
Preface

This book offers an introduction to the use of matrix theory and linear algebra in modeling the dynamics of biological populations. Matrix algebra has been used in population dynamics since the seminal work of H. Bernardelli [8], E. G. Lewis [103], and P. H. Leslie [100], [101] in the 1940s. Particularly influential was Leslie's work on the dynamics of populations structured by age categories. Later, in 1965, L. P. Lefkovich demonstrated how the methodology can be applied to populations structured by other means as well, such as body size or weight, life cycle stages, disease states, spatial location, and/or any number of physiological and behavioral characteristics [99]. Today matrix models continue to play an expanding major role in theoretical and applied population dynamics [13], [14], [15], [28], [106].

The book does not serve as a broad introduction to the subject of structured population dynamics. That would entail covering a large variety of other types of mathematical equations, including partial differential equations, delay or functional differential equations, integral equations, and integro-differential equations [9], [10], [12], [28], [55], [83], [84], [94], [105], [109], [110], [122], [130], [133], and require more mathematical background (and a much larger book). With a focus on matrix models, the book requires only first courses in multivariable calculus and matrix theory (or linear algebra) as prerequisites. Additional material needed that might not be found in a first course in these subjects is

covered when required (e.g., topics from Perron–Frobenius theory). Although a student would benefit from a first course in differential equations (in that basic topics in dynamics would then be familiar), the book is mathematically self contained with regard to dynamical systems concepts (equilibria, stability, bifurcations, etc.). It is aimed at the upper-division undergraduate or first-year graduate student level of mathematical maturity. The book could be used in a variety of ways, including as

- a text for a special topics course;
- a supplement to a mathematical biology course;
- a resource for a general modeling course;
- independent reading and research projects;
- a source of applications of matrix theory and difference equations.

I have used the material in the book, over many decades, in a variety of teaching and mentoring settings at the University of Arizona, including an undergraduate biomathematics course in the Department of Mathematics and a mathematical modeling course in the Department of Ecology and Evolutionary Biology; undergraduate independent study courses for both mathematics and biological majors; undergraduate honors projects and theses; REU research projects; and research training courses for first-year graduate students in the Interdisciplinary Program in Applied Mathematics.

In this book, a student will learn the basics of modeling methodology (i.e., how to set up a matrix model from biological underpinnings) and the fundamentals of the analysis of discrete time dynamical systems (equilibria, stability, bifurcations, etc.). In addition to numerous examples that illustrate these fundamentals, several applications appear at the end of each chapter that illustrate the full cycle of model setup, mathematical analysis, and interpretation. These applications were carefully selected so as to illustrate not only the mathematical techniques and theorems presented in the chapter but to showcase some specific questions and problems of historical and/or contemporary interest in theoretical and applied population dynamics.

A focus throughout the book is on the long-term fate of a population (i.e., its asymptotic dynamics), and a central recurrent theme in all chapters concerns the problem of extinction versus survival. Which of these

outcomes a model equation predicts typically depends on the parameters (coefficients) appearing in the model equation, and a change in one (or more) of these parameters can change the predicted outcome from extinction to survival or vice versa. Bifurcation theory is a mathematical discipline that focuses specifically on dynamic changes caused by changes in an equation's parameters; hence, bifurcation theory serves as a natural context in which to study population dynamic models, including the basic question of extinction versus survival. Each chapter has as its centerpiece a basic bifurcation theorem that addresses the issue of extinction versus survival. (A twist occurs in Chapter 4 on epidemic models where the extinction state is replaced by a so-called disease-free state.) The strength of these basic bifurcation theorems is their generality and relative ease of application. They therefore serve as a baseline starting point for the analysis of virtually any model. The shortcoming of the basic bifurcation theorems is that they do not give a complete global picture of a model's dynamics. This global picture depends heavily on the particular details of the model equation under consideration and requires further analysis.

The topics presented in the Chapters 1–3 are, in my view, the bare bones of matrix models and structured population dynamics, both the modeling methodology and the analysis of model equations. These chapters give a student a solid foundation on which to pursue further topics, either in higher level textbooks and scientific/mathematical literature or as original research projects. Although the models and equations treated are in discrete time and deal with populations structured by discrete classes only, they serve as a starting point for more general models involving continuous time and/or population structuring, which are mathematically more difficult and challenging.

Chapters 4 and 5 give two example directions for further topic development in structured population dynamics. Models of diseases, used in the study of epidemics, are structured population models (the structuring done with respect to disease states). While commonly done using ordinary differential equations, discrete time models are also used (e.g., see [9]). Chapter 4 gives an introduction to this topic for discrete disease classes. (Discrete time models with continuously distributed disease classes lead to integro-difference equation type models [e.g., see [94], [108]]). Chapter 5 extends population dynamic models to include Darwinian evolution by natural selection. The modeling methodology given

in this chapter has only recently been developed for discrete time models [129] and, to my knowledge, appears at this time in no student level book. Both of these chapters open the door to innumerable research projects for young investigators, given that there are so many pathogens and diseases that threaten any biological population and given that evolution is the central principle in biology.

There are numerous other topics of interest and importance in population dynamics that are not covered in this book. For example, models that include immigration/emigration and harvesting, periodic (seasonal) or stochastically fluctuating parameters, a spatial component, or multispecies interactions are not covered. The reasons, besides the length of the book, are that these topics demand higher mathematical prerequisites or, in some case, are not yet so well developed for matrix models. The topics covered in the book will, however, give a student a solid foundation on which to pursue these and other topics found in higher level textbooks or in the scientific/mathematical literature.

I am highly grateful for the comments that I received from several reviewers of early drafts of the book. Their critiques and suggestions were very helpful in preparing an improved final version.

Jim Michael Cushing
Professor Emeritus
Department of Mathematics
Interdisciplinary Program in Applied Mathematics
University of Arizona
Tucson, AZ 85721 USA