf{A}[\boldsymbol{\theta}, \mathbf{n}] = \begin{pmatrix} 0 & 0 & b\exp(-c_{el}n_1 - c_{ea}n_3) \\ 1 - \mu_l & 0 & 0 \\ 0 & \exp(-c_{pa}n_3) & 1 - \mu_a \end{pmatrix} \tag{10.39}$$

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)

$$b = 6.598$$

$$c_{ea} = 1.155 \times 10^{-2}$$

$$c_{el} = 1.209 \times 10^{-2}$$

$$c_{pa} = 4.7 \times 10^{-3}$$

$$\mu_a = 7.729 \times 10^{-3}$$

$$\mu_l = 2.055 \times 10^{-1}$$

produce a stable equilibrium

$$\hat{\mathbf{n}} = \begin{pmatrix} 22.6 \\ 18.0 \\ 385.2 \end{pmatrix}. \tag{10.40}$$

The sensitivity of $\hat{\mathbf{n}}$ is calculated using (10.16). 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 $\mathbf{c}^\mathsf{T} = (9\ 1\ 4.5)$, and calculate the sensitivity and elasticity of $\hat{N}_m$ using (10.37) and (10.31).

Figure 10.1 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.
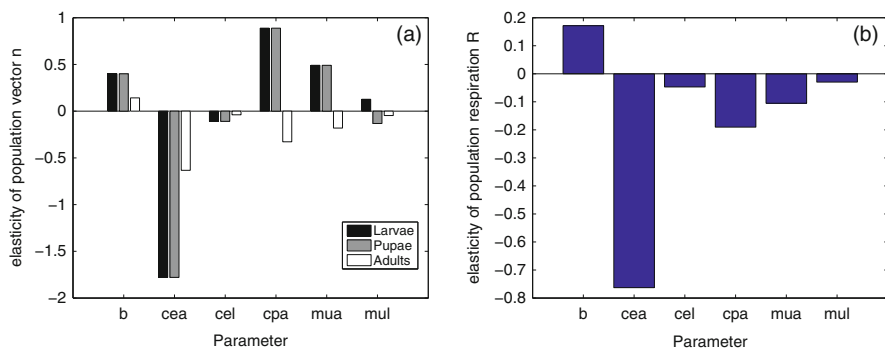

Fig. 10.1 Sensitivity analysis of equilibrium for the flour beetle *Tribolium* in Example 2. (**a**) The elasticity of the equilibrium $\hat{\mathbf{n}}$ to the parameters (see Example 2 for definitions). (**b**) The elasticity of the equilibrium population respiration rate $\hat{N}_m$ to the parameters

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 parameters (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. ■

10.2.6 Continuous-Time Models

We have focused on discrete-time models throughout this book. An analogous perturbation analysis can be carried out on continuous-time models of the form

$$\frac{d\mathbf{n}}{dt} = \mathbf{A}\left[\mathbf{n}(t)\right]\mathbf{n}(t) \tag{10.41}$$

Verdy and Caswell (2008) present a parallel presentation of the continuous and discrete models. The linearization at $\hat{\mathbf{n}}$ is, once again, given by (10.10). If all the eigenvalues of $\mathbf{M}$ have negative real parts, the equilibrium is locally stable.

The sensitivity of the equilibrium $\hat{\mathbf{n}}$ is

$$\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^\mathsf{T}} = \left\{-\mathbf{A} - \left(\hat{\mathbf{n}}^\mathsf{T} \otimes \mathbf{I}_s\right)\frac{\partial \operatorname{vec}\mathbf{A}}{\partial \mathbf{n}^\mathsf{T}}\right\}^{-1}\left(\hat{\mathbf{n}}^\mathsf{T} \otimes \mathbf{I}_s\right)\frac{\partial \operatorname{vec}\mathbf{A}}{\partial \boldsymbol{\theta}^\mathsf{T}}, \tag{10.42}$$

with $\mathbf{A}$ and all its derivatives evaluated at the equilibrium $\hat{\mathbf{n}}$. Substituting (10.10) for $\mathbf{M}$ gives

$$\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^\mathsf{T}} = -\mathbf{M}^{-1}\left(\hat{\mathbf{n}}^\mathsf{T} \otimes \mathbf{I}_s\right)\frac{\partial \operatorname{vec}\mathbf{A}}{\partial \boldsymbol{\theta}^\mathsf{T}}, \tag{10.43}$$

and $\mathbf{M}$ is nonsingular unless 0 is an eigenvalue of $\mathbf{M}$, which corresponds to a bifurcation point of the equilibrium.

10.3 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 Sect. 10.8.

A static feedback model can be written

$$\mathbf{n}(t+1) = \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t), \mathbf{g}(t)] \, \mathbf{n}(t) \tag{10.44}$$

$$\mathbf{g}(t) = \mathbf{g}[\boldsymbol{\theta}, \mathbf{n}(t)] \tag{10.45}$$

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

$$\hat{\mathbf{n}} = \mathbf{A}[\boldsymbol{\theta}, \hat{\mathbf{n}}, \hat{\mathbf{g}}]\hat{\mathbf{n}} \tag{10.46}$$

$$\hat{\mathbf{g}} = \mathbf{g}[\boldsymbol{\theta}, \hat{\mathbf{n}}]. \tag{10.47}$$

Differentiating these expressions gives

$$d\hat{\mathbf{n}} = \mathbf{A}(d\hat{\mathbf{n}}) + (d\mathbf{A})\hat{\mathbf{n}} \tag{10.48}$$

$$d\hat{\mathbf{g}} = \frac{\partial \hat{\mathbf{g}}}{\partial \boldsymbol{\theta}^{\mathsf{T}}}d\boldsymbol{\theta} + \frac{\partial \hat{\mathbf{g}}}{\partial \mathbf{n}}d\hat{\mathbf{n}}. \tag{10.49}$$

Applying the vec operator to (10.48) and expanding $d\text{vec}\,\mathbf{A}$ gives

$$d\hat{\mathbf{n}} = \left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right) \left[\frac{\partial \text{vec}\,\mathbf{A}}{\partial \boldsymbol{\theta}^{\mathsf{T}}}d\boldsymbol{\theta} + \frac{\partial \text{vec}\,\mathbf{A}}{\partial \mathbf{g}^{\mathsf{T}}}d\hat{\mathbf{g}} \right] + \mathbf{A}d\hat{\mathbf{n}}. \tag{10.50}$$

Substituting (10.49) for $d\hat{\mathbf{g}}$ and rearranging gives

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

$$+ \left[\mathbf{A} + \left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right) \frac{\partial \text{vec}\,\mathbf{A}}{\partial \mathbf{g}^{\mathsf{T}}} \frac{\partial \hat{\mathbf{g}}}{\partial \mathbf{n}^{\mathsf{T}}} \right] d\hat{\mathbf{n}}. \tag{10.51}$$

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

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

$$\times \left(\hat{\mathbf{n}} \otimes \mathbf{I}_s\right) \left[\frac{\partial \text{vec}\,\mathbf{A}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} + \frac{\partial \text{vec}\,\mathbf{A}}{\partial \mathbf{g}^{\mathsf{T}}} \frac{\partial \hat{\mathbf{g}}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} \right]. \tag{10.52}$$

In this expansion, $\mathbf{A}$, $\mathbf{g}$, and all derivatives are evaluated at $(\hat{\mathbf{n}}, \hat{\mathbf{g}})$. A comparison of (10.52) with (10.16) 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 (2008), 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

$$\frac{d\hat{\mathbf{g}}}{d\boldsymbol{\theta}^\mathsf{T}} = \frac{\partial\hat{\mathbf{g}}}{\partial\boldsymbol{\theta}^\mathsf{T}} + \frac{\partial\hat{\mathbf{g}}}{\partial\mathbf{n}}\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^\mathsf{T}} \qquad (10.53)$$

where $d\hat{\mathbf{g}}/d\boldsymbol{\theta}^\mathsf{T}$ is given by (10.49) and $(d\hat{\mathbf{n}}/d\boldsymbol{\theta}^\mathsf{T})$ by (10.52).

10.4   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). They are also the basis of cohort-component population projections that include immigration.

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 may be density-dependent. All three cases can lead to equilibrium populations.

10.4.1   Density-Independent Subsidized Populations

The model,

$$\mathbf{n}(t+1) = \mathbf{A}[\boldsymbol{\theta}]\mathbf{n}(t) + \mathbf{b}[\boldsymbol{\theta}], \qquad (10.54)$$

includes a subsidy vector $\mathbf{b}$ giving the input of individuals to the population.[8] 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.[9] This equilibrium satisfies

$$\hat{\mathbf{n}} = \mathbf{A}\hat{\mathbf{n}} + \mathbf{b} \tag{10.55}$$

$$= (\mathbf{I}_s - \mathbf{A})^{-1}\,\mathbf{b}. \tag{10.56}$$

Differentiating (10.55) and applying the vec operator yields

$$d\hat{\mathbf{n}} = \left(\hat{\mathbf{n}}^\mathsf{T} \otimes \mathbf{I}_s\right) d\mathrm{vec}\,\mathbf{A} + \mathbf{A}\left(d\hat{\mathbf{n}}\right) + d\mathbf{b} \tag{10.57}$$

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

$$\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^\mathsf{T}} = (\mathbf{I}_s - \mathbf{A})^{-1}\left\{\left(\hat{\mathbf{n}}^\mathsf{T} \otimes \mathbf{I}_s\right)\frac{d\mathrm{vec}\,\mathbf{A}}{d\boldsymbol{\theta}^\mathsf{T}} + \frac{d\mathbf{b}}{d\boldsymbol{\theta}^\mathsf{T}}\right\}. \tag{10.58}$$

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.[10] 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

---

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

[9]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.

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

Pollard interpolated this distribution to 1-year age classes, and combined it with a 1954 life table for Australian males (only one woman, the redoubtable geologist Dorothy Hill in 1956, had been elected to the Academy prior to 1969) to construct a model of the form (10.54). He 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 Fig. 10.2a.

