Sensitivity Analysis in Periodic Matrix Models: A Postscript to Caswell and Trevisan

M. LESNOFF*
Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD – EMVT) TA/30A
34398 Montpellier Cedex 5, France

and
International Livestock Research Institute (ILRI)
P.O. Box 5689, Addis Ababa, Ethiopia
m.lesnoff@cgiar.org

P. EZANNO
Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD – EMVT) TA/30A
34398 Montpellier Cedex 5, France
pauline.ezanno@cirad.fr

H. CASWELL
Biology Department, MS #34
Woods Hole Oceanographic Institution
Woods Hole, MA 02543-1049, U.S.A.
hcaswell@whoi.edu

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Abstract—Periodic matrix population models are a useful approach to modelling cyclic variations in demographic rates. Caswell and Trevisan [1] introduced the perturbation analysis (sensitivities and elasticities) of the per-cycle population growth rate for such models. Although powerful, their method can be time-consuming when the dimension of the matrices is large or when cycles are composed of many phases. We present a more efficient method, based on a very simple matrix product. We compared the two methods for matrices of different sizes. We observed a reduction in calculation time on the order of 24% with the new method for a set of 26 within-year Leslie matrices of size 287 x 287. The time saving may become particularly significant when sensitivities are used in Monte Carlo or bootstrap simulations. © 2003 Elsevier Science Ltd. All rights reserved.

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Periodic matrix population models are a useful approach to modelling cyclic variations in demographic rates, such as are caused by seasonality within the year or by interannual cyclic variability. See [2, Chapter 13] for a review of biological applications. Caswell and Trevisan [1]

*Author to whom all correspondence should be addressed. Please send to author’s second address.
†See [1].
introduced the perturbation analysis (sensitivities and elasticities) of population growth rate for periodic models; the objective of our postscript is to introduce a simpler way to calculate these sensitivities and elasticities.

We suppose here that the cycle is composed of $K$ "phases" (e.g., a year composed of $K = 4$ seasons, or of $K = 26$ two-week phases). The phases need not be of the same duration. The matrices $B_1, B_2, \ldots, B_K$ denote the population projection matrices for the different phases. That is, matrix $B_i$ projects the population from phase $i$ to phase $i + 1$; the phases are cyclic, so that $B_K$ projects the population from phase $K$ back to phase 1. The starting point of the cycle is arbitrary. Consider a cycle starting at the beginning of phase $k$ and let $x(t)$ denote the population state vector at time $t$. The dynamics over the whole cycle are given by

$$x(t + K) = B_{k-1}B_{k-2} \ldots B_1B_KB_{K-1} \ldots B_kx(t),$$

$$= \Lambda_K x(t).$$

The asymptotic properties of such models have been described in Skellam [3] and Caswell [1,2,4]. Under weak conditions of primitivity, the asymptotic population growth rate $\lambda$ (on the per-cycle scale) is the common dominant eigenvalue of the product-matrices $A_k$ (all the $A_k$ have the same eigenvalues).

Our concern here is to calculate the sensitivities of $\lambda$ to changes in the entries of each of the matrices $B_k$. Using the notation in [1], let $a_{ij}^{(k)}$ denote the $(i, j)$ entry of the product-matrix $A_k$ and $S_{Ak}$ the sensitivity matrix of $A_k$, i.e., the matrix whose $(i, j)$ entry is the partial derivative $\partial a_{ij}^{(k)} / \partial b_{ij}^{(k)}$. This matrix can be calculated directly from the eigenvectors of $A_k$, but because the entries of $A_k$ are complicated combinations of the phase-specific demographic rates, these sensitivities are difficult to interpret. Of more interest is the sensitivity matrix $S_{Bk}$ (the matrix whose $(i, j)$ entry is the partial derivative $\partial \lambda / \partial b_{ij}^{(k)}$, where $b_{ij}^{(k)}$ denotes the $(i, j)$ entry of $B_k$). Caswell and Trevisan [1] showed that these sensitivity matrices are given by

$$S_{Bk} = (B_{k-1}B_{k-2} \ldots B_1B_KB_{K-1} \ldots B_{k+1})^T S_{Ak} \quad k = 1, \ldots, K. \quad (3)$$

Equation (3) is powerful and easy to implement in appropriate software. However, it requires the calculation of $K$ sensitivity matrices $S_{Ak}$. This calculation could become time-consuming when the dimension of matrices $B_k$ is large and when there are many phases in the annual cycle. Next, we present a more efficient method.

Since the sensitivity $\partial \lambda / \partial a_{ij}^{(k)}$ is independent of which cyclic permutation of the $B$ matrices is considered, we suppose here for notational simplicity, and without loss of generality, that the cyclic projection matrix is $A_1 = BKB_{K-1} \ldots B_1 \equiv A$. The population growth rate $\lambda$ can be seen as a composite function of the variables $a_{mn}$ and $b_{ij}^{(k)}$, i.e.,

$$\lambda = \lambda \left( a_{mn} \left( b_{ij}^{(k)} \right) \right), \quad i, j, m, n = 1, \ldots, q; \quad k = 1, \ldots, K, \quad (4)$$

where $q$ is the dimension of matrices $A_k$ and $B_k$.

From the chain rule, the partial derivative of $\lambda$ with respect to $b_{ij}^{(k)}$ is

$$\frac{\partial \lambda}{\partial b_{ij}^{(k)}} = \sum_{m,n} \frac{\partial \lambda}{\partial a_{mn}} \frac{\partial a_{mn}}{\partial b_{ij}^{(k)}}. \quad (5)$$

Our problem is to find the derivatives $\partial a_{mn} / \partial b_{ij}^{(k)}$ in a more efficient way than that of Caswell and Trevisan [1]. To do so, we rewrite matrix $A$ as

$$A = CB_kG,$$
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