SENSITIVITY ANALYSIS OF PERIODIC MATRIX MODELS[1]

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Abstract. Periodic matrix models are used to describe the effects of cyclic environmental variation, both seasonal and interannual, on population dynamics. If the environmental cycle is of length m, with matrices $\mathbf{B}^{(1)}$, $\mathbf{B}^{(2)}$, ..., $\mathbf{B}^{(m)}$ describing population growth during the m phases of the cycle, then population growth over the whole cycle is given by the product matrix $\mathbf{A} = \mathbf{B}^{(m)}\mathbf{B}^{(m-1)}\cdots\mathbf{B}^{(1)}$.

The sensitivity analysis of such models is complicated because the entries in $\mathbf{A}$ are complicated combinations of the entries in the matrices $\mathbf{B}^{(i)}$, and thus do not correspond to easily interpreted life history parameters. In this paper we show how to calculate the sensitivity and elasticity of population growth rate to changes in the entries in the individual matrices $\mathbf{B}^{(i)}$ making up a periodic matrix product. These calculations reveal seasonal patterns in sensitivity that are impossible to detect with sensitivity analysis based on the matrix $\mathbf{A}$. We also show that the vital rates interact in important ways: the sensitivity to changes in a rate at one point in the cycle may depend strongly on changes in other rates at other points in the cycle.

Key words: eigenvalues; elasticity; matrix population models; seasonality; sensitivity; variable environments.

Introduction

Virtually all populations experience some periodic environmental variation. The periodicity may reflect seasonal variation within a year or be a component of interannual variability. The demography of such a population depends on its vital rates at each phase of the cycle (e.g., at each season of the year). Skellam (1966) showed how to model such populations using periodic products of population projection matrices. The purpose of this paper is to present a method for the sensitivity analysis of these periodic matrix models.

Suppose that the cycle is composed of m "phases" (e.g., a year composed of $m = 12$ mo) and that $\mathbf{B}^{(1)}$, ..., $\mathbf{B}^{(m)}$ are the population projection matrices for each phase. The dynamics of the population over the whole cycle are described by a periodic matrix product

$$\mathbf{n}(t + m) = [\mathbf{B}^{(m)}\mathbf{B}^{(m-1)}\cdots\mathbf{B}^{(1)}]\mathbf{n}(t) \qquad (1)$$

$$= \mathbf{A}^{(1)}\mathbf{n}(t). \qquad (2)$$

The matrix product $\mathbf{A}^{(1)}$ projects the population through the entire cycle. The superscript on $\mathbf{A}$ indicates the phase at which the projection starts. In the case of the 12-mo annual cycle, suppose that $\mathbf{B}^{(1)}$ projects the population from 1 January to 1 February, $\mathbf{B}^{(2)}$ from 1 February to 1 March, and so on. The periodic product matrix $\mathbf{A}^{(1)}$ projects the population from 1 January to 1 January, $\mathbf{A}^{(2)}$ projects from 1 February to 1 February, and so on. The matrices $\mathbf{A}^{(1)}$, $\mathbf{A}^{(2)}$, ..., $\mathbf{A}^{(m)}$ may differ

greatly in form, although they all yield the same rate of increase (Caswell 1989:198–202). Note that it is not necessary for all the $\mathbf{B}^{(h)}$ to use the same projection interval.

Periodic matrix models have been used for two main purposes. One is to incorporate within-year seasonal variation in the vital rates (e.g., Darwin and Williams 1964, Sarukhan and Gadgil 1974, McFadden 1991, Ang and De Wreede 1993, Sandberg et al. 1993, R. M. Andrews, *unpublished manuscript*, N. J. Gotelli, A. R. Davis, and H. Caswell, *unpublished manuscript*). In these studies the vital rates are measured over intervals that are short in comparison to the seasonal cycle and strung together to describe population growth over the whole cycle. Periodic models have also been used as an approximation to interannual variability. In these studies (e.g., Bierzychudek 1982, Huenneke and Marks 1987, Silva et al. 1991) matrices are typically available for several years or under several environmental conditions. Assuming that the matrices reflect the range of environments encountered, the matrices are multiplied together to describe population growth in a hypothetical environment that cycles among the environmental states observed. This cyclic environment model can be considered an approximation to a more appropriate stochastic model, in which matrices for each year are drawn at random from a set of matrices. Silva et al. (1991) compare the periodic model with a stochastic model and find close agreement for a particular set of data on tropical savanna grasses, but this cannot be assumed true in general (cf. Tuljapurkar and Orzack 1980, Tuljapurkar 1990).