As parameters, consider the age-specific mortality rates $\mu_i = -\log P_i$, and define the parameter vector $\boldsymbol{\theta} = \left(\mu_1 \; \mu_2 \; \ldots \right)^{\mathsf{T}}$. Equation (10.58) then gives the sensitivity of the equilibrium population to changes in age-specific mortality. The
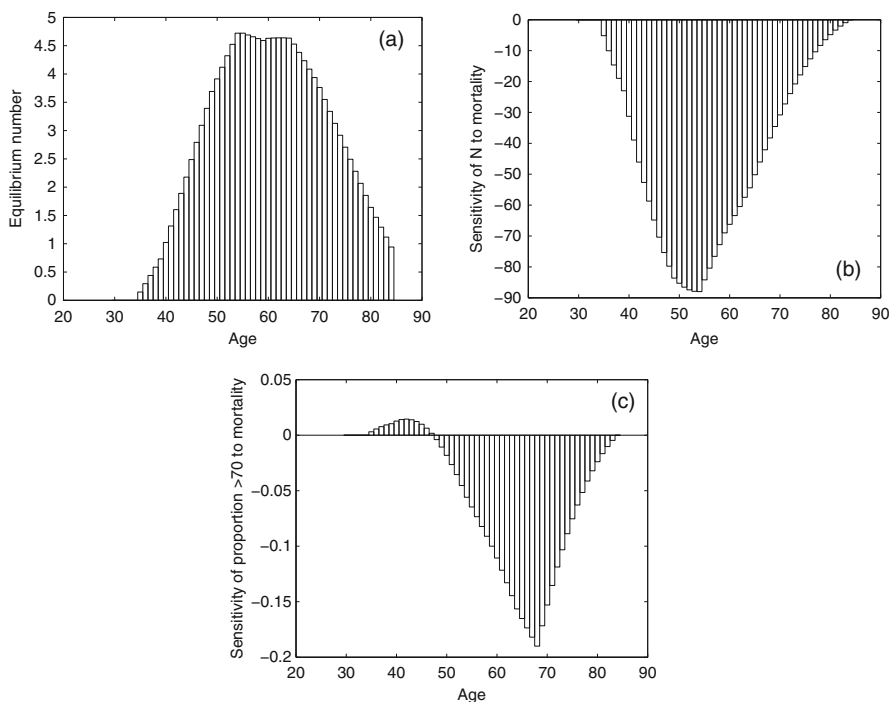

Fig. 10.2 Analysis of the equilibrium of a linear subsidized model for the Australian Academy of Science, based on Pollard (1968). (**a**) The equilibrium age structure of the Academy, assuming recruitment of 6 members per year. (**b**) The sensitivity, to changes in age-specific mortality, of the number of members. (**c**) The sensitivity, to changes in age-specific mortality, of the proportion of members over 70 years old

sensitivity of the total size of the Academy, $\hat{N} = \mathbf{1}^\mathsf{T}\hat{\mathbf{n}}$, calculated using (10.31), is shown in Fig. 10.2b. 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 (10.33), is shown in Fig. 10.2c. Increases in mortality before age 48 would increase the proportion of members over 70, while increases in mortality after age 48 would decrease it.[11] ∎

10.4.2   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[12] 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

$$\mathbf{b}(t) = \left(\phi F(t)\ 0\ \cdots\ 0\right)^\mathsf{T}, \tag{10.59}$$

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,

$$F(t) = A - \mathbf{g}^\mathsf{T}\mathbf{n}(t) \tag{10.60}$$

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 (10.60) into (10.59) and rearranging gives

$$\mathbf{n}(t+1) = \mathbf{B}\mathbf{n}(t) + \left(\phi A\ 0\ \cdots\ 0\right)^\mathsf{T} \tag{10.61}$$

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[11]It is possible to calculate the average age of the Academy, and its sensitivity, using results to be introduced in Sect. 10.5.4. The response is very similar to that of the proportion over age 70.

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

where

$$\mathbf{B} = \begin{pmatrix} -\phi g_1 & -\phi g_2 & \cdots & -\phi g_s \\ a_{21} & a_{22} & \cdots & a_{2s} \\ \vdots & \vdots & \ddots & \vdots \\ a_{s1} & a_{s2} & \cdots & a_{ss} \end{pmatrix}. \tag{10.62}$$

Although it includes competition for space, the model is linear. The equilibrium $\hat{\mathbf{n}}$ of (10.61) is stable if the spectral radius of $\mathbf{B}$ is less than one.[13] The formula (10.58) 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 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 (Fig. 10.3a). 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 the parameters be age-specific survival probabilities, so that $\boldsymbol{\theta} = \begin{pmatrix} P_1 & \cdots & P_{52} \end{pmatrix}$. Some of the possible sensitivities are shown in Fig. 10.3. 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 (Fig. 10.3b). A perturbation to a parameter, call it ξ, that affects survival at all ages would have the effect

$$\frac{d\hat{\mathbf{n}}}{d\xi} = \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} \frac{d\boldsymbol{\theta}}{d\xi} = \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}} \mathbf{1} \tag{10.63}$$

where $\mathbf{1}$ 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 (Fig. 10.3c).

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

The sensitivity of $\hat{\mathbf{n}}$ to the larval settlement rate ϕ is obtained from (10.58) by setting $d\text{vec}\,\mathbf{B}/d\boldsymbol{\phi} = \mathbf{0}_{s^2 \times 1}$, and

$$\frac{d\mathbf{b}}{d\phi} = \left(\hat{F}\ 0\ \cdots\ 0 \right)^{\mathsf{T}}$$

Not surprisingly, increases in ϕ increase $\hat{\mathbf{n}}$, with the largest effect on the young age classes (Fig. 10.3d). The sensitivity of $\hat{\mathbf{n}}$ to the radial growth rate ρ is obtained by writing

$$\frac{d\text{vec}\,\mathbf{B}}{d\rho} = \frac{d\text{vec}\,\mathbf{B}}{d\mathbf{g}^{\mathsf{T}}} \frac{d\mathbf{g}}{d\rho} \tag{10.64}$$

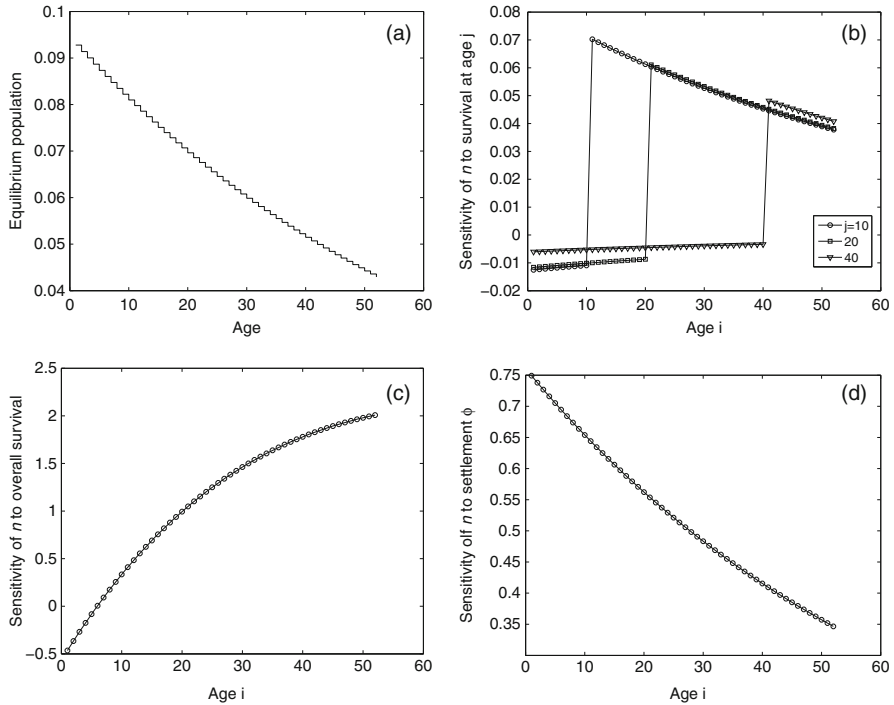This sensitivity is negative, with the greatest impact on young age classes (Fig. 10.3e).

Fig. 10.3 Sensitivity analysis of a subsidized population of the intertidal barnacle *Balanus glandula*. (**a**) The equilibrium population $\hat{\mathbf{n}}$ (scaled relative to a unit of area $A = 1$). (**b**) The sensitivity of $\hat{b}on$ to a change in survival at ages $j = 10, 20, 40$. (**c**) The sensitivity of $\hat{\mathbf{n}}$ to changes in overall survival at all ages. (**d**) The sensitivity of $\hat{\mathbf{n}}$ to the settlement rate ϕ per unit area. A sensitivity analysis of a subsidized population of the intertidal barnacle *Balanus glandula*.
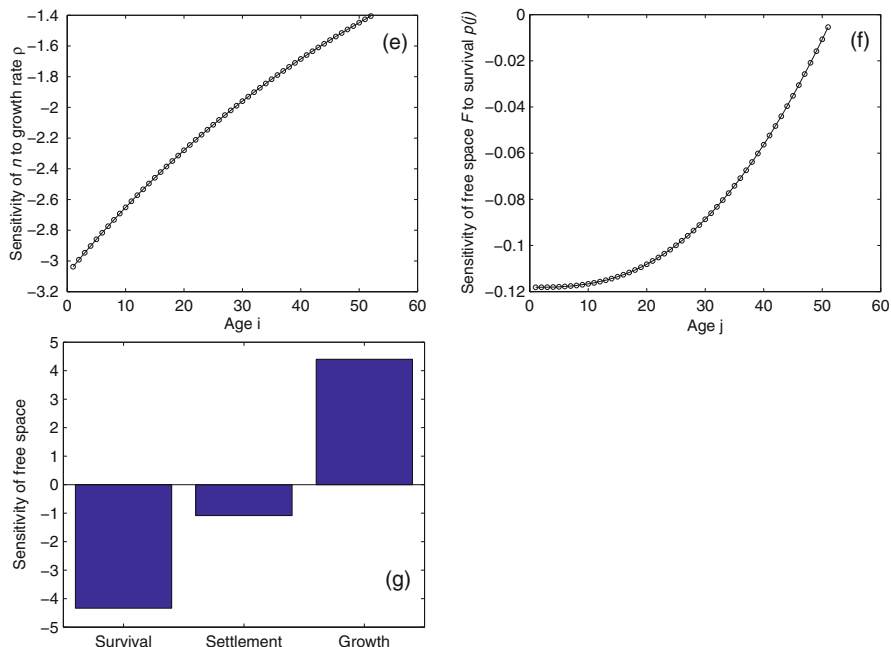
Fig. 10.3 (continued) (e) The sensitivity of $\hat{\mathbf{n}}$ to the radial growth rate ρ. (f) The sensitivity of the equilibrium free space $\hat{F}$ to age-specific survival. (g) The sensitivity of $\hat{F}$ to changes in overall survival, settlement rate, and radial growth rate. Based on data of Gaines and Roughgarden (1985)

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

$$\frac{d\hat{F}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \frac{d\hat{F}}{d\mathbf{n}^{\mathsf{T}}} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = -\mathbf{g}^{\mathsf{T}} \frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}} \tag{10.65}$$

Increases in survival reduce the amount of free space at equilibrium; the effect is largest for changes in survival of young age classes (Fig. 10.3f). Figure 10.3g 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 $\hat{F}$. ∎

10.4.3   Density-Dependent Subsidized Models

Once individuals arrive in the population, they may experience a variety of density-dependent effects, that can be incorporated in a model

$$\mathbf{n}(t+1) = \mathbf{A}\left[\boldsymbol{\theta}, \mathbf{n}(t)\right]\mathbf{n}(t) + \mathbf{b}. \tag{10.66}$$

The sensitivity result (10.58) applies to this model by substituting

$$d\text{vec}\,\mathbf{A} = \frac{\partial \text{vec}\,\mathbf{A}}{\partial \boldsymbol{\theta}^\mathsf{T}} d\boldsymbol{\theta} + \frac{\partial \text{vec}\,\mathbf{A}}{\partial \mathbf{n}^\mathsf{T}} d\hat{\mathbf{n}} \tag{10.67}$$

into (10.57) and solving for $d\hat{\mathbf{n}}$, to obtain

$$\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^\mathsf{T}} = \left(\mathbf{I}_s - \mathbf{A} - \left(\hat{\mathbf{n}}^\mathsf{T} \otimes \mathbf{I}_s \right) \frac{\partial \text{vec}\,\mathbf{A}}{\partial \mathbf{n}^\mathsf{T}} \right)^{-1} \left\{ \left(\hat{\mathbf{n}}^\mathsf{T} \otimes \mathbf{I}_s \right) \frac{\partial \text{vec}\,\mathbf{A}}{\partial \boldsymbol{\theta}^\mathsf{T}} + \frac{d\mathbf{b}}{d\boldsymbol{\theta}^\mathsf{T}} \right\}.$$
$$\tag{10.68}$$

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

10.5   Stable Structure and Reproductive Value

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, the dynamics of the *proportional* population structure are nonlinear (Tuljapurkar 1997). We can take advantage of this to analyze the sensitivity of proportional structures by writing them as equilibria of nonlinear maps.

