Chapter 8
Periodic Models

8.1 Introduction

Periodic matrix models are often used to study cyclical temporal variation (seasonal or interannual), sometimes as a (perhaps crude) approximation to stochastic models. However, formally periodic models also appear when multiple processes (e.g., demography and dispersal) operate within a single projection interval. The models take the form of periodic matrix products. A familiar example is when population projection over an annual interval is described as a product of seasonal operators. The perturbation analysis of periodic models (Caswell and Trevisan 1994; Lesnoff et al. 2003; Caswell and Shyu 2012) must specify both the vital rates affected by the perturbation and the timing of the perturbation within the cycle. This chapter presents a general approach to the perturbation analysis of both linear and nonlinear periodic models. The results consist of a series of analyses of some of the most commonly encountered periodic models.

If the environment is time-invariant on the scale of a chosen projection interval (e.g., from year to year), the result is a periodic matrix population model in which the seasonal product repeats itself. Such a model can be written as

$$\mathbf{n}(t+1) = \mathbf{B}_p \cdots \mathbf{B}_2 \mathbf{B}_1 \mathbf{n}(t) \tag{8.1}$$

Here, $\mathbf{B}_i$ is the matrix at phase i of the cycle and p is the period. The period is the number of phases in the cycle; i.e., the number of matrices in the periodic matrix product in (8.1). Neither the identities nor the number of stages need be the same from one phase to the next, so the matrices $\mathbf{B}_i$ may be rectangular rather than square.

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The phases need not be the same length, so the period may or may not be measured in units of time. For example, in the model of Pico et al. (2002), each season is of 2 months duration, and the period ($p = 6$) corresponds directly to a time scale. In contrast, the model of Hunter and Caswell (2005a) has three phases, with durations of 3 weeks, 5 weeks, and 10 months, respectively. The period ($p = 3$) of that model does not correspond to a time scale, but it identifies the number of matrices in the periodic product and appears in calculations in the same role as $p = 6$ in the model of Pico et al. (2002).

The projection matrix over the entire periodic cycle is[1]

$$\mathbf{A} = \mathbf{B}_p \cdots \mathbf{B}_2 \mathbf{B}_1 \tag{8.2}$$

The earliest studies of periodic matrix models were due to Darwin and Williams (1964), Skellam (1966), and MacArthur (1968). In recent years, with little fanfare, periodic models have emerged as an important tool for incorporating multiple processes within a single projection interval. Uses of periodic models include the following.

1. Seasonal variation. Plants and animals experience obvious and dramatic seasonal variation in their demographic rates. Periodic models have been used to describe this variation, with seasons variously defined in terms of monthly periods, calendar seasons, or in terms of environmental events such as rainfall or flood patterns (e.g., Smith et al. 2005).

   Although annual or near-annual species are obvious candidates for periodic models, within-year time scales may also be important for long-lived species. For example, Hunter and Caswell (2005a) incorporated chick development events on a time scale of weeks into a periodic model for the sooty shearwater, which has a lifetime of decades. Similarly, Jenouvrier et al. (2010, 2014) have used periodic models to capture the timing of events in the breeding cycle within a portion of the year in the long-lived emperor penguin.

[1]Although we will not address it in this chapter, the model (8.1) can be written in a way that explicitly defines the starting phase in the cycle. As written, $\mathbf{A}$ in (8.2) projects from phase 1 to phase 1; if desired we could write this as $\mathbf{A}_1$ and define matrices

$$\begin{aligned} \mathbf{A}_2 &= \mathbf{B}_1 \mathbf{B}_p \cdots \mathbf{B}_2 \\ &\vdots \\ \mathbf{A}_p &= \mathbf{B}_{p-1} \cdots \mathbf{B}_1 \mathbf{B}_p \end{aligned}$$

The $\mathbf{A}_i$ are obtained by cyclic permutations of the sequence $\{\mathbf{B}_p, \ldots, \mathbf{B}_1\}$; each of these projects from a different phase in the cycle. Some demographic properties (e.g., the population growth rate λ) are invariant with respect to such permutations; others (e.g., the eigenvectors) are not (Caswell 2001). In this chapter, we will start with phase 1 and refer to $\mathbf{A}$ rather than $\mathbf{A}_1$.

2. Periodic interannual variability. Periodic models based on sequences of annual observations have been used to study effects of inter-event intervals, where events include fires, floods, ENSO events, etc.
3. Harvest and management. These activities often take place at specified points within an annual or interannual cycle. Periodic models have been used to study the effects of their timing; one of the earliest periodic models being devoted to seasonal harvesting (Darwin and Williams 1964).
4. Conditional probabilities. Periodic matrix products appear when models are written as products of conditional probabilities. In stage-classified models, for example, a transition matrix $\mathbf{U}$, is written as the product of a diagonal matrix $\boldsymbol{\Sigma}$ (with survival probabilities $\boldsymbol{\sigma}$ on the diagonal) and a matrix $\mathbf{G}$ of transition probabilities conditional on survival:

$$\mathbf{U} = \mathbf{G}\boldsymbol{\Sigma} \tag{8.3}$$

which creates a period-2 periodic matrix product within the model.
5. Multistate vec-permutation models. When individuals are classified by two or more criteria (e.g., stage and location), the dynamics over the projection interval can be described in terms of the processes affecting each criterion (e.g., transitions and movement). The result is a periodic model that uses the vec-permutation matrix to generate a block-structured projection matrix over the entire interval. See Chap. 6 for analysis of such models.
6. Nonlinear models. Henson and Cushing (1997) developed a model for *Tribolium* in an experimental system in which container size was varied periodically. Shyu et al. (2013) developed a nonlinear seasonal model of an invasive plant to account for the timing of both density effects and management actions within the year. In such models, cyclic dynamics can be produced both by the environmental periodicity and the nonlinearities (e.g., Cushing 2006).

8.1.1 Perturbation Analysis

As in Fig. 8.1, we suppose that in phase i of the cycle, the parameter vector takes on the value $\boldsymbol{\theta}_i$ and determines the matrix $\mathbf{B}_i$. The projection matrix $\mathbf{A}$ is the product, in the specified order, of the $\mathbf{B}_i$. Although the output $\boldsymbol{\xi}$ is calculated from $\mathbf{A}$, the parameter dependence operates through the $\mathbf{B}_i$ (Fig. 8.1). The sensitivity of $\boldsymbol{\xi}$ to the elements of $\mathbf{A}$ is in general not of interest, because those elements are complicated expressions involving the elements of all the $\mathbf{B}_i$, and thus mix disparate biological processes. Here we calculate the sensitivity of demographic outcomes to the entries of the $\mathbf{B}_i$.