In either of these applications, the long-term growth rate of the population over the period of the cycle is given by the largest eigenvalue, $\lambda^{(h)}$, of the matrix $\mathbf{A}^{(h)}$. Since the eigenvalues of all the $\mathbf{A}^{(h)}$ ($h = 1, 2, \ldots, m$) are identical, we will ignore the superscript on λ. If any of the $\mathbf{A}^{(h)}$ are primitive, then λ is strictly larger than the modulus of any other eigenvalue, and the population eventually converges to this growth rate and to a stable stage distribution. Conditions for the primitivity of $\mathbf{A}$ in terms of the $\mathbf{B}^{(h)}$ are discussed in Keller (1980), Taylor (1985), and Caswell (1989). If the $\mathbf{A}^{(h)}$ are imprimitive and/or reducible, the dominant eigenvalue still provides a measure of population growth, but the convergence results are more complicated. In either case, the population structure within the cycle is periodic with period m.

SENSITIVITY AND ELASTICITY ANALYSIS OF PERIODIC MATRIX PRODUCTS

The importance of λ as a measure of population growth rate and of fitness has made sensitivity analysis an integral part of demographic analysis. The sensitivity of λ to a change in an entry a_{ij} of the matrix $\mathbf{A}$ is

$$\frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle}, \tag{3}$$

where $\mathbf{w}$ and $\mathbf{v}$ are the right and left eigenvectors of $\mathbf{A}$ corresponding to λ (the stable stage distribution and reproductive value, respectively), and $\langle \mathbf{w}, \mathbf{v} \rangle$ denotes the scalar product of $\mathbf{w}$ and $\mathbf{v}$ (Caswell 1978, 1989).

This formula can be applied directly to the periodic matrix $\mathbf{A}$ in Eq. 2. However, the sensitivity of λ to changes in the a_{ij} is not what we want. Because the a_{ij} incorporate *all* pathways by which individuals in stage j at time t can contribute individuals to stage i at time $t + m$, they are complex mixtures of life history characters. The sensitivity of λ to changes in such a complex mixture has no simple interpretation. Consider a simple example: a two-stage population projected over two seasons (summer and winter), with matrices

$$\mathbf{B}^{(w)} = \begin{pmatrix} F_1^{(w)} & F_2^{(w)} \\ G_1^{(w)} & P_2^{(w)} \end{pmatrix} \quad \mathbf{B}^{(s)} = \begin{pmatrix} F_1^{(s)} & F_2^{(s)} \\ G_1^{(s)} & P_2^{(s)} \end{pmatrix}, \tag{4}$$

where the F_i are fertilities, G_1 is the probability of growth, and P_2 is the survival probability of large individuals. The product matrix (with the projection starting from the summer) is

$$\mathbf{A}^{(s)} = \begin{pmatrix} F_1^{(s)}F_1^{(w)} + G_1^{(s)}F_2^{(w)} & F_2^{(s)}F_1^{(w)} + P_2^{(s)}F_2^{(w)} \\ F_1^{(s)}G_1^{(w)} + G_1^{(s)}P_2^{(w)} & F_2^{(s)}G_1^{(w)} + P_2^{(s)}P_2^{(w)} \end{pmatrix}. \tag{5}$$

Each entry of $\mathbf{A}^{(s)}$ is a sum of two terms, each of which is a product of two different vital rates. This confounding of vital rates only gets worse for larger matrices or longer cycles. For a $s \times s$ matrix with period m, each entry in $\mathbf{A}$ is a sum of s^{m-1} terms, each of which is a product of m vital rates. Some simplification occurs when the matrices have lots of zero entries (as in a

Leslie matrix), but the fact remains that each entry in $\mathbf{A}$ is a function of many of the vital rates.

Thus, changing an element of $\mathbf{A}$ changes a complicated combination of growth, survival, and fertility terms. The sensitivity of λ to such changes is, at best, difficult to interpret. Much more useful is the sensitivity of λ to changes in the entries in each of the individual matrices $\mathbf{B}^{(h)}$, $h = 1, \ldots, m$. These sensitivities show the impact on population growth of *changes in each vital rate at each point in the environmental cycle*. Note that this is different from the sensitivity of the eigenvalues of the $\mathbf{B}^{(h)}$ to changes in their entries (as calculated, for example, by Sauer and Slade [1985, 1986]). Although the eigenvalues of the $\mathbf{B}^{(h)}$ can be used to summarize the conditions at that point in the periodic cycle, they do not describe the population growth resulting from the entire cycle.