10.5.1   Stable Structure

The sensitivity of the stable stage distribution has been approached as an eigenvector perturbation problem (e.g., Caswell 1982, 2001; Kirkland and Neumann 1994), but those calculations are complicated. Analysis of the equilibrium of the nonlinear model (10.69) is much easier.

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

$$\mathbf{p}(t+1) = \frac{\mathbf{A}\mathbf{p}(t)}{\|\mathbf{A}\mathbf{p}(t)\|}. \tag{10.69}$$

The stable stage distribution is an equilibrium of (10.69); it satisfies

$$\hat{\mathbf{p}} = \frac{\mathbf{A}\hat{\mathbf{p}}}{\mathbf{1}^\mathsf{T}\mathbf{A}\hat{\mathbf{p}}} \tag{10.70}$$

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

$$d\hat{\mathbf{p}} = \frac{1}{\left(\mathbf{1}^\mathsf{T}\mathbf{A}\hat{\mathbf{p}}\right)^2} \left[\mathbf{1}^\mathsf{T}\mathbf{A}\hat{\mathbf{p}}(d\mathbf{A})\hat{\mathbf{p}} + \mathbf{1}^\mathsf{T}\mathbf{A}\hat{\mathbf{p}}\mathbf{A}(d\hat{\mathbf{p}}) - \mathbf{A}\hat{\mathbf{p}}\mathbf{1}^\mathsf{T}(d\mathbf{A})\hat{\mathbf{p}} - \mathbf{A}\hat{\mathbf{p}}\mathbf{1}^\mathsf{T}\mathbf{A}(d\hat{\mathbf{p}})\right]$$
(10.71)

Note that $\mathbf{A}\hat{\mathbf{p}} = \lambda\hat{\mathbf{p}}$ and $\mathbf{1}^\mathsf{T}\mathbf{A}\hat{\mathbf{p}} = \lambda$, where λ is the dominant eigenvalue of $\mathbf{A}$. Making these substitutions and applying the vec operator to both sides gives

$$\lambda\, d\hat{\mathbf{p}} = \left[\left(\hat{\mathbf{p}}^\mathsf{T} \otimes \mathbf{I}_s\right) - \left(\hat{\mathbf{p}}^\mathsf{T} \otimes \hat{\mathbf{p}}\mathbf{1}^\mathsf{T}\right)\right] d\text{vec}\,\mathbf{A} + \left[\mathbf{A} - \hat{\mathbf{p}}\mathbf{1}^\mathsf{T}\mathbf{A}\right] d\hat{\mathbf{p}}$$
(10.72)

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

$$\frac{d\hat{\mathbf{p}}}{d\boldsymbol{\theta}^\mathsf{T}} = \left(\lambda\mathbf{I}_s - \mathbf{A} + \hat{\mathbf{p}}\mathbf{1}^\mathsf{T}\mathbf{A}\right)^{-1}\left(\hat{\mathbf{p}}^\mathsf{T} \otimes \mathbf{I}_s - \hat{\mathbf{p}}^\mathsf{T} \otimes \hat{\mathbf{p}}\mathbf{1}^\mathsf{T}\right)\frac{d\text{vec}\,\mathbf{A}}{d\boldsymbol{\theta}^\mathsf{T}}$$
(10.73)

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 (Fig. 10.4). Applying (10.73) 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, ..., 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 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. ∎

10.5.2   Reproductive Value

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

$$\hat{\mathbf{v}}^\mathsf{T} = \frac{\hat{\mathbf{v}}^\mathsf{T}\mathbf{A}}{\hat{\mathbf{v}}^\mathsf{T}\mathbf{A}\mathbf{e}_1}$$
(10.74)

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

$$d\hat{\mathbf{v}}^\mathsf{T} = \frac{1}{\left(\hat{\mathbf{v}}^\mathsf{T}\mathbf{A}\mathbf{e}_1\right)^2}\left[\hat{\mathbf{v}}^\mathsf{T}\mathbf{A}\mathbf{e}_1(d\hat{\mathbf{v}}^\mathsf{T})\mathbf{A} + \hat{\mathbf{v}}^\mathsf{T}\mathbf{A}\mathbf{e}_1\hat{\mathbf{v}}^\mathsf{T}(d\mathbf{A})\right.$$
$$\left. - (d\hat{\mathbf{v}}^\mathsf{T})\mathbf{A}\mathbf{e}_1\hat{\mathbf{v}}^\mathsf{T}\mathbf{A} - \hat{\mathbf{v}}^\mathsf{T}(d\mathbf{A})\mathbf{e}_1\hat{\mathbf{v}}^\mathsf{T}\mathbf{A}\right]$$
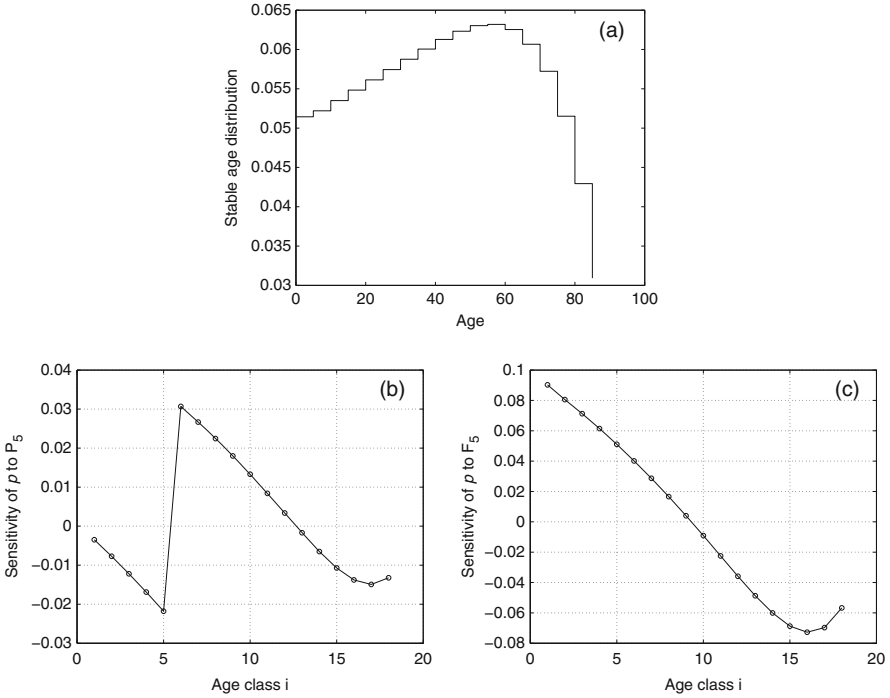(10.75)

Fig. 10.4 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)

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 vec $\mathbf{v}^\mathsf{T} = \mathbf{v}$) gives

$$\lambda d\mathbf{v} = \left[\left(\mathbf{I}_s \otimes \hat{\mathbf{v}}^\mathsf{T}\right) - \left(\hat{\mathbf{v}}\mathbf{e}_1^\mathsf{T} \otimes \hat{\mathbf{v}}^\mathsf{T}\right)\right] d\text{vec }\mathbf{A} + \left(\mathbf{A}^\mathsf{T} - \hat{\mathbf{v}}\mathbf{e}_1^\mathsf{T}\mathbf{A}^\mathsf{T}\right) d\mathbf{v}. \tag{10.76}$$

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

$$\frac{d\hat{\mathbf{v}}}{d\boldsymbol{\theta}^\mathsf{T}} = \left(\lambda\mathbf{I}_s - \mathbf{A}^\mathsf{T} + \hat{\mathbf{v}}\mathbf{e}_1^\mathsf{T}\mathbf{A}^\mathsf{T}\right)^{-1}\left[\left(\mathbf{I}_s \otimes \hat{\mathbf{v}}^\mathsf{T}\right) - \left(\hat{\mathbf{v}}\mathbf{e}_1^\mathsf{T} \otimes \hat{\mathbf{v}}^\mathsf{T}\right)\right]\frac{d\text{vec }\mathbf{A}}{d\boldsymbol{\theta}^\mathsf{T}} \tag{10.77}$$

In stable population theory, in the calculation of second derivatives of population growth rate (Shyu and Caswell 2014), and in the analysis of multitype branching processes for demographic stochasticity (Caswell and Vindenes 2018), it is necessary to use the sensitivity of $\mathbf{v}$ subject to the scaling

$$\mathbf{v}^\mathsf{T}\mathbf{w} = 1. \tag{10.78}$$

The resulting derivative is

$$\frac{d\mathbf{v}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\lambda\mathbf{I} - \mathbf{A}^{\mathsf{T}} + \lambda\mathbf{v}\mathbf{w}^{\mathsf{T}}\right)^{-1}$$

$$\times \left(\left[\left(\mathbf{I} - \mathbf{v}\mathbf{w}^{\mathsf{T}}\right) \otimes \mathbf{v}^{\mathsf{T}}\right] - \lambda\left(\mathbf{v} \otimes \mathbf{v}^{\mathsf{T}}\right)\frac{d\mathbf{w}}{d\mathrm{vec}^{\mathsf{T}}\mathbf{A}}\right)\frac{d\mathrm{vec}\,\mathbf{A}}{d\boldsymbol{\theta}^{\mathsf{T}}}. \quad (10.79)$$

(see Caswell and Vindenes 2018 for derivation).

