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Mathematical Models in Population Biology and Epidemiology. By Fred Brauer and Carlos Castillo-Chávez. Springer, New York, 2001, xxiii + 416 pp., ISBN 0-387-98902-1, $59.95.

Reviewed by **Shandelle M. Henson**

Recently I stood with mathematician Jim Cushing and ecologist Bob Costantino in the cool dimness of the Mt. Wilson Observatory, looking across the railing into the telescope room. After a period of silence, Bob turned to us and said, "Astronomers looked up at the sky and assumed there was order. So they formulated and tested mathematical models. Ecologists look out at nature and say, 'This stuff is too complex to explain and predict.' That's self-defeating. Surely there is enough low-dimensional order out there to allow prediction of ecological dynamics. When the mindset changes—as it surely will—scientific progress will follow."

As I consider recent advances in ecology, I have the growing sense that these words may be prophetic. Ecology may well stand at the threshold of an enormously productive mathematical revolution.

For those unfamiliar with the issues, some explanation is in order. Mathematics and ecology have had an uneasy relationship. It is true that each discipline has benefited from the other. On the one hand, the models and questions of ecology have contributed substantial motivation to the mathematical theory of dynamical systems. On the other hand, mathematics has contributed a number of important theoretical insights and tenets to ecology. However, actual quantitative connections between dynamic models and data have been scarce. While the discipline of physics has long embraced mathematical models and controlled laboratory experiments as primary tools for the explanation and prediction of dynamic physical phenomena, ecology has been slow to follow.

In fact, the hypothesis that population fluctuations are shaped largely by low-dimensional deterministic forces has caused considerable controversy for nearly a century. During the last few decades, however, this hypothesis has been rigorously and successfully tested in laboratory populations through the application of dynamical systems theory and statistics. Careful studies involving mathematical models, controlled laboratory population experiments, and statistical techniques have unequivocally identified many low-dimensional deterministic phenomena in population data. These phenomena include equilibria, cycles, transitions between dynamic regimes (bifurcations), multiple attractors, resonance, basins of attraction, saddle influences, stable and unstable manifolds, transient phenomena, and even chaos. Robust qualitative and quantitative predictions have become possible for several laboratory systems; see, for example, [**1**]–[**5**], [**8**], and [**10**]–[**12**].

A major goal of laboratory studies, of course, is to gain clear insights that might be applied to fluctuations in field populations. Despite the very real difficulties of developing quantitatively accurate models for field systems, many researchers are optimistic that we are gaining the necessary conceptual tools and insights. If some of the recent successes in the laboratory can be extended to the field, unprecedented advances in field ecology may lie just around the corner.

So what does this have to do with textbooks for mathematical modeling? In this exciting climate of accelerating change, students of biology in general and ecology in particular should be trained in the mathematical methods just as physics majors are. Interdisciplinary courses on mathematical models in biology are springing up at many university campuses. These classes are important to the future of the discipline of ecology. Not all the students thus trained will go on to do mathematical modeling in their careers; but hopefully they will have lost any prejudice they might have harbored against the method of abstraction and will point their own students to the importance of mathematical training. In other words, classes in mathematical modeling can help change the academic culture of biology and ecology departments.

I have had the pleasure of teaching such courses at the College of William and Mary and Andrews University. The subject seems to be popular, and it has attracted some excellent students. We cover the basics of deterministic discrete- and continuous-time linear and nonlinear models, both scalar equations and systems. Topics include analytic solutions of linear equations, equilibria, linearization, stability, phase portraits, bifurcations, simulations, and modeling methodology. We spend a good deal of time discussing the philosophy of science: how are mathematics and science different, how are they similar, and how should mathematics be used in science? We talk about logic, epistemology, and various notions of certainty. The students become familiar with the literature, work together in interdisciplinary research groups, and learn to give research talks. It would be nice to run a second semester of the course, covering issues of stochasticity, parametrization, validation, and the connection of models with data. Teaching this course has been fun and rewarding.

It has also been a challenge. Frankly, teaching a good interdisciplinary course in mathematics and biology can be tough. It seems to me that the ideal classroom is a mix of biology and mathematics majors. Each discipline learns to respect the other; the mathematics students learn some biology and the biology students some mathematics; and all of them get a taste of the exciting synergy of interdisciplinary collaboration. At any rate, even if one did wish to separate the biology and mathematics students, many universities do not have the resources to run two such courses. The problem with having a mixed clientele, of course, is pitching the material at the right level of mathematical difficulty. Usually the biology majors will have had one or two semesters of calculus. Mathematics majors who are drawn to such a course, in contrast, tend to be more advanced in their mathematical curriculum; they are often seniors looking for an interesting mathematics elective.

Although the inequalities of mathematical background present a real opportunity for an intellectually invigorating classroom, they can also create various sorts of problems. Feelings of insecurity and attitudes of disdain among the students are not uncommon. The biology students who take such a course are usually pretty serious and sometimes even intellectually passionate, but they often feel insecure about the mathematics. And, it is pretty common for one or two lazy or anti-intellectual mathematics majors to enroll just because it sounds like an easy elective. These students sometimes attempt to cloak a refusal to learn with a mantle of mathematicians' disdain. (This is easy to see through, but it certainly is annoying.) It is often unclear how fast the instructor should go through the material, and to what depth; and each group of students may have different needs in this regard.