In this chapter we analyze linear periodic models of the form (8.1) and the cyclic dynamics of nonlinear seasonal models with delayed density effects. We will briefly discuss the generalization of the multistate age×stage-classified models

Table 8.1 Table of symbols in this chapter

Symbol	Meaning
s_i	Number of stages at phase i of the cycle
p	Period of the cycle
q	Dimension of parameter vector $\boldsymbol{\theta}$
r	Number of locations in spatial model
$\boldsymbol{\theta}_i$	Parameter vector evaluated at phase i
$\mathbf{B}_i$	Projection matrix from phase i to phase $i+1$, or in location i
$\mathbf{C}_i^j$	Ordered product $\mathbf{B}_j \cdots \mathbf{B}_i$ of matrices from i to j
$\mathbf{M}_i$	Dispersal matrix for stage i
$\mathbf{A}$	Projection matrix over entire cycle
$\mathbf{A}_i$	Projection matrix over cycle, starting at phase i
$\mathbf{R}_i$	Matrix of LTRE contributions from phase i
$\mathbf{E}_{s,i}$	$s \times s$ matrix with 1 in (i,i) position and 0 elsewhere
$\mathbf{I}_s$	Identity matrix of dimension s
$\mathcal{D}(\mathbf{x})$	Diagonal matrix with $\mathbf{x}$ on the diagonal
$\mathbf{1}$	Vector of ones
$\mathbb{B}$, $\mathbb{M}$, etc.	Block-structured matrices
$\circ$	Hadamard, or element-by-element product
$\otimes$	Kronecker product

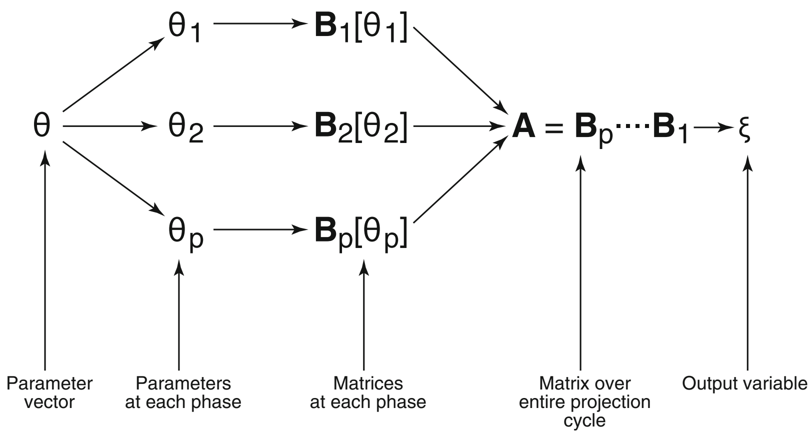

Fig. 8.1 A vector $\boldsymbol{\theta}$ of parameters determines an output variable $\boldsymbol{\xi}$, which may be a scalar, vector, or matrix. The parameter vector will generally take on different values at each phase in the cycle, and determine the phase-specific matrix $\mathbf{B}_i$. These matrices determine the projection matrix $\mathbf{A}$ as a periodic matrix product; the output variable is computed from $\mathbf{A}$. The perturbation problem is to compute the sensitivity or elasticity of $\boldsymbol{\xi}$ to $\boldsymbol{\theta}$

explored in Chap. 6 to an arbitrary number of classifications. We extend the LTRE decomposition analysis to the periodic case, making it possible to analyze effects of parameter changes at any point in a periodic environment.

8.2 Linear Models

Consider the basic model (8.1) with projection matrix (8.2). The period of the cycle is p. To allow for differences in the state vector at different phases within the cycle, define the number of stages at phase i as s_i. Thus the matrix $\mathbf{B}_i$ is of dimension $s_{i+1} \times s_i$, with the subscript i interpreted mod(p) (that is, $(p+1)\ \mathrm{mod}(p) = 1$).

Let $\boldsymbol{\xi}$ (dimension $m \times 1$) denote an output variable calculated from $\mathbf{A}$, where $\boldsymbol{\xi}$ might be a scalar, a vector, or a vectorized matrix. Let $\boldsymbol{\theta}$ be a parameter vector (dimension $q \times 1$). The derivative of $\boldsymbol{\xi}$ with respect to $\boldsymbol{\theta}$ is the $m \times q$ matrix

$$\frac{d\boldsymbol{\xi}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\frac{d\xi_i}{d\theta_j} \right) \qquad i = 1, \ldots, m; \; j = 1, \ldots, q \tag{8.4}$$

By the chain rule, the effects of the parameters on $\boldsymbol{\xi}$ are captured in the matrix product

$$\frac{d\boldsymbol{\xi}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \frac{d\boldsymbol{\xi}}{d\mathrm{vec}^{\mathsf{T}}\mathbf{A}} \frac{d\mathrm{vec}\,\mathbf{A}}{d\boldsymbol{\theta}^{\mathsf{T}}}. \tag{8.5}$$

The first term in (8.5) is the derivative of the output variable $\boldsymbol{\xi}$ with respect to the matrix $\mathbf{A}$ from which it is calculated. The second term in (8.5) is the derivative of the periodic product matrix $\mathbf{A}$ with respect to the parameter vector $\boldsymbol{\theta}$. To obtain this, differentiate (8.2), to obtain

$$\begin{aligned} d\mathbf{A} = \mathbf{B}_p \cdots \mathbf{B}_2 \, (d\mathbf{B}_1) \\ +\mathbf{B}_p \cdots (d\mathbf{B}_2)\, \mathbf{B}_1 \\ \vdots \\ + \left(d\mathbf{B}_p\right) \mathbf{B}_{p-1} \cdots \mathbf{B}_1 \end{aligned} \tag{8.6}$$

It is convenient to define the matrix $\mathbf{C}_i^j$ as the ordered product (from right to left) of the $\mathbf{B}$ matrices from i up to j:

$$\mathbf{C}_i^j = \mathbf{B}_j \cdots \mathbf{B}_i \qquad i \le j \tag{8.7}$$

and set $\mathbf{C}_1^0 = \mathbf{C}_{p+1}^p = \mathbf{I}_{s_1}$. Then (8.6) becomes

$$d\mathbf{A} = \mathbf{C}_2^p \,(d\mathbf{B}_1) + \mathbf{C}_3^p \,(d\mathbf{B}_2)\, \mathbf{C}_1^1 \cdots + \left(d\mathbf{B}_p\right) \mathbf{C}_1^{p-1} \tag{8.8}$$

Applying the vec operator to both sides gives

$$d\mathrm{vec}\,\mathbf{A} = \sum_{i=1}^{p} \left[\left(\mathbf{C}_1^{i-1} \right)^{\mathsf{T}} \otimes \mathbf{C}_{i+1}^p \right] d\mathrm{vec}\,\mathbf{B}_i \tag{8.9}$$

Equation (8.9) accounts automatically for the possibly different dimensions of the $\mathbf{B}_i$. The resulting derivative with respect to the parameter vector $\boldsymbol{\theta}$ is

$$\frac{d\text{vec}\,\mathbf{A}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \sum_{i=1}^{p} \left[\left(\mathbf{C}_1^{i-1} \right)^{\mathsf{T}} \otimes \mathbf{C}_{i+1}^{p} \right] \frac{d\text{vec}\,\mathbf{B}_i}{d\boldsymbol{\theta}^{\mathsf{T}}}. \tag{8.10}$$

where $d\text{vec}\,\mathbf{B}_i / d\boldsymbol{\theta}^{\mathsf{T}}$ is the derivative of the matrix $\mathbf{B}_i$ with respect to the parameter vector $\boldsymbol{\theta}$, evaluated at $\boldsymbol{\theta}_i$. Equation (8.10) sums the contributions of the derivatives of all of the phase-specific matrices $\mathbf{B}_i$ with respect to $\boldsymbol{\theta}$, thus accounting for all the ways in which $\boldsymbol{\theta}$ may affect the demographic rates at each point in the cycle. As written, (8.10) gives the result of perturbing $\boldsymbol{\theta}$ at each point in the cycle. The effect of a phase-specific perturbation is easily obtained by summing only over phases in which $\boldsymbol{\theta}_i$ is modified.