The sensitivity of λ to changes in the entries of each of the seasonal matrices is not difficult to calculate. We will state the result here and leave its derivation to the Appendix. Let us introduce the following notation. Let $\mathbf{S}_A^{(h)}$, $h = 1, 2, \ldots, m$, denote the sensitivity matrix of $\mathbf{A}^{(h)}$. That is, $\mathbf{S}_A^{(h)}$ is a matrix whose entries are the sensitivities of λ to changes in the corresponding entries in $\mathbf{A}^{(h)}$. Let $\mathbf{S}_B^{(h)}$, $h = 1, 2, \ldots, m$, denote the sensitivity matrix for $\mathbf{B}^{(h)}$. That is, $\mathbf{S}_B^{(h)}$ is the matrix whose entries are the sensitivities of λ to changes in the entries of $\mathbf{B}^{(h)}$; this is the matrix we want to calculate. This sensitivity matrix is given by

$$\mathbf{S}_B^{(h)} = [\mathbf{B}^{(h-1)}\mathbf{B}^{(h-2)} \cdots \mathbf{B}^{(1)}\mathbf{B}^{(m)}\mathbf{B}^{(m-1)}$$
$$\cdots \mathbf{B}^{(h+1)}]^T \mathbf{S}_A^{(h)}, \tag{6}$$

where T denotes the matrix transpose.

In words, to calculate the sensitivity of λ to changes in each element of $\mathbf{B}^{(h)}$, first cyclically permute the individual matrices until $\mathbf{B}^{(h)}$ appears first in the series (i.e., at the right-hand end of the product matrix). Then calculate the sensitivity matrix $\mathbf{S}_A^{(h)}$ corresponding to this product and premultiply it by the transpose of the product of the individual matrices *excluding* $\mathbf{B}^{(h)}$.

Eq. 6 can also be used to obtain the elasticities, or proportional sensitivities (Caswell et al. 1984, De Kroon et al. 1986), of λ to changes in the entries of $\mathbf{B}^{(h)}$, since the elasticities are given by

$$e_{ij} = \frac{b_{ij}}{\lambda} \frac{\partial \lambda}{\partial b_{ij}}. \tag{7}$$

For any single matrix, the elasticities of λ with respect to changes in the entries of the matrix sum to 1 and measure the proportional contribution of the matrix entries to population growth (De Kroon et al. 1986, Caswell 1989). In the case of periodic matrix products, we show in the Appendix that the elasticities of λ with respect to the entries of $\mathbf{B}^{(i)}$ sum to 1 for each i.

One important implication of this result is that the seasonal patterns of sensitivity reflect interactions among the vital rates. That is, the sensitivity of λ to

one rate, at one point in the cycle, is affected by changes in other rates at other points in the cycle. As an example, consider the simple model (Eq. 5), with

$$\mathbf{B}^{(s)} = \begin{pmatrix} 2.0 & 0.5 \\ 0.5 & 0.5 \end{pmatrix} \text{ and } \mathbf{B}^{(w)} = \begin{pmatrix} 0.2 & 5.0 \\ 0.5 & 0.5 \end{pmatrix}. \quad (8)$$

Here, only fertility (the entries in the first row) varies between summer and winter. The two sensitivity matrices are

$$\mathbf{S}_B^{(s)} = \begin{pmatrix} 0.46 & 0.17 \\ 4.18 & 1.55 \end{pmatrix} \text{ and } \mathbf{S}_B^{(w)} = \begin{pmatrix} 1.70 & 0.53 \\ 1.31 & 0.41 \end{pmatrix}. \quad (9)$$

Although the seasonal growth and survival terms (the entries in the second row) do not vary between seasons, their sensitivity values do, because of an interaction with the periodic variation in fertility. In this simple case, some of this variation has a simple interpretation. In the winter, reproduction is low in stage 1 and high in stage 2, so λ is particularly sensitive to increases in growth during the summer, which puts individuals into stage 2 in time to take advantage of the higher winter reproduction. Other differences in the sensitivities have similar interpretations (cf. MacArthur 1968). In more-complicated periodic models the interaction of the varying vital rates and the shifting stage distribution is more complex, but the sensitivity formula (Eq. 6) takes all this complexity into account.

