PERGAMON

Mathematical and Computer Modelling 37 (2003) 945–948

MATHEMATICAL AND COMPUTER MODELLING

www.elsevier.nl/locate/mcm

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

(Received April 2002; revised and accepted December 2002)

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 × 287. The time saving may become particularly significant when sensitivities are used in Monte Carlo or bootstrap simulations.

Keywords—Sensitivity, Elasticity, Periodic matrix models, Population dynamics, Population growth rate.

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].

PII: S0895-7177(03)00110-9

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 $\mathbf{B}_1, \mathbf{B}_2, \ldots, \mathbf{B}_K$ denote the population projection matrices for the different phases. That is, matrix $\mathbf{B}_i$ projects the population from phase i to phase $i+1$; the phases are cyclic, so that $\mathbf{B}_K$ 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 $\underline{\mathbf{x}}(t)$ denote the population state vector at time t. The dynamics over the whole cycle are given by [1]

$$\underline{\mathbf{x}}(t+K) = \mathbf{B}_{k-1}\mathbf{B}_{k-2}\ldots\mathbf{B}_1\mathbf{B}_K\mathbf{B}_{K-1}\ldots\mathbf{B}_k\underline{\mathbf{x}}(t), \tag{1}$$

$$\equiv \mathbf{A}_k\underline{\mathbf{x}}(t). \tag{2}$$

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 λ (on the per-cycle scale) is the common dominant eigenvalue of the product-matrices $\mathbf{A}_k$ (all the $\mathbf{A}_k$ have the same eigenvalues).

Our concern here is to calculate the sensitivities of λ to changes in the entries of each of the matrices $\mathbf{B}_k$. Using the notation in [1], let $a_{ij}^{(k)}$ denote the (i,j) entry of the product-matrix $\mathbf{A}_k$ and S_{A_k} the sensitivity matrix of $\mathbf{A}_k$, 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 $\mathbf{A}_k$, but because the entries of $\mathbf{A}_k$ 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 $\mathbf{B}_k$). Caswell and Trevisan [1] showed that these sensitivity matrices are given by

$$\mathbf{S}_{\mathbf{B}_k} = (\mathbf{B}_{k-1}\mathbf{B}_{k-2}\ldots\mathbf{B}_1\mathbf{B}_K\mathbf{B}_{K-1}\ldots\mathbf{B}_{k+1})^{\top}\mathbf{S}_{\mathbf{A}_k} \qquad k = 1,\ldots,K. \tag{3}$$

Equation (3) is powerful and easy to implement in appropriate software. However, it requires the calculation of K sensitivity matrices $\mathbf{S}_{\mathbf{A}_k}$. This calculation could become time-consuming when the dimension of matrices $\mathbf{B}_k$ 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 $\mathbf{B}$ matrices is considered, we suppose here for notational simplicity, and without loss of generality, that the cyclic projection matrix is $\mathbf{A}_1 = \mathbf{B}_K\mathbf{B}_{K-1}\ldots\mathbf{B}_1 \equiv \mathbf{A}$. The population growth rate λ can be seen as a composite function of the variables a_{mn} and $b_{ij}^{(k)}$, i.e.,

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

where q is the dimension of matrices $\mathbf{A}_k$ and $\mathbf{B}_k$.

From the chain rule, the partial derivative of λ 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 $\mathbf{A}$ as

$$\mathbf{A} = \mathbf{C}\mathbf{B}_k\mathbf{G}, \tag{6}$$

where the matrices $\mathbf{C}$ and $\mathbf{G}$ are defined as

$$\mathbf{C} = \begin{cases} \mathbf{B}_K\mathbf{B}_{K-1}\dots\mathbf{B}_{k+1}, & \text{if } k \neq K, \\ \mathbf{I}, & \text{if } k = K, \end{cases} \tag{7}$$

$$\mathbf{G} = \begin{cases} \mathbf{B}_{k-1}\mathbf{B}_{k-2}\dots\mathbf{B}_1, & \text{if } k \neq 1, \\ \mathbf{I}, & \text{if } k = 1, \end{cases} \tag{8}$$

($\mathbf{I}$ denotes the identity matrix).

Since $\mathbf{C}$ and $\mathbf{G}$ do not contain the term $b_{ij}^{(k)}$ (by definition), the matrix $\frac{\partial \mathbf{A}}{\partial b_{ij}^{(k)}}$ (i.e., the matrix whose (m,n) entry is $\frac{\partial a_{mn}}{\partial b_{ij}^{(k)}}$) can be written [5]

$$\frac{\partial \mathbf{A}}{\partial b_{ij}^{(k)}} = \mathbf{C}\frac{\partial \mathbf{B}_k}{\partial b_{ij}^{(k)}}\mathbf{G}. \tag{9}$$

All entries of matrix $\frac{\partial \mathbf{B}_k}{\partial b_{ij}^{(k)}}$ are null except the (i,j) entry which has the value 1. From equations (5) and (9), and by the rule of matrix multiplication, it follows that

$$\frac{\partial \lambda}{\partial b_{ij}^{(k)}} = \sum_{m,n} c_{mi} g_{jn} \frac{\partial \lambda}{\partial a_{mn}} \tag{10}$$

or, in matrix notation,

$$\mathbf{S}_{\mathbf{B}_k} = \mathbf{C}^\top \mathbf{S}_A \mathbf{G}^\top. \tag{11}$$

The elasticity, or proportional sensitivity, of λ to the $b_{ij}^{(k)}$ can be calculated directly in the form of the elasticity matrix

$$\mathbf{E}_{\mathbf{B}_k} = \frac{1}{\lambda}\mathbf{B}_k \circ \mathbf{S}_{\mathbf{B}_k}, \tag{12}$$

where $\circ$ denotes the Hadamard, or element-by-element product.