Substituting (8.10) into the formula (8.5) gives the general expression for the sensitivity of $\boldsymbol{\xi}$ to changes affecting any or all of the $\mathbf{B}_i$:

$$\frac{d\boldsymbol{\xi}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \frac{d\boldsymbol{\xi}}{d\text{vec}^{\mathsf{T}}\mathbf{A}} \left(\sum_{i=1}^{p} \left[\left(\mathbf{C}_1^{i-1} \right)^{\mathsf{T}} \otimes \mathbf{C}_{i+1}^{p} \right] \frac{d\text{vec}\,\mathbf{B}_i}{d\boldsymbol{\theta}^{\mathsf{T}}} \right). \tag{8.11}$$

The elasticity of $\boldsymbol{\xi}$ to $\boldsymbol{\theta}$ is the matrix

$$\frac{\epsilon\boldsymbol{\xi}}{\epsilon\boldsymbol{\theta}^{\mathsf{T}}} = \left(\frac{\theta_j}{\xi_i} \frac{d\xi_i}{d\theta_j} \right) \tag{8.12}$$

$$= \mathcal{D}\left(\boldsymbol{\xi}\right)^{-1} \frac{d\boldsymbol{\xi}}{d\text{vec}^{\mathsf{T}}\mathbf{A}} \left(\sum_{i=1}^{p} \left[\left(\mathbf{C}_1^{i-1} \right)^{\mathsf{T}} \otimes \mathbf{C}_{i+1}^{p} \right] \frac{d\text{vec}\,\mathbf{B}_i}{d\boldsymbol{\theta}^{\mathsf{T}}} \right) \mathcal{D}\left(\boldsymbol{\theta}\right) \tag{8.13}$$

where $\mathcal{D}(\mathbf{x})$ is a diagonal matrix with $\mathbf{x}$ on the diagonal and zeros elsewhere. Because elasticities are logarithmic derivatives, they apply only when $\boldsymbol{\xi} > 0$ and $\boldsymbol{\theta} \geq 0$.

8.2.1 A Simple Harvest Model

The projection matrix for a simple harvest model (e.g., Hauser et al. 2006) can be written

$$\mathbf{A} = \mathbf{B}\left(\mathbf{I} - \mathbf{H}\right). \tag{8.14}$$

The matrix $\mathbf{B}$ describes demography in the absence of harvest. The matrix $\mathbf{H} = \mathcal{D}(\mathbf{h})$ is a harvest matrix, where h_i is the probability that an individual of stage i

is harvested.[2] Either $\mathbf{B}$, $\mathbf{H}$, or both may be functions of a vector $\boldsymbol{\theta}$ of parameters. Differentiating (8.14) and applying the vec operator gives

$$d\mathrm{vec}\,\mathbf{A} = -\left(\mathbf{I}_s \otimes \mathbf{B}\right) d\mathrm{vec}\,\mathbf{H} + \left[(\mathbf{I}-\mathbf{H})^{\mathsf{T}} \otimes \mathbf{I}_s\right] d\mathrm{vec}\,\mathbf{B}. \tag{8.15}$$

The diagonal matrix $\mathbf{H}$ can be written

$$\mathbf{H} = \mathbf{I}_s \circ \left(\mathbf{1}_s \mathbf{h}^{\mathsf{T}}\right) \tag{8.16}$$

where $\mathbf{1}_s$ is a $s \times 1$ vector of ones and $\circ$ denotes the Hadamard product. The differential of $\mathbf{H}$ in (8.16) is

$$d\mathrm{vec}\,\mathbf{H} = \mathcal{D}\left(\mathrm{vec}\,\mathbf{I}_s\right)\left(\mathbf{I}_s \otimes \mathbf{1}_s\right) d\mathbf{h}. \tag{8.17}$$

Combining (8.16) and (8.15) and applying the chain rule gives the derivative with respect to $\boldsymbol{\theta}$:

$$\frac{d\mathrm{vec}\,\mathbf{A}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \underbrace{-\left(\mathbf{I}_s \otimes \mathbf{B}\right)\mathcal{D}\left(\mathrm{vec}\,\mathbf{I}_s\right)\left(\mathbf{I}_s \otimes \mathbf{1}_s\right)\frac{d\mathbf{h}}{d\boldsymbol{\theta}^{\mathsf{T}}}}_{\text{perturbations of }\mathbf{h}} + \underbrace{\left[(\mathbf{I}-\mathbf{H})^{\mathsf{T}} \otimes \mathbf{I}_s\right]\frac{d\mathrm{vec}\,\mathbf{B}}{d\boldsymbol{\theta}^{\mathsf{T}}}}_{\text{perturbations of }\mathbf{B}}. \tag{8.18}$$

The conditional probability model (8.3) has the same form as the harvest model (8.14), so a similar analysis applies to it as well:

$$d\mathrm{vec}\,\mathbf{U} = \left(\mathbf{I} \otimes \mathbf{G}\right)\mathcal{D}\left(\mathrm{vec}\,\mathbf{I}\right)\left(\mathbf{I} \otimes \mathbf{1}\right) d\boldsymbol{\sigma} + \left(\boldsymbol{\Sigma} \otimes \mathbf{I}\right) d\mathrm{vec}\,\mathbf{G}. \tag{8.19}$$

However, the conditional transition matrix $\mathbf{G}$ is column-stochastic (all columns sum to 1), because all loss of individuals is accounted for by $\boldsymbol{\Sigma}$. Thus relevant perturbations must be parameterized so that the stochasticity is preserved. For example, if $\mathbf{G}$ describes growth in the standard size-classified model (Caswell 2001, Section 4.2), e.g.,

$$\mathbf{G} = \begin{pmatrix} 1-\gamma_1 & 0 & 0 \\ \gamma_1 & 1-\gamma_2 & 0 \\ 0 & \gamma_2 & 1-\gamma_3 \end{pmatrix} \tag{8.20}$$

then perturbations of the γ_i will preserve stochasticity of $\mathbf{G}$. If $\mathbf{G}$ has no such convenient parameterization, then changes in the entries of $\mathbf{G}$ must be compensated for by changes elsewhere in the same column (see Caswell 2001; Hill et al. 2004;

[2] Alternatively, let μ_i be the mortality due to harvest experienced by an individual in stage i. Then $\mathbf{H} = \exp\left[-\mathcal{D}\left(\boldsymbol{\mu}\right)\right]$. Harvest imposes an additional, additive hazard on top of the natural mortality contained in $\mathbf{B}$.

Theorem 4.5 of Caswell 2013). For explicit formulas for compensation, see Chap. 11 of this volume; for an application, see van Daalen and Caswell (2017).

The harvest model (8.14) can be extended to describe harvest imposed at a specified phase within a p-cycle. Suppose that harvest takes place between phase m and phase $m+1$, so that

$$\mathbf{A} = \mathbf{B}_p \cdots \mathbf{B}_{m+1} \; (\mathbf{I} - \mathbf{H}) \; \mathbf{B}_m \cdots \mathbf{B}_1 \tag{8.21}$$

(see Darwin and Williams (1964) for an early example of this kind of seasonal harvest model). Using the same approach, it can be shown that

$$\begin{aligned} \frac{d\mathrm{vec}\,\mathbf{A}}{d\boldsymbol{\theta}^{\mathsf{T}}} &= -\left[\left(\mathbf{C}_1^m\right)^{\mathsf{T}} \otimes \mathbf{C}_{m+1}^p\right] \frac{d\mathrm{vec}\,\mathbf{H}}{d\boldsymbol{\theta}^{\mathsf{T}}} \\ &\quad + \left[\mathbf{I}_{s_1} \otimes \mathbf{C}_{m+1}^p \left(\mathbf{I} - \mathbf{H}\right)\right] \sum_{i=1}^{m} \left[\left(\mathbf{C}_1^{i-1}\right)^{\mathsf{T}} \otimes \mathbf{C}_{i+1}^m\right] \frac{d\mathrm{vec}\,\mathbf{B}_i}{d\boldsymbol{\theta}^{\mathsf{T}}} \\ &\quad + \left[\left(\left(\mathbf{I} - \mathbf{H}\right) \mathbf{C}_1^m\right)^{\mathsf{T}} \otimes \mathbf{I}_{s_1}\right] \sum_{i=m+1}^{p} \left[\left(\mathbf{C}_{m+1}^{i-1}\right)^{\mathsf{T}} \otimes \mathbf{C}_{i+1}^p\right] \frac{d\mathrm{vec}\,\mathbf{B}_i}{d\boldsymbol{\theta}^{\mathsf{T}}} \end{aligned} \tag{8.22}$$

The expression (8.17) can be substituted for $d\mathrm{vec}\,\mathbf{H}$ in (8.22), and the resulting expression for $d\mathrm{vec}\,\mathbf{A}/d\boldsymbol{\theta}^{\mathsf{T}}$ substituted into (8.5).

