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Mathematics in population biology, by Horst R. Thieme, Princeton Series in Theoretical and Computational Biology, Princeton Univ. Press, Princeton and Oxford, 2003, 568 pp., \$49.50 (paper), ISBN 0-691-09291-5; \$95.00 (cloth), ISBN 0-691-09290-7

Humans have noted the rise and fall of plant and animal numbers since the dawn of civilization. While many illustrious names are associated with early mathematical theories of population growth (such as Fibonacci, Euler, Halley, and Malthus), the first half of the twentieth century is generally regarded as the Golden Age of mathematical ecology and population dynamics [1]. These decades saw the formulation of what are now viewed as the classical theories in these disciplines. Equations such as the famous logistic differential equation, the Volterra predator-prey equations, and the Lotka-Volterra competition equations had a tremendous influence on the development of both theoretical and applied ecology. They stimulated the formulation of (and provided theoretical support to) many, if not most, of the fundamental tenets that underlie these disciplines – in one guise or another – to this day. These tenets include exponential (unregulated) population growth, carrying capacity (regulated growth), the principle of competitive exclusion, the concept of ecological niche and limiting similarity, the classification of species as r or K selectors, the oscillatory dynamics of predator-prey interactions, the paradox of enrichment, and stable age distributions, to name only a few.

Ecological systems are complex. The variety of biological organisms on our planet, and of the ecological interactions among them and their environments, is staggering. In order to gain a deeper understanding of the complexities of the biological world, mathematicians and theoretical ecologists throughout the twentieth century modified the classical models in innumerable ways and also developed new models and modeling methodologies.

All mathematical models of necessity make simplifying assumptions, and as a result there is a relentless trade-off between biological accuracy and mathematical tractability. The classical models of Lotka and Volterra are described by systems of autonomous ordinary differential equations in which the state variables are total population sizes (or densities). One way to organize the simplifying assumptions underlying such models is with respect to the uniformities and homogeneities that are postulated (either explicitly or implicitly). For example, three important assumptions underlying Lotka/Volterra models – indeed underlying many of the

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models found in mathematical ecology – concern homogeneities in space, time, and the characteristics of individual organisms. In such models there is no attempt to account for the spatial distribution or movement of biological organisms; it is assumed that environmental and biological parameters are constant in time (so that the equations are autonomous), and all individuals in the populations are treated as identical organisms. Much of the development in theoretical ecology and populations that followed the Golden Age focussed on relaxing these simplifying assumptions in one way or another.

For example, there is now a large body of literature dealing with population dynamic models that include spatial structure and population dispersal. The spatial distribution of populations and their movements within habitats are of considerable interest to ecologists, as well as to many others interested in such important issues as the spread of diseases and undesirable organisms, threats to endangered species, the management of renewable resources, the design of conservation preserves, and so on. In this literature one finds many types of equations (e.g. partial differential, integro-differential, and integral-difference equations) and challenging problems of interest to mathematicians, including the formation of spatial patterns, the structure of travelling waves, speed of propagation, etc. More recently, researchers have also employed cellular automata type models to study the spatial distribution and movement of biological populations.

There is also a substantial literature dealing with the non-autonomous equations that arise when physical environments or vital biological parameters such as birth, growth, and death rates vary temporally. Periodically forced differential and integral equations capture the effects of oscillations that are regular: daily fluctuations in light and temperature, monthly oscillations of tides, annual changes of the seasons, and so on. At the opposite extreme, stochastic equations model stochastic fluctuations that occur all too frequently in ecological systems. These kinds of models provide interesting and challenging mathematical problems, and they raise questions concerning the extent to which fundamental principles in population dynamics and ecology, formulated on the basis of autonomous deterministic models, remain valid for non-autonomous and/or stochastic models.

There is also now a well-established body of literature concerned with dynamic models of populations in which all individuals are no longer treated as identical to one another. Individuals that make up biological populations generally differ with regard to their physiological and behavioral characteristics. They therefore differ in the ways that they interact with their physical environment and with other individuals (of their own species as well as with those of other species). As a result, vital processes such as birth, death, growth, metabolism, resource consumption, movement, etc., all vary among individuals within a population. Birth rates of younger individuals are generally quite different from those of older individuals, mortality rates of larger individuals are usually different from those of smaller individuals, and so on. These differences can be considerable, with variances sometimes greater within a population than among different populations.