How should a mathematics professor deal with such problems? I have tried various methods. Most importantly, one must create an atmosphere of interprofessional respect. It helps if the professor has credibility as an interdisciplinary researcher and collaborates with colleagues from biology. It is also helpful if biologist colleagues sit in on the course, or team teach it, or give guest lectures. I try to cover the biology as well as the mathematics and to present the modeling techniques in a unified scientific framework. Along with respect, it is important to create an atmosphere of security. Biology students must be certain that it is okay to ask questions about the mathematics, that there is no reason to be ashamed because they don't know as much math as the mathematics majors. They need to be encouraged to jump in with both feet, simply learn as much as they can, and be intellectually passionate as scientists. The mathematics majors should be encouraged to learn some science, and to dig deeply into some of the fascinating and difficult mathematical topics (such as chaos) that come up in biology.

Traditional lecturing—normally my most effective teaching mode—must proceed at a more leisurely pace, and can be punctuated by frequent "breaks." Students come up to the board to work problems, we discuss issues of human population growth, I probe the students' understanding of various issues by calling on them individually. Sometimes when going through a long algebraic derivation, I will ask each student in turn: "Clara, what is the next step in solving for λ?" "Matt, what does the eigenvalue tell you about the dynamical system?" When one has a good feel for the level of each student, one can usually ask questions to which he or she can give appropriate and substantive answers. These frequent changes of pace keep the attention of those with more mathematical background and help those with less to absorb the material. Because of the dampening effect of lazy students who are not really interested in the subject, I have started personally interviewing students before they begin the class. I tell each student what the class will be like and what I expect in terms of participation and intellectual engagement. I also warn that the nontraditional nature of the class might make it a miserable experience for someone who is not excited about biology.

Finally, there is the problem of choosing an appropriate textbook. At first I imagined I would simply choose a textbook and follow it, as we tend to do in mathematics. Edelstein-Keshet [**6**], perhaps the main workhorse in the area, nicely integrates the mathematics with the applications and brings together a treasure-trove of material. It has a prerequisite of "basic calculus," but it was too difficult for my students who had done well in a year of calculus at William and Mary. Hastings [**9**] requires a year of calculus and suggests having some previous exposure to ecological ideas. This well-written book was created for Hastings's population ecology students, and it is a favorite with my biology majors. It is too elementary in terms of computation and theory for mathematics majors, although it provides excellent supplemental reading for these students.

The book under review is a new entry in this field. Fred Brauer and Carlos Castillo-Chávez have written a solid, comprehensive book organized around the three topics of single species models, interacting species models, and structured population models. They cover discrete and continuous time equations, linear models and linearization, qualitative analysis and phase space, bifurcations, and delay equations. Biological applications and classic topics include epidemiology, vaccination schemes, harvesting, delayed recruitment, Lotka-Voterra models, chemostats, competition, predator-prey systems, mutualism, Kolmogorov models, invasion and coexistence, the community matrix, and age structured McKendrick-Von Foerster models (including numerical schemes). Some chapters include case studies of such topics as the eutrophication of a lake, oscillations in flour beetle populations, Nicholson's blowflies, and the spruce budworm. Most chapters contain several interesting projects; for example, estimating the population of the U.S.A. and models for blood cell populations, neurons, and pulse vaccination.

The book reads as a well-written and fairly traditional undergraduate mathematics textbook, with theorems and some proofs (although many theorems are stated without proof). Its prerequisites are "a year of calculus, some background in elementary differential equations, and a little matrix theory." It would work well as a text for an upper division undergraduate topics course in applied dynamics, or as a graduate course for mathematically advanced ecology students. It served as an excellent reference and source for problems and projects in my own undergraduate interdisciplinary class. However, my students found it more difficult than Edelstein-Keshet [**6**].

The conclusion of the textbook hunt for my particular situation has been the following: (1) the kind of course I want to teach is too fluid to run in lockstep with a textbook; (2) no book will be at the right level for all the students in my class; indeed, there is no "right level"; (3) textbooks are useful for assigning readings and problems, as sources for student projects, and as reference books for the scholarly libraries of my upcoming young research biologists and applied mathematicians. In the Spring 2002 semester I used two texts: the book under review and Hastings [**9**]. I assigned readings and homework problems out of both books as appropriate, but did not base my lectures on either book. Instead, I ended up writing my own set of notes tailored to the interdisciplinary mix of students. This approach seemed to work well.

Brauer and Castillo-Chávez write in the preface: "This book is intended to inspire students in the biological sciences to incorporate mathematics in their approach to science . . . . A secondary goal is to expose students of mathematics to the process of modeling in the natural and social sciences." This statement cheers me, and I am reminded of the words of the evolutionary statistician R. A. Fisher [**7**, p. ix], when he said of mathematics and biology: "I can imagine no more beneficial change in scientific education than that which would allow each to appreciate something of the imaginative grandeur of the realms of thought explored by the other."

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> ——Lev Grossman, "Crunching the Numbers," *Time*, 23 December 2002, p. 51.