8.3 Multistate Models

We have encountered several examples of models in which individuals are classified by two criteria (age and stage, stage and environmental state, stage and location, etc.). These multistate models can be constructed by the vec-permutation matrix approach; see Chaps. 5 and 6 or Hunter and Caswell (2005b) and Caswell et al. (2018).

Suppose individuals classified by two criteria; e.g., stages $(1, \ldots, s)$ and locations $(1, \ldots, r)$. One might describe population dynamics in terms of stage transitions within locations, and spatial movement within stages, with the two processes acting sequentially. Thus individuals first survive and reproduce according to their stage-specific demography, and then disperse among locations, and then repeat. Let $\mathbf{B}_i$ be the $s \times s$ matrix describing transitions and reproduction within location i, and $\mathbf{M}_j$ the $r \times r$ matrix describing movement probabilities for stage j. Let $\mathbb{B}$ and $\mathbb{M}$ be the $sr \times sr$ block diagonal matrices with the $\mathbf{B}_i$ and the $\mathbf{M}_j$, respectively, on the diagonal.

The population is projected by

$$\mathbf{n}(t+1) = \mathbf{K}^{\mathsf{T}} \mathbb{M} \mathbf{K} \mathbb{B} \; \mathbf{n}(t).. \tag{8.23}$$

The matrix $\mathbf{K}$ is the vec-permutation matrix, or commutation matrix, (Henderson and Searle 1981; Magnus and Neudecker 1979), which satisfies

$$\text{vec}\,\mathcal{N}^{\mathsf{T}} = \mathbf{K}\ \text{vec}\,\mathcal{N} \tag{8.24}$$

For the calculation of $\mathbf{K}$, see Sect. 2.2.3.

The model (8.23) is formally periodic, with the operation of $\mathbb{B}$ and $\mathbb{M}$ alternating; thus the projection matrix is

$$\mathbf{A} = \mathbf{K}^{\mathsf{T}}\mathbb{M}\mathbf{K}\mathbb{B}. \tag{8.25}$$

The dependence of $\mathbf{A}$ on the parameters $\boldsymbol{\theta}$ can take place through $\mathbf{B}_i\,[\boldsymbol{\theta}]$, $\mathbf{M}_i\,[\boldsymbol{\theta}]$, or both.

The general sensitivity formula (8.5) requires the derivative $d\mathbf{A}/d\boldsymbol{\theta}^{\mathsf{T}}$. Differentiating (8.25) gives

$$d\mathbf{A} = \mathbf{K}^{\mathsf{T}}\,(d\mathbb{M})\,\mathbf{K}\mathbb{B} + \mathbf{K}^{\mathsf{T}}\mathbb{M}\mathbf{K}\,(d\mathbb{B})\,. \tag{8.26}$$

Applying the vec operator gives

$$d\text{vec}\,\mathbf{A} = \left(\mathbb{B}^{\mathsf{T}}\mathbf{K}^{\mathsf{T}} \otimes \mathbf{K}^{\mathsf{T}}\right) d\text{vec}\,\mathbb{M} + \left(\mathbf{I}_{sp} \otimes \mathbf{K}^{\mathsf{T}}\mathbb{M}\mathbf{K}\right) d\text{vec}\,\mathbb{B} \tag{8.27}$$

We want to express $d\text{vec}\,\mathbb{B}$ and $d\mathbb{M}$ in terms of the derivatives of their diagonal entries $\mathbf{B}_i$ and $\mathbf{M}_j$. This can be done using equations (14) and (15) of Caswell and van Daalen (2016). Define the matrices $\mathbf{P}_i$ and $\mathbf{Q}_i$, of dimension $rs \times s$ and $s \times rs$, respectively,

$$\mathbf{P}_i = \begin{pmatrix} \mathbf{0}_{s(i-1)\times s} \\ \mathbf{I}_s \\ \mathbf{0}_{s(r-i)\times s} \end{pmatrix} \qquad \mathbf{Q}_i = \begin{pmatrix} \mathbf{0}_{s\times(i-1)s} & \mathbf{I}_s & \mathbf{0}_{s\times(r-i)s} \end{pmatrix}. \tag{8.28}$$

Then

$$d\text{vec}\,\mathbb{B} = \sum_{i=1}^{r} \left(\mathbf{Q}_i^{\mathsf{T}} \otimes \mathbf{P}_i\right) d\text{vec}\,\mathbf{B}_i. \tag{8.29}$$

Similarly, for $\mathbb{M}$, define matrices $\mathbf{R}_i$ and $\mathbf{S}_i$

$$\mathbf{R}_i = \begin{pmatrix} \mathbf{0}_{r(i-1)\times r} \\ \mathbf{I}_r \\ \mathbf{0}_{r(s-i)\times r} \end{pmatrix} \qquad \mathbf{S}_i = \begin{pmatrix} \mathbf{0}_{r\times(i-1)r} & \mathbf{I}_r & \mathbf{0}_{r\times(s-i)r} \end{pmatrix}. \tag{8.30}$$

Then

$$d\text{vec}\,\mathbb{M} = \sum_{i=1}^{s} \left(\mathbf{S}_i^{\mathsf{T}} \otimes \mathbf{R}_i\right) \text{vec}\,\mathbf{M}_i. \tag{8.31}$$

Substituting (8.29) and (8.31) into the expression (8.27) for $d\text{vec}\,\mathbf{A}$ gives the final result

$$\frac{d\text{vec}\,\mathbf{A}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \underbrace{\mathbf{X}_1 \sum_{j=1}^{s} \left(\mathbf{S}_j^{\mathsf{T}} \otimes \mathbf{R}_j\right) \frac{d\text{vec}\,\mathbf{M}_j}{d\boldsymbol{\theta}^{\mathsf{T}}}}_{\text{perturbations of the } \mathbf{M}_j} + \underbrace{\mathbf{X}_2 \sum_{i=1}^{r} \left(\mathbf{Q}_i^{\mathsf{T}} \otimes P_i\right) \frac{d\text{vec}\,\mathbf{B}_i}{d\boldsymbol{\theta}^{\mathsf{T}}}}_{\text{perturbations of the } \mathbf{B}_i} \tag{8.32}$$

where $\mathbf{X}_1$ and $\mathbf{X}_2$ are constant matrices,

$$\mathbf{X}_1 = \left(\mathbb{B}^{\mathsf{T}}\mathbf{K}^{\mathsf{T}} \otimes \mathbf{K}^{\mathsf{T}}\right) \tag{8.33}$$

$$\mathbf{X}_2 = \left(\mathbf{I}_{sr} \otimes \mathbf{K}^{\mathsf{T}}\mathbb{M}\mathbf{K}\right) \tag{8.34}$$

that need be calculated only once. Although $\mathbf{X}_1$, $\mathbf{X}_2$, and the Kronecker products appearing in the summations are large, they are also extremely sparse. The sparse matrix capabilities in MATLAB can take advantage of this fact. Substituting (8.32) into (8.5) gives the sensitivity of an output variable $\boldsymbol{\xi}$ to changes in parameters that perturb any or all of the $\mathbf{M}_j$ and $\mathbf{B}_i$.