10.5.3   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 (Keyfitz and Flieger 1990, p. 32). 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

$$D = \frac{\mathbf{a}^{\mathsf{T}}\hat{\mathbf{p}}}{\mathbf{b}^{\mathsf{T}}\hat{\mathbf{p}}} \quad (10.80)$$

where $\mathbf{a}$ is a vector with ones for the dependent ages and zeros otherwise, and $\mathbf{b}$ is its complement. Applying Eq. (10.33) for the sensitivity of a ratio gives

$$\frac{dD}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\frac{\mathbf{b}^{\mathsf{T}}\hat{\mathbf{p}}\mathbf{a}^{\mathsf{T}} - \mathbf{a}^{\mathsf{T}}\hat{\mathbf{p}}\mathbf{b}^{\mathsf{T}}}{(\mathbf{b}^{\mathsf{T}}\hat{\mathbf{p}})^2}\right)\frac{d\hat{\mathbf{p}}}{d\boldsymbol{\theta}^{\mathsf{T}}}. \quad (10.81)$$

where $d\hat{\mathbf{p}}/\boldsymbol{\theta}^{\mathsf{T}}$ is given by (10.73).

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 (Fürnkranz-Prskawetz and Sambt 2014). For an example applied to a population projection for Spain, see Caswell and Sanchez Gassen (2015). The analysis also 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 (10.81). It can be extended to transient dynamics, where the age distribution, and thus the dependency ratio, varies over time (Caswell 2007), as is the case in population projections (Caswell and Sanchez Gassen 2015). Finally, the sensitivity (10.81) makes it possible to carry out LTRE analyses to decompose

differences in dependency ratios into components due to differences in each of the vital rates (see Chaps. 2, 8, and 9).

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 Fig. 10.5. 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[14] 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. ∎

10.5.4 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,

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[14]Or, equivalently, reductions in mortality. For these parameter values, the sensitivity to mortality is approximately the sensitivity to survival with the opposite sign.
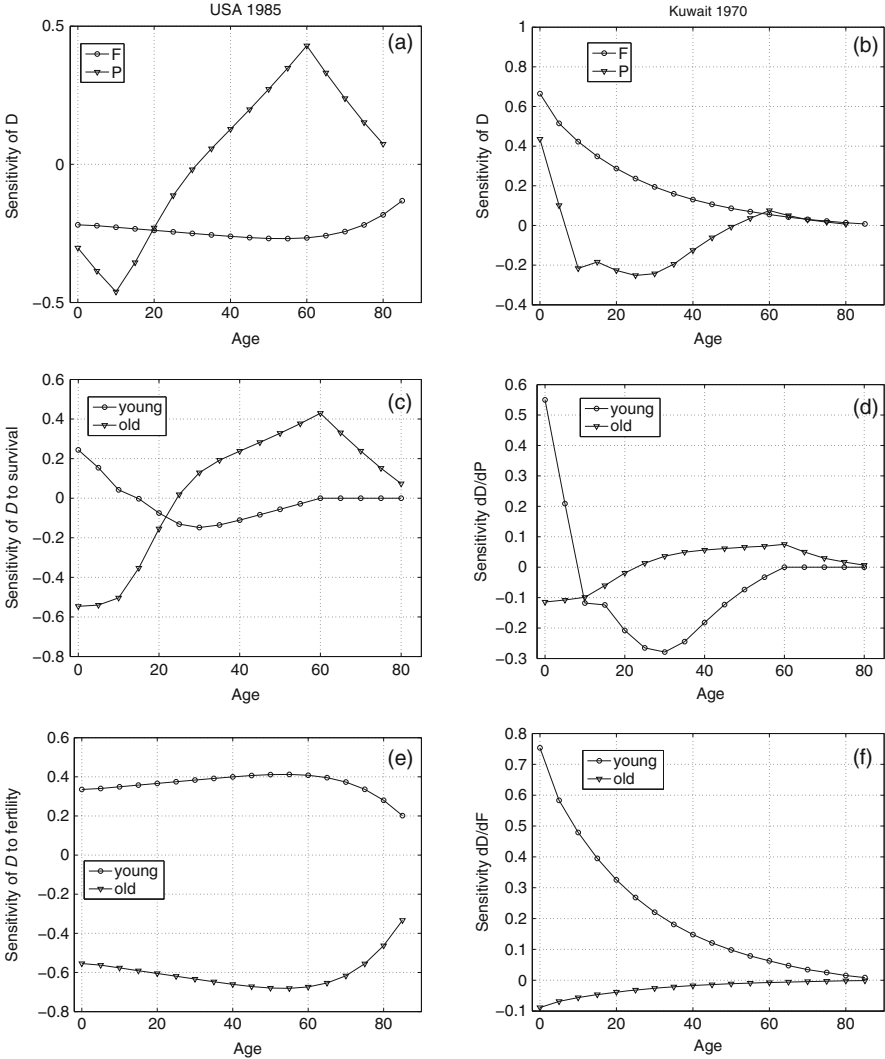
Fig. 10.5 Sensitivity of the dependency ratio D, and of its old and young components, to age-specific survival and fertility. Left: calculated from the stable age distribution of the United States in 1985. Right: calculated from the stable age distribution of Kuwait in 1970. (**a**) and (**b**): Sensitivity 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)

$$\bar{a}_{\mathbf{f}} = \frac{\mathbf{c}^{\mathsf{T}} \left(\mathbf{f} \circ \hat{\mathbf{p}} \right)}{\mathbf{1}^{\mathsf{T}} \left(\mathbf{f} \circ \hat{\mathbf{p}} \right)} \tag{10.82}$$

where

$$\mathbf{c}^{\mathsf{T}} = \left(1 \ 2 \ \cdots \ s \right),$$

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 $d(\mathbf{a} \circ \mathbf{b}) = \mathcal{D}(\mathbf{a})d\mathbf{b} + \mathcal{D}(\mathbf{b})d\mathbf{a}$. The result is

$$\frac{d\bar{a}_{\mathbf{f}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\frac{\mathbf{1}^{\mathsf{T}} \left(\mathbf{f} \circ \hat{\mathbf{p}} \right) \mathbf{c}^{\mathsf{T}} - \mathbf{c}^{\mathsf{T}} \left(\mathbf{f} \circ \hat{\mathbf{p}} \right) \mathbf{1}^{\mathsf{T}}}{\left(\mathbf{f}^{\mathsf{T}} \hat{\mathbf{p}} \right)^2} \right) \left(\mathcal{D}(\mathbf{f}) \frac{d\hat{\mathbf{p}}}{d\boldsymbol{\theta}^{\mathsf{T}}} + \mathcal{D}(\hat{\mathbf{p}}) \frac{d\mathbf{f}}{d\boldsymbol{\theta}^{\mathsf{T}}} \right) \tag{10.83}$$

where $d\hat{\mathbf{p}}/d\boldsymbol{\theta}^{\mathsf{T}}$ is given by (10.73).

This result can be generalized in several ways. Setting $\mathbf{f} = \mathbf{1}$ makes the age-specific property that of simply being alive, and $\bar{a}_1 = \mathbf{c}^{\mathsf{T}} \mathbf{1}$ is then the mean age of the stable population, the sensitivity of which is

$$\frac{d\bar{a}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \mathbf{c}^{\mathsf{T}} \frac{d\hat{\mathbf{p}}}{d\boldsymbol{\theta}^{\mathsf{T}}} \tag{10.84}$$

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

$$\mathbf{c}^{\mathsf{T}} = \left(x_1 \ x_2 \ \cdots \ x_s \right) \tag{10.85}$$

where x_i is the value associated with stage i.

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 Fig. 10.6. 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.   ∎
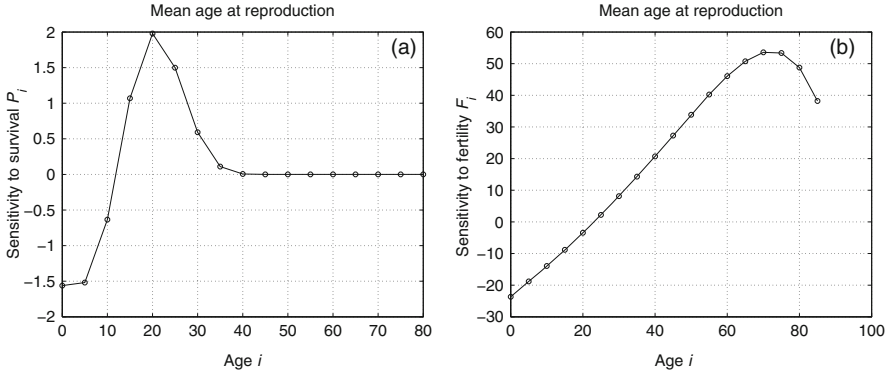
Fig. 10.6 Sensitivity of the mean age at reproduction to changes in age-specific survival and fertility, for the life table of the population of the United States, 1985. (Data from Keyfitz and Flieger 1990)

10.5.5 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

$$V_{\mathbf{f}} = \overline{a_{\mathbf{f}}^2} - (\bar{a}_{\mathbf{f}})^2 \,. \tag{10.86}$$

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

$$\overline{a_{\mathbf{f}}^2} = \frac{(\mathbf{c} \circ \mathbf{c})^{\mathsf{T}} \left(\mathbf{f} \circ \hat{\mathbf{p}}\right)}{\mathbf{1}^{\mathsf{T}} \left(\mathbf{f} \circ \hat{\mathbf{p}}\right)} \tag{10.87}$$

and then differentiating

$$dV_{\mathbf{f}} = d\left(\overline{a_{\mathbf{f}}^2}\right) - 2\bar{a}_{\mathbf{f}} \ (d\bar{a}_{\mathbf{f}}) \,. \tag{10.88}$$

The final result is

$$\frac{dV_{\mathbf{f}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\frac{\mathbf{1}^{\mathsf{T}}(\mathbf{f} \circ \hat{\mathbf{p}})(\mathbf{c} \circ \mathbf{c})^{\mathsf{T}} - (\mathbf{c} \circ \mathbf{c})^{\mathsf{T}} \left(\mathbf{f} \circ \hat{\mathbf{p}}\right) \mathbf{1}^{\mathsf{T}}}{\left(\mathbf{f}^{\mathsf{T}}\hat{\mathbf{p}}\right)^2}\right)$$

$$\times \left(\mathcal{D}\left(\mathbf{f}\right)\frac{d\hat{\mathbf{p}}}{d\boldsymbol{\theta}^{\mathsf{T}}} + \mathcal{D}\left(\hat{\mathbf{p}}\right)\frac{d\mathbf{f}}{d\boldsymbol{\theta}^{\mathsf{T}}}\right) - 2\bar{a}_{\mathbf{f}}\frac{d\bar{a}_{\mathbf{f}}}{d\boldsymbol{\theta}^{\mathsf{T}}}\,. \tag{10.89}$$

where $d\hat{\mathbf{p}}/d\boldsymbol{\theta}^{\mathsf{T}}$ is given by (10.73) and $d\bar{a}_{\mathbf{f}}/d\boldsymbol{\theta}^{\mathsf{T}}$ is given by (10.83).

