Review: Matrix Theory in Population Modelling
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COMMENTARY

MATRIX THEORY IN POPULATION MODELLING

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A consideration of MATRIX POPULATION MODELS: CONSTRUCTION, ANALYSIS AND INTERPRETATION; *by Hal Caswell; Sinauer Associates Inc., Sunderland (Massachusetts)*; $50.00 (hardcover), $28.95 (paper); xv + 328 p.; ill.; index; ISBN: 0-87893-094-9.

WHAT THEORETICAL biologist has not, when delivering a lunch-hour seminar to the local graduate students, felt a noticeable stiffening in the air when the word "eigenvector" is introduced? Even when most of the audience has sat through the standard sophomore linear algebra course, there is still a reluctance to come to grips, in their professional work, with the abstract formalism they remember from that course.

But the fact is that the formalism of matrix algebra provides a powerful and elegant approach to the study of the generation-by-generation changes in structured populations. The approach is powerful because a large number of diverse results can be extracted from a few general methods and principles; it is elegant because the general theory— for example the way in which operations on the left and the right of a matrix interact — is simple and beautiful. The purpose of this book is to demonstrate this fact to those very graduate students we mentioned above, and in our opinion it succeeds fairly well. It is an interesting, timely, and generally readable account of the various ways that matrix models can be and are used in studying the biology of populations, and it provides a comprehensive overview of the current state of population modelling.

The book's first four chapters will reassure even the most mathematically reluctant of biology graduate students that they too can make use of some dimly remembered topics from some math course or other. In these chapters, Caswell discusses the creation of mathematical models presenting, of course, the various assumptions needed to use a linear model. He also includes a clear and useful discussion of the types of information that can be drawn from it once the model is created (forecasting versus projection). He addresses, as well, the vexing problems associated with finding the appropriate parameters to insert in the model.

The later chapters, aimed at a much more mathematically sophisticated readership, will be of interest to the expert as well as to the novice, since they collect and integrate a variety of topics. Chapter 5 shows how the z-transform (analogous to the probability generating function), together with the life-cycle graph, can provide a mathematically neat and biologically meaningful analysis of the characteristic equation. Chapter 6 moves from a discussion of the main sensitivity results, the response of λ to perturbations in the entries of the matrix, to evolutionary demography, the study of the change in the mean value of a trait such as fecundity or mortality, under the action of selection in an age-structured population. The subject matter of both of these chapters is mathematically quite beautiful.

Chapter 7 addresses the importance of assigning a confidence interval to an estimated intrinsic rate of growth, and discusses some techniques for obtaining a reasonable assignment. The discussion in Chapter 8 brings together some very difficult results concerning possible mathematical definitions of the intrinsic rate of growth of a population and makes them more intelligible and accessible than was possible in the original papers. And Chapter 9, on density-dependent models, brings together a number of important recent results and examples.

There is a remarkable example in Chapter 9. Example 9.5 describes a simple two age-class population with the dynamic

$$\begin{bmatrix} n_1(t+1) \\ n_2(t+1) \end{bmatrix} = \begin{bmatrix} \mu e^{-N/10} & 2\mu e^{-N/10} \\ 9/10 & 0 \end{bmatrix} \begin{bmatrix} n_1(t) \\ n_2(t) \end{bmatrix}$$

where t is time, n_i is the age i population size and $N = n_1 + n_2$. Age 1 individuals have a probability 0.9 of survival to age 2, and the fecundity (the top row) is density dependent with age 2 individuals twice as fecund as age 1. This example was first studied by Levin (1981) as a fishery model, and it turns out to have a wonderful sequence of behaviors, "from quasiperiodicity to chaos" (p. 248) as the fecundity parameter μ is increased, and provides the reader with a clear look at the Hopf bifurcation and a good feeling for the different possible routes to chaos. It is a timely example because of the recent interest, in a number of disciplines, in chaotic behavior of dynamical systems.

The above example can be compared with the more familiar one-dimensional (one species or one age-class) population model

$$N(t+1) = F(\mu, N(t))$$

studied by May (1974, 1976) and May and Oster (1976). Even when the function F is quite simple (but non-linear: e.g., quadratic) the system can move (as μ is increased) from a stable equilibrium, through a sequence of period doubling intervals, and finally to chaotic behavior. The surprising thing is that essentially the same progression occurs for a wide class of functions F. But the analogous model for two-dimensional behavior is mathematically less well understood, and the sequence of possible behaviors can be much more complex. For ecologists who wish to understand this extraordinary topic better, the above matrix example is just the right follow-up to the one-dimensional models of May.

We have one general criticism. We feel the book would have been much improved if many of the general matrix results used had been put in chapters of their own, and presented in a direct, precise, and formal style. Not only would this have made it much easier for the reader to look up the various results when needed, but it would also have exposed more clearly the underlying theory, and thereby facilitated a general understanding of how different concepts fit together. In fact, the most basic matrix results are already collected in an appendix, but our suggestion is that this chapter should have gone much farther than it did.