8.4 Nonlinear Models and Delayed Density Dependence

Anticipating the more extensive treatment in Chap. 10, we consider the effects of nonlinearity in periodic models. You may want to return to this section after Sect. 10.7, which analyzes periodic oscillations arising from time-invariant nonlinearities. When periodic environmental changes interact with such oscillations, the results can be complicated, and such interactions are the focus of the present section.

In a periodic nonlinear model, each of the $\mathbf{B}_i$ in (8.2) may depend on density. Especially in seasonal models, the vital rates in the matrix $\mathbf{B}_i$ may depend on densities not only at phase i, but at previous phases within the cycle as well. For example, in a study of the invasive plant garlic mustard (*Alliaria petiolata*) Shyu et al. (2013) found that seed production of fruiting plants in the fall reflected the density experienced by vegetative rosettes in the early spring.

To develop a model including such delayed density dependence, define

$$\mathbf{n}_i(t) = \text{population at season } i \text{ in year } t \tag{8.35}$$

Starting at season 1, the dynamics are given by

$$\begin{aligned}
\mathbf{n}_1(t+1) &= \mathbf{B}_p \mathbf{n}_p(t) \\
\mathbf{n}_2(t) &= \mathbf{B}_1 \mathbf{n}_1(t) \\
&\vdots \\
\mathbf{n}_p(t) &= \mathbf{B}_{p-1} \mathbf{n}_{p-1}(t)
\end{aligned} \tag{8.36}$$

Density-dependence, in a general form, means that the matrices $\mathbf{B}_i$ may be functions of densities over one cycle prior to season i:

$$\begin{aligned}
\mathbf{B}_1 &= \mathbf{B}_1 \left[\mathbf{n}_1(t), \mathbf{n}_p(t-1), \ldots, \mathbf{n}_2(t-1) \right] \\
\mathbf{B}_2 &= \mathbf{B}_2 \left[\mathbf{n}_2(t), \mathbf{n}_1(t), \mathbf{n}_p(t-1), \ldots, \mathbf{n}_3(t-1) \right] \\
&\vdots \\
\mathbf{B}_p &= \mathbf{B}_p \left[\mathbf{n}_p(t), \mathbf{n}_{p-1}(t), \ldots, \mathbf{n}_1(t) \right]
\end{aligned} \tag{8.37}$$

A fixed point on the interannual time scale, from t to $t+1$, is a p-cycle on the seasonal scale, satisfying

$$\begin{aligned}
\hat{\mathbf{n}}_1 &= \mathbf{B}_p \left[\hat{\mathbf{n}}_1, \ldots, \hat{\mathbf{n}}_p \right] \; \hat{\mathbf{n}}_p \\
\hat{\mathbf{n}}_2 &= \mathbf{B}_1 \left[\hat{\mathbf{n}}_1, \ldots, \hat{\mathbf{n}}_p \right] \; \hat{\mathbf{n}}_1 \\
&\vdots \\
\hat{\mathbf{n}}_p &= \mathbf{B}_{p-1} \left[\hat{\mathbf{n}}_1, \ldots, \hat{\mathbf{n}}_p \right] \; \hat{\mathbf{n}}_{p-1}
\end{aligned} \tag{8.38}$$

A k-cycle on the interannual time scale is a kp-cycle on the seasonal time scale, the points of which are numbered $\hat{\mathbf{n}}_1, \ldots, \hat{\mathbf{n}}_{kp}$. The corresponding sequence of matrices, in which the annual cycle $\mathbf{B}_1, \ldots, \mathbf{B}_p$ is repeated k times, is defined as $\mathbf{B}_1, \ldots, \mathbf{B}_{kp}$. With this notation, (8.38) still holds, with kp instead of p entries.

Differentiating (8.38) yields

$$d\hat{\mathbf{n}}_i = (d\mathbf{B}_{i-1})\, \hat{\mathbf{n}}_{i-1} + \mathbf{B}_{i-1} \left(d\hat{\mathbf{n}}_{i-1} \right) \qquad i = 1, \ldots, p \tag{8.39}$$

where the subscripts on $\hat{\mathbf{n}}$ and $\mathbf{B}$ are interpreted modulo p. Applying the vec operator to (8.39) yields

$$d\hat{\mathbf{n}}_i = \left(\hat{\mathbf{n}}_{i-1}^{\mathsf{T}} \otimes \mathbf{I}_s \right) d\operatorname{vec} \mathbf{B}_{i-1} + \mathbf{B}_{i-1} d\hat{\mathbf{n}}_{i-1}. \tag{8.40}$$

The sensitivity analysis of the cycle involves a set of block-structured matrices, the form of which is easily generalized from the special case with $p = 3$. Assuming $p = 3$ and noting that $\mathbf{B}$ depends on all the $\hat{\mathbf{n}}_i$ as well as on the parameter vector $\boldsymbol{\theta}$, the total differential of $\mathbf{B}_{i-1}$ in (8.40) is

$$d\text{vec}\,\mathbf{B}_{i-1} = \frac{\partial \text{vec}\,\mathbf{B}_{i-1}}{\partial \mathbf{n}_1^{\mathsf{T}}} d\hat{\mathbf{n}}_1 + \frac{\partial \text{vec}\,\mathbf{B}_{i-1}}{\partial \mathbf{n}_2^{\mathsf{T}}} d\hat{\mathbf{n}}_2 + \frac{\partial \text{vec}\,\mathbf{B}_{i-1}}{\partial \mathbf{n}_3^{\mathsf{T}}} d\hat{\mathbf{n}}_3 + \frac{\partial \text{vec}\,\mathbf{B}_{i-1}}{\partial \boldsymbol{\theta}^{\mathsf{T}}} d\boldsymbol{\theta} \tag{8.41}$$

For notational convenience, define the matrices

$$\mathbf{H}_i = \left(\hat{\mathbf{n}}_i^{\mathsf{T}} \otimes \mathbf{I}_s\right) \qquad i = 1, \ldots, p \tag{8.42}$$

Substituting (8.41) into (8.40) produces the set of equations

$$\begin{aligned}
d\hat{\mathbf{n}}_1 &= \mathbf{H}_3 \frac{\partial \text{vec}\,\mathbf{B}_3}{\partial \boldsymbol{\theta}^{\mathsf{T}}} d\boldsymbol{\theta} + \mathbf{H}_3 \sum_{j=1}^{p} \frac{\partial \text{vec}\,\mathbf{B}_3}{\partial \mathbf{n}_j^{\mathsf{T}}} d\hat{\mathbf{n}}_j + \mathbf{B}_3 d\hat{\mathbf{n}}_3 \\
d\hat{\mathbf{n}}_2 &= \mathbf{H}_1 \frac{\partial \text{vec}\,\mathbf{B}_1}{\partial \boldsymbol{\theta}^{\mathsf{T}}} d\boldsymbol{\theta} + \mathbf{H}_1 \sum_{j=1}^{p} \frac{\partial \text{vec}\,\mathbf{B}_1}{\partial \mathbf{n}_j^{\mathsf{T}}} d\hat{\mathbf{n}}_j + \mathbf{B}_1 d\hat{\mathbf{n}}_1 \\
d\hat{\mathbf{n}}_1 &= \mathbf{H}_2 \frac{\partial \text{vec}\,\mathbf{B}_2}{\partial \boldsymbol{\theta}^{\mathsf{T}}} d\boldsymbol{\theta} + \mathbf{H}_2 \sum_{j=1}^{p} \frac{\partial \text{vec}\,\mathbf{B}_2}{\partial \mathbf{n}_j^{\mathsf{T}}} d\hat{\mathbf{n}}_j + \mathbf{B}_2 d\hat{\mathbf{n}}_2
\end{aligned} \tag{8.43}$$