10.6   Frequency-Dependent Two-Sex Models

In sexually reproducing species, a particular sort of nonlinearity arises 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.,

$$\mathbf{A}[\boldsymbol{\theta}, c\mathbf{n}] = \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}] \qquad \text{for any } c \neq 0. \tag{10.90}$$

Such models have been 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[15] 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.

Note that matrix models that include Mendelian genetics are also homogeneous of degree zero, but it is confusing to call them frequency-dependent, because doing so creates confusion with the genetic phenomenon of frequency-dependent fitness, which is a different thing altogether (de Vries and Caswell 2018).

10.6.1   Sensitivity of the Population Structure

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

$$\hat{\mathbf{p}} = \frac{\mathbf{A}[\boldsymbol{\theta}, \hat{\mathbf{p}}] \; \hat{\mathbf{p}}}{\|\mathbf{A}[\boldsymbol{\theta}, \hat{\mathbf{p}}] \; \hat{\mathbf{p}}\|} \tag{10.91}$$

where $\hat{p}_i \geq 0$ and $\mathbf{1}^{\mathsf{T}}\hat{\mathbf{p}} = 1$. Differentiating (10.91) gives

$$d\hat{\mathbf{p}} = \frac{\mathbf{1}^{\mathsf{T}}\mathbf{A}\hat{\mathbf{p}}\left[(d\mathbf{A})\hat{\mathbf{p}} + \mathbf{A}(d\hat{\mathbf{p}})\right] - \mathbf{A}\hat{\mathbf{p}}\left[\mathbf{1}^{\mathsf{T}}(d\mathbf{A})\hat{\mathbf{p}} + \mathbf{1}^{\mathsf{T}}\mathbf{A}(d\hat{\mathbf{p}})\right]}{\left(\mathbf{1}^{\mathsf{T}}\mathbf{A}\hat{\mathbf{p}}\right)^2}. \tag{10.92}$$

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[15]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). See also Martcheva (1999).

Making the substitutions $\mathbf{A}\hat{\mathbf{p}} = \lambda\hat{\mathbf{p}}$ and $\mathbf{1}^{\mathsf{T}}\mathbf{A}\hat{\mathbf{p}} = \lambda$ and rearranging gives

$$\lambda d\hat{\mathbf{p}} = (d\mathbf{A})\hat{\mathbf{p}} + \mathbf{A}(d\hat{\mathbf{p}}) - \hat{\mathbf{p}}\mathbf{1}^{\mathsf{T}}(d\mathbf{A})\hat{\mathbf{p}} - \hat{\mathbf{p}}\mathbf{1}^{\mathsf{T}}\mathbf{A}(d\hat{\mathbf{p}}). \tag{10.93}$$

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

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

$$\times \left[\hat{\mathbf{p}}^{\mathsf{T}} \otimes \left(\mathbf{I}_s - \hat{\mathbf{p}}\mathbf{1}^{\mathsf{T}}\right)\right]\frac{\partial\text{vec}\,\mathbf{A}}{\partial\boldsymbol{\theta}^{\mathsf{T}}} \tag{10.94}$$

where $\mathbf{A}$ and all derivatives are evaluated at $\hat{\mathbf{p}}$. Note that (10.94) differs from the expression (10.73) for the stable stage distribution in the linear model only in the term involving $\partial\text{vec}\,\mathbf{A}/\partial\mathbf{p}^{\mathsf{T}}$, which of course is zero in the linear model.

10.6.2   Population Growth Rate in Two-Sex Models

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

$$d\lambda = \mathbf{v}^{\mathsf{T}}(d\mathbf{A})\hat{\mathbf{p}} \tag{10.95}$$

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

$$d\lambda = \left(\hat{\mathbf{p}}^{\mathsf{T}} \otimes \mathbf{v}^{\mathsf{T}}\right)d\text{vec}\,\mathbf{A}. \tag{10.96}$$

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

$$\frac{d\lambda}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\hat{\mathbf{p}}^{\mathsf{T}} \otimes \mathbf{v}^{\mathsf{T}}\right)\left[\frac{\partial\text{vec}\,\mathbf{A}}{\partial\boldsymbol{\theta}^{\mathsf{T}}} + \frac{\partial\text{vec}\,\mathbf{A}}{\partial\hat{\mathbf{p}}^{\mathsf{T}}}\frac{d\hat{\mathbf{p}}}{d\boldsymbol{\theta}^{\mathsf{T}}}\right] \tag{10.97}$$

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 (10.94).

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.

Fig. 10.7 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
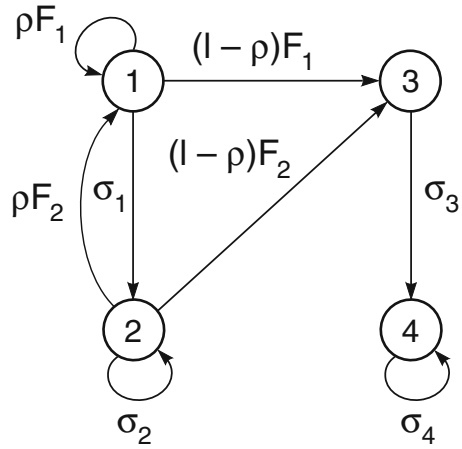
(2007) used this fact to explore the effect of male fertility patterns on the evolution of aging; the sensitivity (10.97) could be used to generalize such results. Recent work by Shyu has coupled these calculations to the methods of adaptive dynamics to examine the evolution of sex ratios (Shyu and Caswell 2016a,b).

Although two-sex models are an important case of homogeneous models, they are not the only case. Keyfitz's (1972) 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 (10.97) 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 Fig. 10.7. 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

$$B(\mathbf{n}) = \min\left(N_f, N_m\right), \tag{10.98}$$

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.

$$F(\mathbf{n}) = \frac{\sigma_0 \phi_i B(\mathbf{n})}{N_f} \tag{10.99}$$

$$= \begin{cases} \sigma_0 \phi_i \frac{N_m}{N_f} & N_f \geq N_m \\ \sigma_0 \phi & N_f < N_m \end{cases} \tag{10.100}$$

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

$$\mathbf{A[n]} = \begin{pmatrix} \rho F_1(\mathbf{n}) & \rho F_2(\mathbf{n}) & 0 & 0 \\ \sigma_1 & \sigma_2 & 0 & 0 \\ (1-\rho)F_1(\mathbf{n}) & (1-\rho)F_2(\mathbf{n}) & 0 & 0 \\ 0 & 0 & \sigma_3 & \sigma_4 \end{pmatrix} \tag{10.101}$$

Legendre et al. (1999) assigned 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.[16] The survival probabilities and equilibrium population structures are

$$\boldsymbol{\sigma} = \begin{pmatrix} 0.35 \\ 0.5 \\ 0.25 \\ 0.4 \end{pmatrix} \qquad \hat{\mathbf{p}} = \begin{pmatrix} 0.320 \\ 0.226 \\ 0.320 \\ 0.134 \end{pmatrix} \tag{10.102}$$

$$\boldsymbol{\sigma} = \begin{pmatrix} 0.25 \\ 0.4 \\ 0.35 \\ 0.5 \end{pmatrix} \qquad \hat{\mathbf{p}} = \begin{pmatrix} 0.320 \\ 0.134 \\ 0.320 \\ 0.226 \end{pmatrix} \tag{10.103}$$

The elasticities of $\hat{\mathbf{p}}$ to each of the parameters, calculated from (10.94), are shown in Table 10.1. 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

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[16]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 10.1 Elasticity of $\hat{\mathbf{p}}$ 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

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 10.2, 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,

$$B(\mathbf{n}) = \frac{2N_f N_m}{N_f + N_m}, \tag{10.104}$$

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

Sometimes the correct calculations lead to apparent paradoxes. Jenouvrier et al. (2010) developed a two-sex model for the Emperor penguin. It was a periodic model, with phases defined by events within the breeding cycle (cf. Chap. 8), and included a

Table 10.2 The elasticity of λ to parameters in the two-sex model for passerine birds, under two mortality scenarios. The correct calculation is based on (10.97). 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

mating function applied to adults at the breeding colony. Because Emperor penguins breed, and share parental care, in the midst of the Antarctic winter,[17] they must be strictly monogamous, and hence Jenouvrier used the minimum as a mating function.

Analysis of the equilibrium growth rate revealed that the sensitivity of λ to adult female survival was negative. This is impossible in a linear model, but happens in this frequency-dependent model because increasing adult female survival increases the proportion of females (already greater than the proportion of males) and thus decreases mating probability. The negative effect of reduced mating overwhelms the positive effect of improved adult survival; the net result is a reduction in population growth rate; see Jenouvrier et al. (2010) for details.   ∎

10.6.3 The Birth Matrix-Mating Rule Model

Pollak (1987, 1990) introduced a powerful conceptual approach to two-sex models, which he called the birth matrix-mating rule (BMMR) model. This model separates the processes of mating, birth, and life cycle stage transitions, and treats them as a periodic process. When generalized to stage-structured models, it contains three main components:

1. A birth matrix whose entries give the expected number of male and female offspring produced by a mating of a male of age (or stage) i and a female of age j.
2. A mating rule function that gives the number of matings u_{ij} between males of age (or stage) i and females of age j.
3. A set of sex-specific mortality schedules, which project surviving individuals to the next age class, or, in our generalization, include other stage-specific life cycle transitions.

---

[17]Dramatically portrayed in the movie, *March of the Penguins*.

A matrix version of the BMMR has recently been developed, using a novel continuous-time formulation of periodic matrix models (Shyu and Caswell 2018). The mating, birth, and transition processes are described, respectively, by matrices **U**, **B**, and **T**. To explore the theoretical consequences of two-sex reproduction, the matrices are parameterized in terms of continuous-time rates rather than discrete-time probabilities. In continuous time, the periodic matrix product that would describe such a process in discrete time converges to a sum of the rate matrices. The dynamics of the population are given by

$$\frac{d\mathbf{n}(t)}{dt} = \mathbf{A}\left[\mathbf{n}(t)\right]\,\mathbf{n}(t) \tag{10.105}$$

where

$$\mathbf{A}\left[\mathbf{n}(t)\right] = \frac{1}{3}\left(\mathbf{T} + \mathbf{B} + \mathbf{U}[\mathbf{n}(t)]\right)\mathbf{n}(t) \tag{10.106}$$

That is, the projection matrix is the mean of the three component matrices, and is nonlinear because of the dependence of union formation (the matrix **U**) on **n**. Shyu and Caswell (2016a,b, 2018) explore this model in the context of sex ratio evolution and of sex-biased harvesting, deriving the sensitivity of the population growth rate as a measure of the selection gradient.