Researchers have employed several different methodologies to derive dynamic models that take into account crucial differences among individuals. The history of these kinds of models extends back to the first half of the twentieth century (for example, to the influential work of A. G. McKendrick and P. H. Leslie). The recognition that the fundamental unit in population biology is the (reproducing)

individual and the desire to relate biological knowledge about individual organisms to the dynamics of the entire population stimulated a resurgence of interest during the last decades of the century in connecting individual level dynamics to population level dynamics. Leslie's early contribution was the introduction of matrix models (or difference equations) to the description of the dynamics of specified categories within a population. His primary interest was with categories based on chronological age, but his methodology extends easily to populations structured by other physiological characteristics (such as body size, weight, life cycle stage, etc.). From a mathematical point of view, these discrete time models constitute an outstanding example of the application of matrix theory. The continuous analogs of matrix models involve first order hyperbolic partial differential equations. These model equations are akin to those found in continuum mechanics, except that they typically involve non-local integrals in both the (nonlinear) differential equations and (nonlinear) boundary conditions. The rigorous mathematical treatment of these equations is a challenge (even with regard to the basic questions of solution existence and uniqueness, to say nothing of the analysis of asymptotic dynamics). Although the modeling methodology has been clarified and much has been accomplished (for example by using nonlinear semi-group methods), the general theory of structured population dynamics is still incomplete in many ways and therefore provides many opportunities for mathematicians to contribute to the further development of theoretical population dynamics and ecology. Other approaches to the dynamics of populations with differing individuals include agent (or individual) based models, in which each individual organism is modeled separately, rules of temporal changes in individual characteristics are adopted, and the population level dynamics are followed by means of computer simulations.

Mathematics and science are disciplinary activities. One consequence of the development of mathematical ecology and population dynamics during the last century was a divergence into different subdisciplines. Within mathematics, mathematical ecology became a somewhat insular cottage industry whose efforts often lacked concrete biological underpinnings. As R. M. May pointed out in his influential monograph, it is easy to cobble together a virtually endless number of theoretical and speculative ecological models from some basic modeling building blocks [2]. After doing this, one can, as a mathematician, have fun in analyzing the resulting equations and thinking (hoping?) that the results have application to problems of interest to biologists. In some light-hearted way this is perhaps not an unreasonable expectation for even a carelessly constructed model, since a mathematician's tongue-in-check definition of a good biologist might be one who can find a biological application of his/her favorite equation. On a more serious side, however, a healthy development of theoretical ecology is obviously not enhanced by the lack of communication between mathematicians and biologists.

Unfortunately, too much of the literature in mathematical ecology consists of mathematical results that mean too little (if anything) to ecologists. Often this literature does not adequately discuss the biological motivation or relevance of the equations studied, nor of the questions addressed, and the results of a mathematical analysis are not interpreted in a meaningful way (if at all). All too often there is no careful and thorough derivation of the model equations from fundamental biological principles and mechanisms, with the result that the models can miss their intended purpose. For example, a biologically reasonable model might, but does not necessarily, result from a familiar model by simply inserting a time delay

in some term of an equation (and casually remarking something about gestation or maturation periods) or by adding white noise to an equation (does this model environmental or demographic stochasticity? sampling error?). Although there are many aspects to the gaps dividing mathematicians and ecologists [3], attention to these issues would certainly help to improve the application of mathematics to the ecological sciences. It is with regard to these issues that the book under review stands out in a favorable way.

The book is the result of courses taught by the author over a number of years at Arizona State University. The courses, and therefore the mathematical material in the book, range from an undergraduate (junior) level to an advanced graduate level. The book is organized, however, around biological rather than mathematical themes. Twenty-three chapters are divided into three parts. A fourth part of the text, entitled “Toolbox”, contains a number of appendices devoted to selected mathematical topics, techniques and theorems.