Equation (11) has the advantage of using the same sensitivity matrix $\mathbf{S}_\mathbf{A}$ for calculating each of the K sensitivity matrices $\mathbf{S}_{\mathbf{B}_k}$. It is only necessary to redefine matrices $\mathbf{C}$ and $\mathbf{G}$, according to equations (6)–(8) for each phase we consider.

As an example, we compared the two methods for Leslie matrices of dimension of 287×287. We supposed within-year variations with $K = 26$ two-week phases. Calculations were carried out with MATLAB 5.3 on a microcomputer with a Pentium III 550 MHz processor (the MATLAB code of a function implementing the new method is presented in the Appendix). The results showed a reduction in calculation time of 1.28 minutes to calculate the $K = 26$ sensitivity matrices $\mathbf{S}_{\mathbf{B}_k}$. This absolute time saving appeared relatively small (updating the computer could also give lower time saving). Nevertheless, it can become more significant when sensitivities are used in Monte Carlo or bootstrap simulations [6] (in the previous example, the reduction in calculation time would become 21.3 hours for 1000 bootstrap replications). The approximation of a continuous-time periodic model with periodic matrix products (in such a case, the number of within-year phases or the matrix size can become very large) would also be a case where the new method could be a useful alternative to the formula of Caswell and Trevisan [1].

APPENDIX

A MATLAB FUNCTION TO CALCULATE THE K SENSITIVITY AND ELASTICITY MATRICES $\mathbf{S}_{\mathbf{B}_k}$ AND $\mathbf{E}_{\mathbf{B}_k}$

The following program takes as arguments the number of phases within the cycle (variable K), the set of matrices $\mathbf{B}_1, \mathbf{B}_2, \dots, \mathbf{B}_K$ (variable B) and the dimension of matrices (variable q; the function was implemented for square matrices but can be easily extent to nonsquare matrices). It returns the sets of matrices $\mathbf{S}_{\mathbf{B}_1}, \mathbf{S}_{\mathbf{B}_2}, \dots, \mathbf{S}_{\mathbf{B}_K}$ (variable S) and $\mathbf{E}_{\mathbf{B}_1}, \mathbf{E}_{\mathbf{B}_2}, \dots, \mathbf{E}_{\mathbf{B}_K}$ (variable E).

```
function [S, E] = persens(K, B, q)

% create product matrix A
A = B(:, :, 1);
for k = 2 : K
  A = B(:, :, k) * A;
end

% sensitivity of lambda to A
[w, d] = eig(A);
[lambda, imax] = max(diag(d));
v = inv(conj(w));
w = w(:, imax);
v = real(v(imax, :))';
sens_A = v * w';
% sensitivity of lambda to B_k
for k = 1 : K
  C = eye(q);
  G = eye(q);
  switch k
  case 1
    for i = 2 : K
      C = B(:, :, i) * C;
    end
  case K
    for i = 1 : (K - 1)
      G = B(:, :, i) * G;
    end
  otherwise
    for i = (k + 1) : K
      C = B(:, :, i) * C
    end
    for i = 1 : (k - 1)
      G = B(:, :, i) * G
    end
  end
  S(:, :, k) = C' * sens_A * G';
  E(:, :, k) = S(:, :, k). * B(:, :, k)/lambda;
end
```

REFERENCES

1. H. Caswell and M.C. Trevisan, Sensitivity analysis of periodic matrix models, *Ecology* **75** (5), 1299–1303, (1994).
2. H. Caswell, *Matrix Population Models. Construction, Analysis and Interpretation*, Second Edition, Sinauer, Sunderland, MA, (2001).
3. J.G. Skellam, *Proceedings of the 5^{th}, Berkeley Symposium on Mathematical Statistics and Probability, Volume 4*, (1966).
4. H. Caswell, *Matrix Population Models. Construction, Analysis and Interpretation*, First Edition, Sinauer, Sunderland, MA, (1989).
5. J.R. Magnus and H. Neudecker, *Matrix Differential Calculus with Applications in Statistics and Econometrics*, Wiley, Chichester, (1995).
6. M. Lesnoff, R. Lancelot, E. Tillard and I.R. Dohoo, A steady-state approach of benefit-cost analysis with a periodic Leslie-matrix model. Presentation and application to the evaluation of a sheep-diseases preventive scheme in Kolda, Senegal, *Prev. Vet. Med.* **46** (2), 113–128, (2000).