This set of equations can be reduced to a single equation by collecting all the points on the kp-cycle into a single vector. Write an array (of dimension $sp \times k$)

$$\mathcal{N} = \begin{array}{l|ccc} & \text{yr. } 1 & & \text{yr. } k \\ \hline \text{season } 1 & \hat{\mathbf{n}}_1 & \cdots & \hat{\mathbf{n}}_1 \\ \vdots & \vdots & & \vdots \\ \text{season } p & \hat{\mathbf{n}}_p & \cdots & \hat{\mathbf{n}}_p \\ \hline \end{array} \tag{8.44}$$

Then write the vector (of dimension $spk \times 1$)

$$\mathbb{N} = \text{vec}\,\mathcal{N} \tag{8.45}$$

In terms of this vector, the set of equations (8.43) can be rewritten

$$\frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left[\mathbf{I}_{skp} - \mathbb{B} - \mathbb{H}\mathbb{C}\right]^{-1} \mathbb{H}\mathbb{D}. \tag{8.46}$$

where $\mathbb{H}$ and $\mathbb{B}$ are the block-circulant matrices

$$\mathbb{H} = \begin{pmatrix} 0 & 0 & \mathbf{H}_3 \\ \mathbf{H}_1 & 0 & 0 \\ 0 & \mathbf{H}_2 & 0 \end{pmatrix} \tag{8.47}$$

$$\mathbb{B} = \begin{pmatrix} 0 & 0 & \mathbf{B}_3 \\ \mathbf{B}_1 & 0 & 0 \\ 0 & \mathbf{B}_2 & 0 \end{pmatrix}, \tag{8.48}$$

and $\mathbb{C}$ and $\mathbb{D}$ are the block matrices

$$\mathbb{C} = \begin{pmatrix} \dfrac{\partial \text{vec}\, \mathbf{B}_1}{\partial \mathbf{n}_1^{\mathsf{T}}} & \cdots & \dfrac{\partial \text{vec}\, \mathbf{B}_1}{\partial \mathbf{n}_3^{\mathsf{T}}} \\ \vdots & \ddots & \vdots \\ \dfrac{\partial \text{vec}\, \mathbf{B}_3}{\partial \mathbf{n}_1^{\mathsf{T}}} & \cdots & \dfrac{\partial \text{vec}\, \mathbf{B}_3}{\partial \mathbf{n}_3^{\mathsf{T}}} \end{pmatrix} \tag{8.49}$$

$$\mathbb{D} = \begin{pmatrix} \dfrac{\partial \text{vec}\, \mathbf{B}_1}{\partial \boldsymbol{\theta}^{\mathsf{T}}} \\ \dfrac{\partial \text{vec}\, \mathbf{B}_2}{\partial \boldsymbol{\theta}^{\mathsf{T}}} \\ \dfrac{\partial \text{vec}\, \mathbf{B}_3}{\partial \boldsymbol{\theta}^{\mathsf{T}}} \end{pmatrix}. \tag{8.50}$$

All the derivatives are evaluated at $\hat{\mathbf{n}}_1, \ldots, \hat{\mathbf{n}}_3$.

8.4.1 Averages

The vector $d\mathbb{N}/d\boldsymbol{\theta}^{\mathsf{T}}$ created by (8.46) contains the sensitivities of all s stages, at each of p seasons within the year, for each of the k years within the inter-annual k-cycle. If this is too much information, one can calculate the sensitivity of averages, or other linear combinations, taken in various ways.

To write these averages, let $\mathbf{b}_m$ be a $m \times 1$ vector of weights. For a simple average of m quantities, each entry of $\mathbf{b}_m$ is $1/m$; for a weighted average, the entries of $\mathbf{b}_m$ would be non-negative numbers summing to 1. More generally, $\mathbf{b}$ may contain arbitrary weights, such as biomass, metabolic rate, economic value, etc. See Chaps. 7 and 10. To calculate averages from $\mathbb{N}$, first apply these vectors to average over rows or columns of $\mathcal{N}$ and then apply the vec operator to express the results as averages over $\mathbb{N}$.

Annual fixed point If the dynamics are a fixed point on the annual time scale, averages can be calculated over stages (using a vector $\mathbf{b}_s$), over seasons (using a vector $\mathbf{b}_p$), or both. The $p \times 1$ vector of averages over stages is

$$\text{avg. over stages} = \text{vec}\left(\mathbf{b}_s^{\mathsf{T}} \mathcal{N}\right) \tag{8.51}$$

$$= \left(\mathbf{I}_p \otimes \mathbf{b}_s^{\mathsf{T}}\right) \mathbb{N} \tag{8.52}$$

The $s \times 1$ vector of averages over seasons is

$$\text{avg. over seasons} = \left(\mathbf{b}_p^{\mathsf{T}} \otimes \mathbf{I}_s\right) \mathbb{N} \tag{8.53}$$

The average over both seasons and stages (a scalar) is

$$\text{avg. over stages and seasons} = \left(\mathbf{b}_p^{\mathsf{T}} \otimes \mathbf{b}_s^{\mathsf{T}}\right) \mathbb{N} \tag{8.54}$$

Because the average is a linear operator, the sensitivities of these averages are obtained by applying the same weights to the derivative $d\mathbb{N}/d\boldsymbol{\theta}^{\mathsf{T}}$ in (8.46):

$$\text{sensitivity of avg. over stages} = \left(\mathbf{I}_p \otimes \mathbf{b}_s^{\mathsf{T}}\right) \frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}} \tag{8.55}$$

$$\text{sensitivity of avg. over seasons} = \left(\mathbf{b}_p^{\mathsf{T}} \otimes \mathbf{I}_s\right) \frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}} \tag{8.56}$$

$$\text{sensitivity of avg. over both} = \left(\mathbf{b}_p^{\mathsf{T}} \otimes \mathbf{b}_s^{\mathsf{T}}\right) \frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\mathsf{T}}} \tag{8.57}$$

Annual *k*-cycle When the dynamics produce a k-cycle on the annual time scale, averages can be calculated over any desired combination of stages, seasons, and years. Table 8.2 gives the resulting expressions for the averages. As in the case of equations (8.55) and (8.56), the sensitivities of these averages to parameters are obtained by applying the same weights to $d\mathbb{N}/d\boldsymbol{\theta}^{\mathsf{T}}$.

