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

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Abstract—Periodic matrix population models are a useful approach to modeling 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 $287 \times 287$. 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 modeling 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]

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†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 [1]

\[
\begin{align*}
x(t + K) &= B_{k-1}B_{k-2}\cdots B_1B_KB_{K-1}\cdots B_kx(t), \\
&= \Lambda_k x(t). \tag{1}
\end{align*}
\]

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 \( S_{A_k} \) the sensitivity matrix of \( A_k \), i.e., the matrix whose \((i, j)\) entry is the partial derivative \( \frac{\partial \lambda}{\partial a_{ij}^{(k)}} \). 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 \( S_{B_k} \) (the matrix whose \((i, j)\) entry is the partial derivative \( \frac{\partial \lambda}{\partial b_{ij}^{(k)}} \) where \( b_{ij}^{(k)} \) denotes the \((i, j)\) entry of \( B_k \)). Caswell and Trevisan [1] showed that these sensitivity matrices are given by

\[
S_{B_k} = (B_{k-1}B_{k-2}\cdots B_1B_KB_{K-1}\cdots B_{k+1})^T S_{A_k} \quad k = 1, \ldots, K. \tag{3}
\]

Equation (3) is powerful and easy to implement in appropriate software. However, it requires the calculation of \( K \) sensitivity matrices \( S_{A_k} \). 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 \( \frac{\partial \lambda}{\partial b_{ij}^{(k)}} \) 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 \( A_1 = B_KB_{K-1}\cdots B_1 \equiv A \). The population growth rate \( \lambda \) can be seen as a composite function of the variables \( a_{mn} \) and \( b_{ij}^{(k)} \), i.e.,

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

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

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

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

\[
A = CB_kG, \tag{6}
\]
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