We are not arguing here for an abstract approach divorced from the central examples of the book. But it is sometimes difficult to do two things at once. In this case, it is difficult to perceive and appreciate the matrix results while coping with the particularities of life-, size-, and stage-classified populations. Yet, in the end, one of the principal contributions that mathematics makes to other disciplines is to provide constructs that are able to describe seemingly disparate situations.

What we have in mind is to take as a basic example a general nonnegative matrix, assumed to have distinct eigenvalues, where the entries a_{ij} are interpreted as the number of type j "descendents" of a type i "parent," along with the graph associated with this matrix, and to derive, in the context of this example, the basic eigenvector results. It turns out that there's a lovely duality between the left and the right. That is, if (column) vectors on the right are interpreted as numbers or frequencies of individuals of different types, then (row) vectors on the left will have an interpretation as price or value. Many of the technical results found throughout the book should be collected together and supported by this interpretation.

As an example, we mention the results in 6.1 on eigenvalue sensitivity. Suppose you increase every entry in the matrix A by one percent. Since this multiplies A by 1.01, it must multiply each of its eigenvalues λ by 1.01. Define the *elasticity* e_{ij} to be the fraction of this one percent increase in λ that is due to the increase of the entry a_{ij}. Then

$$e_{ij} = v_i a_{ij} w_j / \lambda$$

where v and w are the left and right eigenvectors, respectively, normalized so that $v \cdot w = 1$. These elasticities (which sum to one) are displayed on the graph of the teasel life cycle in 6.1, and give the reader a good feeling for the relative significance of the different pathways in the cycle.

From time to time we found the mathematics to be more difficult to read than it might be. In our view this is because the author has never really come to terms with how mathematically sophisticated his reader is, and has often settled on an uncertain compromise between a rigorous development and a heuristic one.

Examples of this are found in the mathematical development of the z-transform in Chapter 5, and in Chapter 6. For example, Section 6.4.2, which discusses Lande's (1982) formula

$$\Delta\bar{z} = \lambda^{-1} G \nabla \lambda$$

for the change in mean phenotype under the action of selection, contains vexing imprecisions. This elegant result is important because it justifies the use of λ as a measure of fitness in an age-structured population in which there is some phenotypic variation. But what exactly is λ? The definition offered on page 165, that it is the dominant eigenvalue of the Leslie matrix A evaluated at the population mean $\bar{z}$, is wrong. On page 167, the formula

$$1 = \sum W_i(z) \lambda^{-i}$$

gives the impression that λ is a function of z, and this is also wrong. Here, W_i is the expected fecundity at age i of a newborn individual of phenotype z. In fact, what is needed for Lande's formula to hold is that λ be defined as the unique positive root of the equation

$$1 = \sum \overline{W}_i \lambda^{-i}$$

which is found on page 170. So defined, λ is in fact the geometric growth rate of the population (in a stable age distribution), but it is not the dominant eigenvalue of any obvious matrix.

Having made these points, our own experience has certainly shown us that in spite of the increasing mathematical sophistication of population biology, it is not an easy task to write for both a biological and a mathematical audience, and Caswell has, on the whole, done rather well. The reader is never talked down to, hard mathematics is brought to bear where it is needed and diligent readers will discover an ability to understand much more than they might have originally expected to.

We have a final suggestion that might be properly addressed to the editor or the publishers. A work of this sort would be improved if the later chapters were more independent. This could be achieved by having a fairly detailed index of notation, and the inclusion of relevant references from the literature at the end of each of the later chapters instead of at the end of the book. The more expert reader would be more easily able to begin the book at the topic of interest.

Reviewing this book has led us to think that it might almost have been an Alexandrian Quartet of books with the same material presented from differing viewpoints of mathematical and biological naivity and sophistication. It is a book that deserves to be widely read and discussed—but, by whom? We would like to see it read by any mathematicians engaged in teaching graduates or undergraduates. The value of the graph associated with a matrix ought never again be doubted by anyone working through Chapters 4 and 5; however, we are hard put to think of a single example of an elementary linear algebra textbook that spends any time on this. Nor have we seen many calculus books that point out the usefulness of partial derivatives to determine the influence of various entries in a matrix on the eigenvalues.

Of course biologists, too—certainly population biologists—should read it. It would be a valuable experience for all biologists to see how quickly one moves from mathematics so simple that one hardly needs it, to mathematics drawn from far enough inside the discipline that half the members of our mathematics department would find concepts that are unfamiliar to them. There can no longer be any question that some familiarity and comfort with these models is needed by all those working on the theoretical underpinnings of population biology. And when all is said, and enthused and complained about, this book is timely, comprehensive, and exceedingly interesting.

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