10.7 Sensitivity of Population Cycles

Equilibria are not the only attractors relevant in nature (e.g., Clutton-Brock et al. 1997) or the laboratory (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.

10.7.1 Sensitivity of the Population Vector

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

$$\hat{\mathbf{n}}_{i+1} = \mathbf{A}\left[\boldsymbol{\theta}, \hat{\mathbf{n}}_i\right]\hat{\mathbf{n}}_i \qquad i = 1, \ldots, k-1$$

$$\hat{\mathbf{n}}_1 = \mathbf{A}\left[\boldsymbol{\theta}, \hat{\mathbf{n}}_k\right]\hat{\mathbf{n}}_k. \tag{10.107}$$

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

$$\frac{d\hat{\mathbf{n}}_1}{d\boldsymbol{\theta}^\mathsf{T}}, \ \ldots, \ \frac{d\hat{\mathbf{n}}_k}{d\boldsymbol{\theta}^\mathsf{T}}. \tag{10.108}$$

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

$$\mathbf{A}_i \equiv \mathbf{A}\left[\boldsymbol{\theta}, \hat{\mathbf{n}}_i\right]. \tag{10.109}$$

The 2-cycle satisfies

$$\hat{\mathbf{n}}_1 = \mathbf{A}_2 \hat{\mathbf{n}}_2 \tag{10.110}$$

$$\hat{\mathbf{n}}_2 = \mathbf{A}_1 \hat{\mathbf{n}}_1 \tag{10.111}$$

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

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

$$+ \mathbf{A}_2 \left(\frac{d\hat{\mathbf{n}}_2}{d\boldsymbol{\theta}^\mathsf{T}}\right) \tag{10.112}$$

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

$$+ \mathbf{A}_1 \left(\frac{d\hat{\mathbf{n}}_1}{d\boldsymbol{\theta}^\mathsf{T}}\right) \tag{10.113}$$

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

$$\frac{d}{d\boldsymbol{\theta}^\mathsf{T}} \begin{pmatrix} \hat{\mathbf{n}}_1 \\ \hat{\mathbf{n}}_2 \end{pmatrix} = \left(\begin{array}{c|c} \mathbf{0} & \mathbf{H}_2 \\ \hline \mathbf{H}_1 & \mathbf{0} \end{array} \right) \begin{pmatrix} \dfrac{\partial\,\mathrm{vec}\,\mathbf{A}_1}{\partial\boldsymbol{\theta}^\mathsf{T}} \\ \dfrac{\partial\,\mathrm{vec}\,\mathbf{A}_2}{\partial\boldsymbol{\theta}^\mathsf{T}} \end{pmatrix}$$

$$+ \left[\left(\begin{array}{c|c} \mathbf{0} & \mathbf{H}_2 \\ \hline \mathbf{H}_1 & \mathbf{0} \end{array} \right) \begin{pmatrix} \dfrac{\partial\,\mathrm{vec}\,\mathbf{A}_1}{\partial\mathbf{n}_1^\mathsf{T}} & \mathbf{0} \\ \mathbf{0} & \dfrac{\partial\,\mathrm{vec}\,\mathbf{A}_2}{\partial\mathbf{n}_2^\mathsf{T}} \end{pmatrix} + \left(\begin{array}{c|c} \mathbf{0} & \mathbf{A}_2 \\ \hline \mathbf{A}_1 & \mathbf{0} \end{array} \right) \right]$$

$$\times \frac{d}{d\boldsymbol{\theta}^\mathsf{T}} \begin{pmatrix} \hat{\mathbf{n}}_1 \\ \hat{\mathbf{n}}_2 \end{pmatrix} \tag{10.114}$$

Solving for the sensitivities gives

$$
\frac{d}{d\boldsymbol{\theta}^{\mathsf{T}}} \begin{pmatrix} \hat{\mathbf{n}}_1 \\ \hat{\mathbf{n}}_2 \end{pmatrix} = \left[\mathbf{I}_{2s} - \begin{pmatrix} 0 & \mathbf{H}_2 \\ \mathbf{H}_1 & 0 \end{pmatrix} \begin{pmatrix} \dfrac{\partial \mathrm{vec}\, \mathbf{A}_1}{\partial \mathbf{n}_1^{\mathsf{T}}} & 0 \\ 0 & \dfrac{\partial \mathrm{vec}\, \mathbf{A}_2}{\partial \mathbf{n}_2^{\mathsf{T}}} \end{pmatrix} \right.
$$

$$
\left. - \begin{pmatrix} 0 & \mathbf{A}_2 \\ \mathbf{A}_1 & 0 \end{pmatrix} \right]^{-1} \begin{pmatrix} 0 & \mathbf{H}_2 \\ \mathbf{H}_1 & 0 \end{pmatrix} \begin{pmatrix} \dfrac{\partial \mathrm{vec}\, \mathbf{A}_1}{\partial \boldsymbol{\theta}^{\mathsf{T}}} \\ \dfrac{\partial \mathrm{vec}\, \mathbf{A}_2}{\partial \boldsymbol{\theta}^{\mathsf{T}}} \end{pmatrix} \qquad (10.115)
$$

where the matrices $\mathbf{A}_i$ and the derivatives of $\mathbf{A}_i$ are all evaluated at $\hat{\mathbf{n}}_i$. The analogy with (10.16) is apparent.

This calculation can be extended to cycles of any period, in terms of block matrices as in (10.115). The pattern of the block matrices is clear from a 3-cycle. Define the following matrices:

$$
\mathbb{N} = \begin{pmatrix} \hat{\mathbf{n}}_1 \\ \hat{\mathbf{n}}_2 \\ \hat{\mathbf{n}}_3 \end{pmatrix} \qquad (10.116)
$$

$$
\mathbb{A} = \begin{pmatrix} 0 & 0 & \mathbf{A}_3 \\ \mathbf{A}_1 & 0 & 0 \\ 0 & \mathbf{A}_2 & 0 \end{pmatrix} \qquad (10.117)
$$

$$
\mathbb{H} = \begin{pmatrix} 0 & 0 & \mathbf{H}_3 \\ \mathbf{H}_1 & 0 & 0 \\ 0 & \mathbf{H}_2 & 0 \end{pmatrix} \qquad (10.118)
$$

$$
\mathbb{C} = \begin{pmatrix} \dfrac{\partial \mathrm{vec}\, \mathbf{A}_1}{\partial \mathbf{n}_1^{\mathsf{T}}} & 0 & 0 \\ 0 & \dfrac{\partial \mathrm{vec}\, \mathbf{A}_2}{\partial \mathbf{n}_2^{\mathsf{T}}} & 0 \\ 0 & 0 & \dfrac{\partial \mathrm{vec}\, \mathbf{A}_3}{\partial \mathbf{n}_3^{\mathsf{T}}} \end{pmatrix} \qquad (10.119)
$$

$$\mathbb{D} = \begin{pmatrix} \dfrac{\partial \text{vec}\, \mathbf{A}_1}{\partial \boldsymbol{\theta}^\mathsf{T}} \\[2ex] \dfrac{\partial \text{vec}\, \mathbf{A}_1}{\partial \boldsymbol{\theta}^\mathsf{T}} \\[2ex] \dfrac{\partial \text{vec}\, \mathbf{A}_1}{\partial \boldsymbol{\theta}^\mathsf{T}} \end{pmatrix}. \tag{10.120}$$

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

$$\frac{d\mathbb{N}}{d\boldsymbol{\theta}^\mathsf{T}} = [\mathbf{I}_{3s} - \mathbb{A} - \mathbb{H}\mathbb{C}]^{-1}\, \mathbb{H}\mathbb{D}. \tag{10.121}$$

10.7.2 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 $s \times k$)

$$\mathbf{G} = \begin{pmatrix} \hat{\mathbf{n}}_1 & \hat{\mathbf{n}}_2 & \cdots & \hat{\mathbf{n}}_k \end{pmatrix}. \tag{10.122}$$

The block vector $\mathbb{N}$ is

$$\mathbb{N} = \text{vec}\, \mathbf{G}. \tag{10.123}$$

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

$$\hat{\mathbf{n}} = \begin{pmatrix} \hat{N}_1 \\ \vdots \\ \hat{N}_k \end{pmatrix} \tag{10.124}$$

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

$$\begin{aligned} \hat{\mathbf{n}} &= \begin{pmatrix} \mathbf{c}^\mathsf{T}\hat{\mathbf{n}}_1 & \cdots & \mathbf{c}^\mathsf{T}\hat{\mathbf{n}}_k \end{pmatrix}^\mathsf{T} \\ &= \text{vec}\, \left(\mathbf{c}^\mathsf{T}\mathbf{G} \right) \\ &= \left(\mathbf{I}_k \otimes \mathbf{c}^\mathsf{T} \right) \text{vec}\, \mathbf{G} \end{aligned}$$

$$= \left(\mathbf{I}_k \otimes \mathbf{c}^\mathsf{T}\right) \mathbb{N} \qquad \text{dimension} = k \times 1. \tag{10.125}$$

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

$$\bar{\mathbf{n}} = \sum_{i=1}^{k} b_i \hat{\mathbf{n}}_i. \tag{10.126}$$

Then

$$\begin{aligned}
\bar{\mathbf{n}} &= \mathbf{Gb} \\
&= \left(\mathbf{b}^\mathsf{T} \otimes \mathbf{I}_s\right) \text{vec}\, \mathbf{G} \\
&= \left(\mathbf{b}^\mathsf{T} \otimes \mathbf{I}_s\right) \mathbb{N} \qquad \text{dimension} = s \times 1
\end{aligned} \tag{10.127}$$

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

$$\begin{aligned}
\bar{N} &= \sum_i b_i \mathbf{c}^\mathsf{T} \hat{\mathbf{n}}_i \\
&= \mathbf{c}^\mathsf{T} \mathbf{Gb} \\
&= \left(\mathbf{b}^\mathsf{T} \otimes \mathbf{c}^\mathsf{T}\right) \mathbb{N}
\end{aligned} \tag{10.128}$$

Thus the sensitivities of the weighted densities, the time-averaged population, and the time-averaged weighted density are obtained by differentiating (10.125), (10.127), and (10.128) as

$$\frac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^\mathsf{T}} = \left(\mathbf{I}_k \otimes \mathbf{c}^\mathsf{T}\right) \frac{d\mathbb{N}}{d\boldsymbol{\theta}^\mathsf{T}} \tag{10.129}$$

$$\frac{d\bar{\mathbf{n}}}{d\boldsymbol{\theta}^\mathsf{T}} = \left(\mathbf{b}^\mathsf{T} \otimes \mathbf{I}_s\right) \frac{d\mathbb{N}}{d\boldsymbol{\theta}^\mathsf{T}} \tag{10.130}$$

$$\frac{d\bar{N}}{d\boldsymbol{\theta}^\mathsf{T}} = \left(\mathbf{b}^\mathsf{T} \otimes \mathbf{c}^\mathsf{T}\right) \frac{d\mathbb{N}}{d\boldsymbol{\theta}^\mathsf{T}} \tag{10.131}$$

where $d\mathbb{N}/\boldsymbol{\theta}^\mathsf{T}$ is given by (10.121).