An Example

A good example of the use of periodic matrix models is provided by McFadden's (1991) study of an intertidal soft coral (*Alcyonium* sp.) in Washington. She divided individuals into five size categories and followed transitions over two seasonal periods (summer and winter). Multiplying the two seasonal matrices together to obtain a yearly matrix, she calculated population growth rates, stable size distributions, and reproductive values for populations at four different sites.

To determine the relative importance of sexual and asexual reproduction, McFadden (1991) used the model to carry out several manipulations of *Alcyonium*'s life history. As part of this analysis, she calculated the elasticity of λ to changes in the entries of the product matrix $\mathbf{A}^{(w)} = \mathbf{B}^{(s)}\mathbf{B}^{(w)}$, where the superscripts s and w indicate summer and winter. For one of her sites (T1), the elasticities calculated from $\mathbf{A}$ (multiplied by 100 to be expressed as percentages, rounded off to show patterns more clearly, and with the largest values in boldface) are

$$100 \cdot \mathbf{E}_A^{(w)} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 2 & 5 & 3 & 1 \\ 0 & 5 & \mathbf{14} & \mathbf{10} & 4 \\ 0 & 3 & \mathbf{10} & \mathbf{11} & 8 \\ 0 & 2 & 4 & 8 & 9 \end{pmatrix}. \quad (10)$$

McFadden (1991) interprets the first row of this matrix as representing sexual reproduction and concludes from

the low elasticity values that sexual reproduction is less important than growth and clonal reproduction. However, the elasticities in Eq. 10 describe the result of proportional changes in the entries of $\mathbf{A}^{(w)}$. Each of those entries is a sum of five products of pairs of parameters from the two seasonal matrices. Thus the effects of sexual reproduction appear throughout the whole matrix, not only in the first row, and the entries in the first row include not only sexual reproduction but also growth and clonal reproduction.

Using Eqs. 6 and 7, it is possible to calculate elasticities of λ with respect to changes in the entries of the seasonal matrices $\mathbf{B}^{(w)}$ and $\mathbf{B}^{(s)}$. These elasticities are

$$100 \cdot \mathbf{E}_B^{(w)} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ 1 & 2 & 3 & 2 & 0 \\ 0 & 3 & 9 & 5 & 1 \\ 0 & 3 & \mathbf{14} & \mathbf{10} & 3 \\ 0 & 3 & 7 & \mathbf{15} & \mathbf{18} \end{pmatrix} \text{ and } \quad (11)$$

$$100 \cdot \mathbf{E}_B^{(s)} = \begin{pmatrix} 0 & 0 & 0 & 0 & 6 \\ 0 & 6 & 3 & 3 & 1 \\ 0 & 2 & \mathbf{16} & 9 & 6 \\ 0 & 0 & 0 & \mathbf{17} & \mathbf{14} \\ 0 & 0 & 0 & 1 & \mathbf{21} \end{pmatrix}. \quad (12)$$

First, we note that while sexual reproduction is still much less important than other transitions, the fertility of the largest individuals in the summer does contribute some 6% to λ. The largest elasticities appear in different locations in the summer and winter. In the winter the most important transitions are growth and survival in the two largest size classes. The largest elasticities in the summer, on the other hand, correspond to stasis in the three largest size classes and to the transition (by shrinkage or fragmentation) from stage 5 to stage 4. Neither of these patterns corresponds to that observed in $\mathbf{E}_A$.

The two seasons can be contrasted by adding elasticities below the diagonal (corresponding to growth), on the diagonal (stasis), and above the diagonal (shrinkage, fragmentation, and reproduction):

	Winter	Summer
Growth	0.4636	0.0349
Stasis	0.3910	0.5976
Shrinkage, etc.	0.1454	0.3675

It appears that growth is most important in the winter, and survival and stasis in the summer. This difference in elasticity patterns between summer and winter could only be detected by analysis of the periodic model.

The point of this example is not to dispute McFadden's (1991) main conclusion: that sexual reproduction is less important than clonal reproduction in *Alcyonium*. For one thing, McFadden supported that conclusion by other evidence, independent of the elas-

ticity analysis of the **A** matrix. For another, in this case the elasticities of the seasonal **B** matrices happen to confirm the main conclusions. That, however, need not always be the case.