8.4.2 A Nonlinear Example

As an example of the calculations for nonlinear systems, imagine an organism with two stages: immature juveniles and reproducing adults. Suppose that the year contains two seasons: a benign, reproduction-heavy Season 1 and a harsh, mortality-heavy Season 2. The life cycle graph is shown in Fig. 8.2. Adults in Season 1 all survive to Season 2 and give birth to new juveniles with per-capita fertility f, which depends on adult density in Season 1 according to $f[\mathbf{n}_1] = ae^{-bn_2}$, where a and b are the maximum fertility and the strength of density-dependence, respectively, and

Table 8.2 Calculation of averages of attractors of nonlinear periodic matrix population models. The upper half of the table shows averages over stages and over seasons when the dynamics are a fixed point on the inter-annual time scale, and thus a p-cycle on the seasonal time scale. The lower half of the table shows averages over all combinations of stages, seasons, and years, when the dynamics are a k-cycle on the inter-annual time scale, and thus a kp-cycle on the seasonal time scale

Average over	Formula	Vectors	Dimension
Stages	$\left(\mathbf{I}_p \otimes \mathbf{b}_s^{\mathsf{T}}\right) \mathbb{N}$	1	$p \times 1$
Seasons	$\left(\mathbf{b}_p^{\mathsf{T}} \otimes \mathbf{I}_s\right) \mathbb{N}$	1	$s \times 1$
Seasons and stages	$\left(\mathbf{b}_p^{\mathsf{T}} \otimes \mathbf{b}_s\right) \mathbb{N}$	1	1×1
Stages	$\left(\mathbf{I}_k \otimes \mathbf{I}_p \otimes \mathbf{b}_s^{\mathsf{T}}\right) \mathbb{N}$	1	$kp \times 1$
Seasons	$\left(\mathbf{I}_k \otimes \mathbf{b}_p^{\mathsf{T}} \otimes \mathbf{I}_s\right) \mathbb{N}$	k	$s \times 1$
Years	$\left(\mathbf{b}_k \otimes \mathbf{I}_p \otimes \mathbf{I}_s\right) \mathbb{N}$	p	$s \times 1$
Seasons and years	$\left(\mathbf{b}_k^{\mathsf{T}} \otimes \mathbf{b}_p^{\mathsf{T}} \otimes \mathbf{I}_s\right) \mathbb{N}$	1	$s \times 1$
Seasons and stages	$\left(\mathbf{I}_k \otimes \mathbf{b}_p^{\mathsf{T}} \otimes \mathbf{b}_s^{\mathsf{T}}\right) \mathbb{N}$	1	$k \times 1$
Years and stages	$\left(\mathbf{b}_k^{\mathsf{T}} \otimes \mathbf{I}_p \otimes \mathbf{b}_s^{\mathsf{T}}\right) \mathbb{N}$	1	$p \times 1$
Stages, seasons, years	$\left(\mathbf{b}_k^{\mathsf{T}} \otimes \mathbf{b}_p^{\mathsf{T}} \otimes \mathbf{b}_s^{\mathsf{T}}\right) \mathbb{N}$	1	1×1

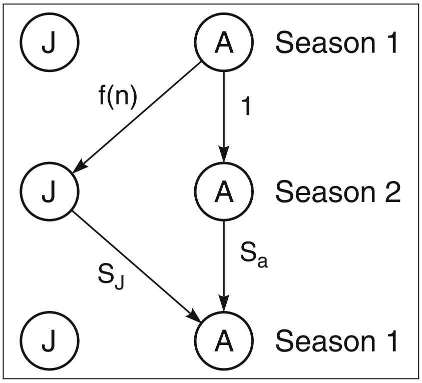

Fig. 8.2 A periodic life cycle graph for a simple two-stage, two-season nonlinear model. J and A denote juveniles and adults, respectively

n_2 is the adult density in Season 1. In the harsher Season 2, juveniles and adults survive with probabilities s_j and s_a. A juvenile that survives to Season 1 matures into an adult.

This life cycle produces seasonal transition matrices $\mathbf{B}_1$ and $\mathbf{B}_2$:

$$\mathbf{B}_1[\mathbf{n}_1] = \begin{pmatrix} 0 & f[\mathbf{n}_1] \\ 0 & 1 \end{pmatrix} \tag{8.58}$$

$$\mathbf{B}_2 = \begin{pmatrix} 0 & 0 \\ s_j & s_a \end{pmatrix} \tag{8.59}$$

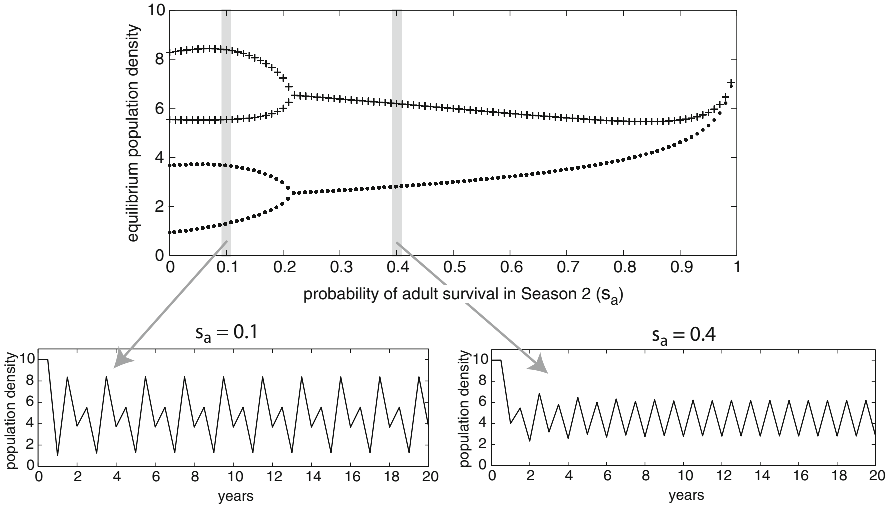

Fig. 8.3 A bifurcation diagram on the seasonal time scale for the two-season, two-stage model of Fig. 8.2. Total densities are plotted for Season 1 (•) and 2 (+). Parameters: $a = 20$, $b = 1$, $s_j = 0.5$; s_a varied from 0 to 1

and the nonlinear periodic model

$$\mathbf{n}_1(t+1) = \mathbf{B}_2\mathbf{n}_2(t)$$
$$\mathbf{n}_2(t) = \mathbf{B}_1\left[\mathbf{n}_1(t)\right]\mathbf{n}_1(t) \tag{8.60}$$

Figure 8.3 is a bifurcation diagram for the system (8.60) in response to changes in adult survival s_a. When adults are long-lived ($s_a \gtrsim 0.22$) there is a 2-cycle on the seasonal scale, corresponding to a fixed point on the annual time scale, satisfying

$$\hat{\mathbf{n}}_1 = \mathbf{B}_2\hat{\mathbf{n}}_2 \tag{8.61}$$

$$\hat{\mathbf{n}}_2 = \mathbf{B}_1[\hat{\mathbf{n}}_1]\hat{\mathbf{n}}_1 \tag{8.62}$$

At $s_a \approx 0.22$ this 2-cycle bifurcates to a 4-cycle on the seasonal time scale, corresponding to a 2-cycle on the annual scale.