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

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

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

$$\hat{\mathbf{n}}_1 = \begin{pmatrix} 325.3 \\ 8.9 \\ 118.5 \end{pmatrix} \qquad \hat{\mathbf{n}}_2 = \begin{pmatrix} 18.2 \\ 158.4 \\ 106.4 \end{pmatrix}, \tag{10.132}$$

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, consider the elasticity of the population vector $\hat{\mathbf{n}}_i$, of the total population $\hat{N}_i = \mathbf{1}^\mathsf{T}\hat{\mathbf{n}}_i$, 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 Fig. 10.8.

First, the elasticities of the $\hat{\mathbf{n}}_i$ differ from stage to stage and from one point on the cycle to another (Fig. 10.8a). 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 Fig. 10.1).

The elasticities of total population are similar at the two points in the cycle (Fig. 10.8b), 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 (Fig. 10.8c).

The elasticities of the time-averaged population vector $\bar{\mathbf{n}}$ (Fig. 10.8d) are similar to those of the equilibrium vector in Fig. 10.1 (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 $\hat{\mathbf{n}}_2$ (Fig. 10.8a).

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

The sensitivity analysis of cycles thus depends very much on the dependent variables of interest. The matrix $d\mathbb{N}/d\boldsymbol{\theta}^\mathsf{T}$ (Fig. 10.8a) 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 (Fig. 10.8b,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 (Fig. 10.8d), and the response of the time-averaged weighted densities finally are described by just 6 numbers. The good news
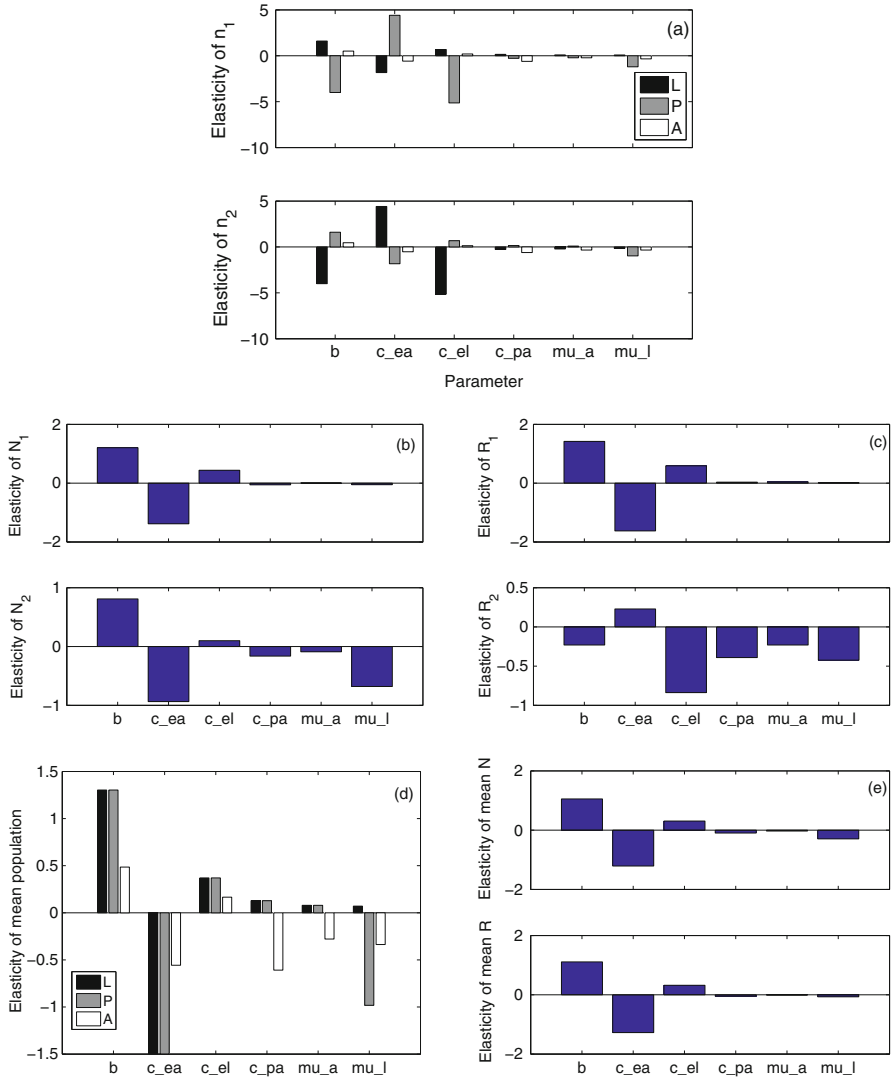
Fig. 10.8 Analysis of a 2-cycle in the *Tribolium* model. (**a**) Elasticity of the density of each stage, with respect to each parameter, at $\hat{\mathbf{n}}_1$ and $\hat{\mathbf{n}}_2$. (**b**) Elasticity of the total population $\hat{N}$ at each point in the cycle. (**c**) Elasticity of the total respiration $\hat{R}$ at each point in the cycle. (**d**) Elasticity of the time-averaged population $\bar{\mathbf{n}}$. (**e**) Elasticity of the time-averaged total population $\bar{N}$ and the time-averaged total respiration $\bar{R}$

is that Eqs. (10.121), (10.125), (10.127), and (10.128) make it easy to compute all
these sensitivities.   ∎

10.7.3   Sensitivity of Temporal Variance in Density

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

$$V(\hat{N}) = E(\hat{N}^2) - \left[E(\hat{N})\right]^2 \tag{10.133}$$

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

$$E(\hat{N}^2) = \sum_{i=1}^{k} b_i \left(\mathbf{c}^{\mathsf{T}}\hat{\mathbf{n}}_i\right)^2 \tag{10.134}$$

$$= (\mathbf{c} \circ \mathbf{c})^{\mathsf{T}}(\mathbf{G} \circ \mathbf{G})\mathbf{b} \tag{10.135}$$

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

$$dE(\hat{N}^2) = 2\left[\mathbf{b}^{\mathsf{T}} \otimes (\mathbf{c} \circ \mathbf{c})^{\mathsf{T}}\right] \mathcal{D}\left(\mathbb{N}\right) d\mathbb{N}. \tag{10.136}$$

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

$$\frac{dV(\hat{N})}{d\boldsymbol{\theta}^{\mathsf{T}}} = 2\left\{\left[\mathbf{b}^{\mathsf{T}} \otimes (\mathbf{c} \circ \mathbf{c})^{\mathsf{T}}\right] \mathcal{D}\left(\mathbb{N}\right) - \bar{N}\left(\mathbf{b}^{\mathsf{T}} \otimes \mathbf{c}^{\mathsf{T}}\right)\right\} \frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}} \tag{10.137}$$

where $d\mathbb{N}/d\boldsymbol{\theta}^{\mathsf{T}}$ is given by (10.121). The extension to higher moments, should one
want to know, say, the sensitivity of the skewness of population size over a cycle, is
possible.

10.7.4   Periodic Dynamics in Periodic Environments

Periodic environments (e.g., seasons within a year) are described by periodic
products of matrices. If the environmental cycle contains p phases, then matrices
$\mathbf{A}_1, \ldots \mathbf{A}_p$ describe the dynamics at each phase, and the periodic product $\mathbf{A}_p \cdots \mathbf{A}_1$
projects the population over an entire cycle. Nonlinear periodic models permit the
$\mathbf{A}_i$ to depend on the population vector at any point in the cycle, including delayed
dependence (e.g., the reproductive success of an individual plant in the fall may
depend on the density it experienced in the spring). A fixed point on the inter-annual
time scale is a p-cycle on the seasonal time scale. A k-cycle on the inter-annual

scale corresponds to a kp-cycle on the seasonal time scale. The sensitivity analysis of these models is given by Caswell and Shyu (2012) and presented here in Chap. 8. For an application to the dynamics of an invasive plant population, see Shyu et al. (2013).

10.8   Dynamic Environmental Feedback Models

The commonly encountered forms of density dependence are usually a shorthand for a feedback between a population and some aspect of its environment.[18] The static feedback model of Sect. 10.3 begins to incorporate environmental feedback, but 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

$$\mathbf{n}(t+1) = \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t), \mathbf{g}(t)]\mathbf{n}(t)$$
$$\mathbf{g}(t+1) = \mathbf{B}[\boldsymbol{\theta}, \mathbf{n}(t), \mathbf{g}(t)]\mathbf{g}(t) \qquad (10.138)$$

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 (10.138) can be found using an approach similar to that applied above to cycles. At equilibrium,

$$\hat{\mathbf{n}} = \mathbf{A}[\boldsymbol{\theta}, \hat{\mathbf{n}}, \hat{\mathbf{g}}]\hat{\mathbf{n}} \qquad (10.139)$$

$$\hat{\mathbf{g}} = \mathbf{B}[\boldsymbol{\theta}, \hat{\mathbf{n}}, \hat{\mathbf{g}}]\hat{\mathbf{g}} \qquad (10.140)$$

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

$$d\hat{\mathbf{n}} = \mathbf{A}\left(d\hat{\mathbf{n}}\right) + \left(\hat{\mathbf{n}}^{\mathsf{T}} \otimes \mathbf{I}_s\right)\left(\frac{\partial\,\mathrm{vec}\,\mathbf{A}}{\partial\boldsymbol{\theta}^{\mathsf{T}}}d\boldsymbol{\theta} + \frac{\partial\mathbf{A}}{\partial\mathbf{n}^{\mathsf{T}}}d\hat{\mathbf{n}} + \frac{\partial\mathbf{A}}{\partial\mathbf{g}^{\mathsf{T}}}d\hat{\mathbf{g}}\right) \quad (10.141)$$

$$d\hat{\mathbf{g}} = \mathbf{B}\left(d\hat{\mathbf{n}}\right) + \left(\hat{\mathbf{g}}^{\mathsf{T}} \otimes \mathbf{I}_q\right)\left(\frac{\partial\,\mathrm{vec}\,\mathbf{B}}{\partial\boldsymbol{\theta}^{\mathsf{T}}}d\boldsymbol{\theta} + \frac{\partial\mathbf{B}}{\partial\mathbf{n}^{\mathsf{T}}}d\hat{\mathbf{n}} + \frac{\partial\mathbf{B}}{\partial\mathbf{g}^{\mathsf{T}}}d\hat{\mathbf{g}}\right). \quad (10.142)$$

Applying the identification theorem and the chain rule gives

---

[18]Early writers even interpreted the simple logistic equation as an interplay between a biotic potential for exponential growth and an environmental resistance due to lack of resources or interaction with predators (e.g., Chapman 1931). Incorporating a fully dynamic feedback greatly expands the range of phenomena that can be explained (see de Roos and Persson (2013) for an extensive development of this approach).