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APPENDIX

DERIVATIONS

We want to calculate the sensitivity of λ to a change in $\mathbf{B}^{(h)}$, $h = 1, 2, \ldots, m$. Since this sensitivity is independent of which cyclic permutation of the **B** matrices we consider, we choose that in which $\mathbf{B}^{(h)}$ is the first in the sequence. We rewrite $\mathbf{A}^{(h)}$ as

$$\mathbf{A}^{(h)} = \mathbf{C}\mathbf{B}^{(h)}, \qquad (A.1)$$

where $\mathbf{C} = \mathbf{B}^{(h-1)}\mathbf{B}^{(h-2)} \cdots \mathbf{B}^{(1)}\mathbf{B}^{(m)}\mathbf{B}^{(m-1)} \cdots \mathbf{B}^{(h+1)}$. Let **w** and **v** be the right and left eigenvectors of $\mathbf{A}^{(h)}$ corresponding to λ and assume that they are scaled so that their scalar product equals 1.

For the sake of clarity, let us supress the superscripts for a moment and write $\mathbf{A} = \mathbf{C}\mathbf{B}$. The sensitivity matrix of **A** is

$$\mathbf{S}_A = \mathbf{v}\mathbf{w}^T \qquad (A.2)$$

where T denotes the matrix transpose.

From the chain rule, it follows that

$$\frac{\partial \lambda}{\partial b_{ij}} = \sum_{k,l} \frac{\partial \lambda}{\partial a_{kl}} \frac{\partial a_{kl}}{\partial b_{ij}}. \qquad (A.3)$$

But, note that

$$a_{kl} = \mathbf{c}_{k.}\mathbf{b}_{.l} \qquad (A.4)$$

where $\mathbf{c}_{k.}$ and $\mathbf{b}_{.l}$ are the kth row of **C** and the lth column of **B**, respectively. Thus $\partial a_{kl}/\partial b_{ij} = 0$ if $l \neq j$. If $l = j$, then $\partial a_{kl}/\partial b_{ij} = c_{ki}$. Thus Eq. A.3 can be written

$$\frac{\partial \lambda}{\partial b_{ij}} = \sum_k \frac{\partial \lambda}{\partial a_{kj}} \frac{\partial a_{kj}}{\partial b_{ij}} \qquad (A.5)$$

$$= \sum_k s_{kj}c_{ki} \qquad (A.6)$$

$$= \langle \mathbf{s}_{.j}, \mathbf{c}_{.i} \rangle \qquad (A.7)$$

But this partial derivative is simply the (i, j) entry in the sensitivity matrix $\mathbf{S}_B^{(h)}$, which can thus be written as the product of the transpose of **C** and the sensitivity matrix $\mathbf{S}_A$:

$$\mathbf{S}_B = \mathbf{C}^T\mathbf{S}_A, \qquad (A.8)$$

which is the formula given in Eq. 6.

Let $\mathbf{E}$ denote the matrix of elasticities of λ with respect to the elements of $\mathbf{B}^{(h)}$, given by Eq. 7. The sum of these elasticities is given by

$$\sum_{i,j} e_{ij} = \frac{1}{\lambda} \, \mathrm{tr}(\mathbf{B}^T \mathbf{S}_B) \qquad (A.9)$$

$$= \frac{1}{\lambda} \, \mathrm{tr}(\mathbf{B}^T \mathbf{C}^T \mathbf{S}_A) \qquad (A.10)$$

$$= \frac{1}{\lambda} \, \mathrm{tr}(\mathbf{A}^T \mathbf{S}_A), \qquad (A.11)$$

where tr( ) denotes the trace. Since $\mathbf{S}_A = \mathbf{v}\mathbf{w}^T$, this expression can be simplified to

$$\sum_{i,j} e_{ij} = \frac{1}{\lambda} \, \mathrm{tr}(\mathbf{A}^T \mathbf{v}\mathbf{w}^T) \qquad (A.12)$$

$$= \frac{1}{\lambda} \, \mathrm{tr}(\lambda \mathbf{v}\mathbf{w}^T) \qquad (A.13)$$

$$= 1. \qquad (A.14)$$

Thus the elasticities of λ with respect to the entries of $\mathbf{B}^{(h)}$ sum to 1 for each h.