To derive the block matrices $\mathbb{C}$ and $\mathbb{D}$ in Eqs. (8.49) and (8.50), define the parameter vector as

$$\boldsymbol{\theta} = \left(s_j \ s_a \ a \ b\right)^{\mathsf{T}}. \tag{8.63}$$

The derivative matrices are

$$\frac{d\,\mathrm{vec}\,\mathbf{B}_1}{d\boldsymbol{\theta}^{\mathsf{T}}} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & e^{-b\hat{n}_2} & -a\hat{n}_2 e^{-b\hat{n}_2} \\ 0 & 0 & 0 & 0 \end{pmatrix} \tag{8.64}$$

$$\frac{d\,\mathrm{vec}\,\mathbf{B}_2}{d\boldsymbol{\theta}^{\mathsf{T}}} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \end{pmatrix} \tag{8.65}$$

$$\frac{d\,\mathrm{vec}\,\mathbf{B}_1}{d\mathbf{n}^{\mathsf{T}}} = \begin{pmatrix} 0 & 0 \\ 0 & 0 \\ 0 & -abe^{-b\hat{n}_2} \\ 0 & 0 \end{pmatrix} \tag{8.66}$$

$$\frac{d\,\mathrm{vec}\,\mathbf{B}_2}{d\mathbf{n}^{\mathsf{T}}} = \mathbf{0} \qquad \text{(dimension } 4 \times 2\text{)} \tag{8.67}$$

We calculate the sensitivities of the equilibrium population at each phase of the cycle using Eq. (8.46) with $s_a = 0.4$ (a 2-cycle on the seasonal time scale; see Fig. 8.3) and with $s_a = 0.1$ (a 4-cycle on the seasonal time scale). The results, and the sensitivities of several averages, are shown in Fig. 8.4.

At the seasonal 2-cycle (annual fixed point), increases in s_j or s_a increase density in Season 1 and reduce density in Season 2, and have little effect on the

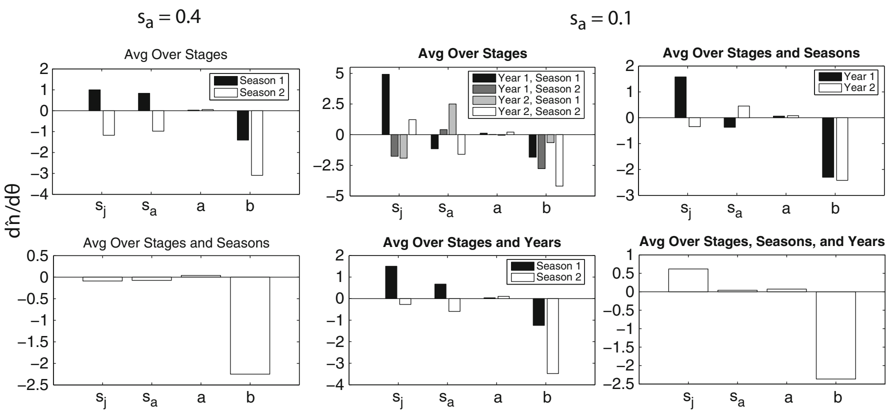

Fig. 8.4 Sensitivities of equilibrium total population size in Seasons 1 and 2, as well as the annual population average, to the demographic parameters s_j, s_a, a, and b. Left: sensitivities when $s_a = 0.4$ (seasonal 2-cycle, annual equilibrium). Right: sensitivities when $s_j = 0.1$ (seasonal 4-cycle, annual 2-cycle)

density averaged over seasons. The maximum fertility level a has little effect at either season, and the density-dependent parameter b has large negative effects throughout.

At the 4-point seasonal cycle (2-cycle on the annual time scale), the patterns are more complicated. We describe them in terms of the $kp = 4$ seasons in the cycle. The maximum fertility a has little effect at any point. The survival probabilities s_j and s_a have effects that are opposite in sign: an increase in s_j increases the density in seasons 1 and 4, and reduces it in seasons 2 and 3. An increase in s_a has the opposite effect. Averaged over years, both s_a and s_j increase density in season 1 and reduce it in season 2, thus increasing the amplitude of the oscillation. Averaged over seasons, s_a and s_j have opposite effects. When averaged over stages, seasons, and years, the effects of s_a cancel each other out, and only s_j and b have appreciable effects.

Even in this simple example, it is clear that parameter changes can have effects that differ among seasons and years. A set of MATLAB scripts to carry out these calculations appears in an online supplement to Caswell and Shyu (2012).

8.5 LTRE Decomposition Analysis

The LTRE decomposition analysis introduced in Sects. 2.9 and 4.5 can be extended to obtain the contributions, to any given outcome, of differences in parameters at each phase of the cycle.

Suppose that $\boldsymbol{\xi}$ is a $m \times 1$ dependent variable (scalar or vector-valued), a function of a parameter vector $\boldsymbol{\theta}$ that takes on values $\boldsymbol{\theta}_1, \ldots, \boldsymbol{\theta}_p$ over the cycle. Use superscripts to denote two conditions,[3] which produce results $\boldsymbol{\xi}^{(1)}$ and $\boldsymbol{\xi}^{(2)}$:

$$\boldsymbol{\theta}_1^{(1)}, \ldots, \boldsymbol{\theta}_p^{(1)} \rightarrow \boldsymbol{\xi}^{(1)} \tag{8.68}$$

$$\boldsymbol{\theta}_1^{(2)}, \ldots, \boldsymbol{\theta}_p^{(2)} \rightarrow \boldsymbol{\xi}^{(2)} \tag{8.69}$$

To first order, the effect on $\boldsymbol{\xi}$ is

$$\boldsymbol{\xi}^{(2)} - \boldsymbol{\xi}^{(1)} \approx \sum_{k=1}^{p} \frac{d\boldsymbol{\xi}}{d\boldsymbol{\theta}_k^{\mathsf{T}}} \left(\boldsymbol{\theta}_k^{(2)} - \boldsymbol{\theta}_k^{(1)} \right) \tag{8.70}$$

The kth term in the summation in (8.70) is the total contribution, over all of the parameters in $\boldsymbol{\theta}$, of parameter differences in phase k of the cycle.

Define $\mathbf{R}_k$ as a $m \times p$ contribution matrix whose entries are the contributions of parameter θ_j in phase k to the effects on outcome variable ξ_i. Then

$$\mathbf{R}_k = \frac{d\boldsymbol{\xi}}{d\boldsymbol{\theta}_k^{\mathsf{T}}} \mathcal{D} \left(\boldsymbol{\theta}_k^{(2)} - \boldsymbol{\theta}_k^{(1)} \right) \tag{8.71}$$

[3]The extension to more than two conditions is easy; see Caswell (2001).

where the derivative is evaluated at the average of $\boldsymbol{\theta}^{(1)}$ and $\boldsymbol{\theta}^{(2)}$. These contributions are a decomposition of the approximate effect in (8.70),

$$\boldsymbol{\xi}^{(2)} - \boldsymbol{\xi}^{(1)} \approx \sum_{k=1}^{p} \mathbf{R}_k \mathbf{1}_p \tag{8.72}$$

The contribution matrix (8.71) requires $d\boldsymbol{\xi}/d\boldsymbol{\theta}_k^{\mathsf{T}}$, that is, the derivative of $\boldsymbol{\xi}$ to the parameter at phase k of the cycle. In the linear model (8.2), this is given by the kth term in the summation in (8.11). In the case of the nonlinear model (8.36), the derivative is obtained from Eq. (8.46) by setting all blocks of $\mathbb{D}$, except those corresponding to phase k, to zero.

8.6 Discussion

The distinguishing feature of periodic models is that the dynamics over a projection interval are given by a periodic product of matrices. The periodic product may reflect the existence of multiple timescales (e.g., seasonal and annual), or the operation of multiple processes (e.g., demography and harvest), or express conditional probabilities, or arise from classifying individuals by multiple criteria. The sensitivity analysis of periodic models must account for the chain of causation (Fig. 8.1) from demographic parameters at each phase in the cycle to the corresponding projection matrices, and thence to the periodic matrix product over the whole cycle, and finally to demographic outcome $\boldsymbol{\xi}$. Matrix calculus makes this easy to do, starting with a simple chain rule expression (see Eq. (8.5)) and then using an appropriate version of (8.9) to calculate the derivative $d\text{vec}\,\mathbf{A}/d\boldsymbol{\theta}^{\mathsf{T}}$.

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