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

$$+ \left(\hat{\mathbf{n}}\otimes\mathbf{I}_s\right)\frac{\partial\operatorname{vec}\mathbf{A}}{\partial\mathbf{g}^{\mathsf{T}}}\frac{d\hat{\mathbf{g}}}{d\boldsymbol{\theta}^{\mathsf{T}}} \tag{10.143}$$

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

$$\mathbf{H} \equiv \left(\hat{\mathbf{n}}^{\mathsf{T}}\otimes\mathbf{I}_s\right) \tag{10.144}$$

$$\mathbf{J} \equiv \left(\hat{\mathbf{g}}^{\mathsf{T}}\otimes\mathbf{I}_q\right) \tag{10.145}$$

Then define

$$\mathbb{A} = \left(\begin{array}{c|c}\mathbf{A} & 0 \\ \hline 0 & \mathbf{B}\end{array}\right) \tag{10.146}$$

$$\mathbb{H} = \left(\begin{array}{c|c}0 & \mathbf{H} \\ \hline \mathbf{J} & 0\end{array}\right) \tag{10.147}$$

$$\mathbb{C} = \left(\begin{array}{c|c}\dfrac{\partial\operatorname{vec}\mathbf{B}}{\partial\mathbf{n}^{\mathsf{T}}} & \dfrac{\partial\operatorname{vec}\mathbf{B}}{\partial\mathbf{g}^{\mathsf{T}}} \\ \hline \dfrac{\partial\operatorname{vec}\mathbf{A}}{\partial\mathbf{n}^{\mathsf{T}}} & \dfrac{\partial\operatorname{vec}\mathbf{A}}{\partial\mathbf{g}^{\mathsf{T}}}\end{array}\right) \tag{10.148}$$

$$\mathbb{D} = \left(\begin{array}{c}\dfrac{\partial\operatorname{vec}\mathbf{A}}{\partial\boldsymbol{\theta}^{\mathsf{T}}} \\ \dfrac{\partial\operatorname{vec}\mathbf{B}}{\partial\boldsymbol{\theta}^{\mathsf{T}}}\end{array}\right) \tag{10.149}$$

$$\mathbb{N} = \left(\begin{array}{c}\hat{\mathbf{n}} \\ \hat{\mathbf{g}}\end{array}\right) \tag{10.150}$$

In terms of these matrices,

$$\frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \mathbb{H}\mathbb{D} + (\mathbb{A} + \mathbb{H}\mathbb{C})\frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}}. \tag{10.151}$$

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

$$\frac{d\mathbb{N}}{d\boldsymbol{\theta}^\mathsf{T}} = \left(\mathbf{I}_{s+q} - \mathbb{A} - \mathbb{HC}\right)^{-1}\mathbb{HD}. \tag{10.152}$$

10.9   Stage-Structured Epidemics

The transmission of infectious diseases is a source of nonlinearity because the rate of transmission depends on the abundance of infected and non-infected individuals. When demographic structure is added to the picture, the models can become complicated because the transmission process, the recovery process, and the consequences of infection may all vary among age classes or stages.

Klepac and Caswell (2011) developed a general framework for stage-classified epidemics, using the vec-permutation formulation (e.g., Chaps. 5 and 6). Individuals were jointly classified by stage and infection category, and nonlinearity was introduced by the disease transmission process. Klepac and Caswell (2011) calculated sensitivities and elasticities of equilibria and cycles of the stage × infection distribution and, of stage-specific prevalence, to parameters specifying demographic, infection, and recovery processes.

Coupling demography and epidemiology requires attention to time scales. Suppose that the demographic processes operate on one time scale: say, years. For some diseases, the infection/recovery process might operate on a much longer time scale (decades). Or the disease might play out on a much shorter time scale (weeks). When the disease time scale is shorter than the demographic time scale, the matrices in Klepac's model that define disease transmission operate many times within a single year; the result is a periodic model on the infection time scale. See Klepac and Caswell (2011) for details.

10.10   Moments of Longevity in Nonlinear Models

The statistics of longevity (e.g., life expectancy) are traditionally calculated from linear age-classified models (see Chap. 4) or from linear stage-classified models (see Chap. 5). In a nonlinear model at equilibrium, the projection matrix is constant and an individual experiences a fixed schedule of vital rates, from which all the usual statistics of longevity can be calculated. Write the density-dependent projection matrix as

$$\mathbf{A}[\boldsymbol{\theta}, \mathbf{n}] = \mathbf{U}[\boldsymbol{\theta}, \mathbf{n}] + \mathbf{F}[\boldsymbol{\theta}, \mathbf{n}] \tag{10.153}$$

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. 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

$$\mathbf{N}[\boldsymbol{\theta}, \hat{\mathbf{n}}] = \left(\mathbf{I}_s - \mathbf{U}[\boldsymbol{\theta}, \hat{\mathbf{n}}]\right)^{-1} \tag{10.154}$$

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

As in Chap. 4, the vector $\boldsymbol{\eta}_1$ containing the mean longevity of each age class or stage is given by

$$\boldsymbol{\eta}_1^\mathsf{T} = \mathbf{1}_s^\mathsf{T} \mathbf{N}[\hat{\mathbf{n}}]. \tag{10.155}$$

The moments of longevity and other indices are calculated from $\mathbf{N}\left(\boldsymbol{\theta}, \hat{\mathbf{n}}\right)$ just as in the linear case. All the sensitivity results of Chaps. 4 and 5 apply directly, except that the derivative of $\mathbf{N}\left(\boldsymbol{\theta}, \hat{\mathbf{n}}\right)$ must include both the direct effects of $\boldsymbol{\theta}$ and the indirect effects through $\hat{\mathbf{n}}$. For convenience, write $\hat{\mathbf{N}}$ and $\hat{\mathbf{U}}$ for the matrices at equilibrium. Then

$$d\operatorname{vec}\hat{\mathbf{N}} = \left(\hat{\mathbf{N}}^\mathsf{T} \otimes \hat{\mathbf{N}}\right) d\operatorname{vec}\hat{\mathbf{U}} \tag{10.156}$$

$$= \left(\hat{\mathbf{N}}^\mathsf{T} \otimes \hat{\mathbf{N}}\right) \left[\frac{d\operatorname{vec}\hat{\mathbf{U}}}{d\boldsymbol{\theta}^\mathsf{T}} d\boldsymbol{\theta} + \frac{d\hat{\mathbf{U}}}{d\hat{\mathbf{n}}^\mathsf{T}} d\hat{\mathbf{n}}\right] \tag{10.157}$$

where $\hat{\mathbf{U}}$, $\hat{\mathbf{N}}$, and the derivatives of $\mathbf{U}$ are all evaluated at equilibrium and $d\hat{\mathbf{n}}/d\boldsymbol{\theta}^\mathsf{T}$ is given by (10.16). Comparing this with equation (4.34) shows that the nonlinearity adds an extra term, capturing the way that changes in $\boldsymbol{\theta}$ affect the vital rates through changes in equilibrium density.

This approach can be used to generalize the results for higher moments of longevity (Chaps. 4, 5, and 11) to the nonlinear case.

10.11 Summary

Table 10.3 lists the perturbation analysis results in this chapter; they comprise a fairly complete analysis for 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.

As in other chapters, most of the results in this chapter follow a straightforward method:

1. Write the model, specifying the dependence of the vital rates on $\boldsymbol{\theta}$ and $\mathbf{n}$.

Table 10.3 Summary of models and main sensitivity results of the chapter. Extending sensitivities to additional dependent variables (ratios, averages, rates, etc.) is described in Sect. 10.2.3. The extension from sensitivities to elasticities is given in Sect. 10.2.5

Model	Sensitivity of …		Equation[s]
Density-dependent	… equilibrium	$\dfrac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(10.16)
$\mathbf{n}(t+1) = \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t)]\,\mathbf{n}(t)$	… cycle	$\dfrac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(10.121)
	… weighted density, time average		(10.125)–(10.128)
	… temporal variance	$\dfrac{dV(\hat{N})}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(10.137)
	… life expectancy	$\dfrac{d\eta_1}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(10.155)
Environmental feedback			
$\mathbf{n}(t+1) = \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t), \mathbf{g}(t)]\,\mathbf{n}(t)$	… equilibrium (static)	$\dfrac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}}, \ \dfrac{d\hat{\mathbf{g}}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(10.52), (10.53)
$\mathbf{g}(t) = \mathbf{g}[\boldsymbol{\theta}, \mathbf{n}(t)]$			
$\mathbf{g}(t+1) = \mathbf{B}[\boldsymbol{\theta}, \mathbf{n}(t), \mathbf{g}(t)]\,\mathbf{g}(t)$	… equilibrium (dynamic)	$\dfrac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(10.152)
Frequency-dependent (two-sex)	… equilibrium structure	$\dfrac{d\hat{\mathbf{p}}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(10.94)
$\mathbf{n}(t+1) = \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t)]\,\mathbf{n}(t)$	… population growth rate	$\dfrac{d\lambda}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(10.97)
$\mathbf{A}[\boldsymbol{\theta}, \mathbf{n}]$ homogeneous of degree zero in $\mathbf{n}$			

Subsidized (linear or nonlinear) $\mathbf{n}(t+1) = \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t)]\,\mathbf{n}(t) + \mathbf{b}[\boldsymbol{\theta}, \mathbf{n}]$	. . . equilibrium population	$\dfrac{d\hat{\mathbf{n}}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(10.58), (10.68)
Proportional structure $\mathbf{p}(t+1) = \dfrac{\mathbf{A}[\boldsymbol{\theta}]\mathbf{p}(t)}{\mathbf{1}^{\mathsf{T}}\mathbf{A}[\boldsymbol{\theta}]\mathbf{p}(t)}$	. . . age- or stage distribution	$\dfrac{d\hat{\mathbf{p}}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(10.73)
	. . . reproductive value	$\dfrac{d\hat{\mathbf{v}}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(10.77)
	. . . dependency ratio	$\dfrac{dD}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(10.81)
	. . . mean age of reproduction	$\dfrac{d\bar{a}_{\mathrm{f}}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(10.83)
	. . . variance in age of reproduction	$\dfrac{dV_{\mathrm{f}}}{d\boldsymbol{\theta}^{\mathsf{T}}}$	(10.89)

2. Write a matrix expression for the demographic outcome of interest (e.g., the equilibrium population).
3. Differentiate this expression.
4. Use the vec operator and Roth's theorem to obtain an expression that involves only the differentials of vectors.
5. Use the chain rule for total differentials to expand the operators (e.g., $dvec\mathbf{A}$) that are functions of both $\boldsymbol{\theta}$ and $\mathbf{n}$, as in (10.14).
6. Use the first identification theorem and the chain rule to extend the results to sensitivities of any desired dependent variable with respect to any set of parameters

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