In Part 1 (“Basic Population Growth Models”) the author provides an extended treatment of single species models. He formulates a general model from basic biological principles (birth, death, immigration, emigration processes) and from it provides careful derivations of the classical models (associated with names such as von Bertalanffy, Verhulst, Beverton-Holt, Gompertz, Allee and others) that form the bases of more complex models and applications. Part 1 concludes with a theme close to the author’s research interest, namely the dynamics of structured populations, developed by means of a case study of an aquatic population subject to a toxic pollutant followed by the formulation and study of a general juvenile/adult structured model.

As the author points out, there is an underlying organization of material throughout the text based on increasing mathematical difficulty that is not apparent in the table of contents. In Part 1 the beginning chapters require only single variable calculus and some elementary knowledge of ordinary differential equations (although basic methods from an introductory course are developed in the book). Subsequent chapters use topics from advanced calculus and more advanced courses in ordinary differential equations. Specifically, the final chapters of Part 1 use phase plane analysis, linearization, Poincaré-Bendixson theory, the Hopf bifurcation theorem, and persistence theory. The required definitions and theorems appear in the “Toolbox” part.

In Part 2 (“Stage Transitions and Demographics”) the author takes up in earnest the topic of structured population dynamics. He carefully develops a methodology for building the submodels concerned with stage transitions of individual organisms that are necessary to formulate models for the (longer term) dynamics at the population level. Considerable attention is paid to models that structure populations according to chronological age, where demographic quantities such as life expectancy and inherent net reproductive rates are related to their dynamic consequences. Models take the form of partial differential equations, integral equations, or time delayed ordinary differential equations. Most of the material in Part 2 concerns linear models, although a chapter is devoted to nonlinear models. The mathematical prerequisites begin at the single variable calculus level and proceed to the advanced calculus level (e.g., Stieljes integrals).

The author includes a considerable amount of material on epidemic (host-parasite) models. Part 3 (“Host-Parasite Population Growth: Epidemiology of Infectious Diseases”) begins with a historical discussion of the impact of infectious

diseases on humans and a formulation of the classic SIR model of Kermack and McKendrick (in which susceptible, infectious, and recovered stages of the disease are dynamically tracked). The remainder of Part 3 consists of the development and study of more complex models that include other important stages of diseases and the demography of the populations (such as age structure). The author carefully defines crucial quantities, such as the net replacement ratio R_0 and the average age of infection, and relates them throughout Part 3 to the dynamics of the epidemic. Among the problems addressed are thresholds for R_0 (above which an epidemic occurs), vaccination strategies (as optimization problems), and characteristics of epidemics (such as the final “size” of an epidemic). The mathematical background required for Part 3 is the most demanding in the book. The reader will need to be familiar with intermediate level ordinary differential equations, some measure theory, and Lebesgue-Stieltjes integration. The “Toolbox” appendices contain the required theorems from these topics, as well as other topics that arise (e.g., convex theory and Perron-Frobenius theory).

Each chapter contains exercises and bibliographic remarks that provide references for further reading. Part 4 contains Maple worksheets that can be used to study some of the models presented in the book. As a result, the book could profitably be used as a text in graduate or advanced undergraduate courses and seminars.

Mathematicians will be pleased to find that definitions and theorems are carefully and rigorously stated (and in some cases proved) in the book. Thus, a unique feature of the book is that neither the rigorous derivation and interpretation of biological models nor the rigorous presentation and use of mathematics are slighted. The author does not present as broad a sweep of population dynamics and theoretical ecology as other textbooks attempt to do. Instead, he offers the reader a more in-depth and accurate presentation of the selected topics than is usually found in other books. Readers with the required mathematical background will be well rewarded by discovering how mathematics can be applied to important problems in population biology. Moreover, they will be in an excellent position to begin or supplement their own research into this field (and many other related fields of bioscience). By focussing on selected chapters, students with less mathematical background will be similarly rewarded (and, in addition, will likely be motivated to learn more mathematics!). The book is a welcome contribution to the growing list of textbooks on the mathematics of population dynamics – a contribution that distinguishes itself by its carefully thought out and rigorous presentation of both the biological and mathematical aspects of the subject.

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