Modeling Techniques and Ecology and Evolutionary Biology

by Drs. Sarah P. Otto and Troy Day

***AIM* —** To provide biologists with a user-friendly book of tools for constructing and analyzing mathematical models.

***JUSTIFICATION* —** The vast majority of biologists (i.e. those without training in mathematics) find theory both impenetrable and inaccessible. Yet, with the advent of computer-aided mathematical tools, almost all biologists have the potential to write and analyze their own mathematical models, if they only knew where to begin. This book aims to bridge the gap for those biologists who wish to embark upon the world of modeling, providing a comfortable guide with sufficient explanations and examples to give the reader the necessary tools for building and analyzing mathematical models. Our aim is to enable any interested reader to learn how mathematical models are born, how they develop, and what they can tell us. Like learning a language, learning mathematical techniques requires practice. Thus, accompanying the book will be electronic modeling tutorials. In each tutorial, the reader will be shown how to perform a technique described in the book using a symbolic-mathematics software package (see below). The reader will be walked through the steps needed to solve important and interesting biological problems by applying the techniques learned. While the book will be aimed at an entry level to mathematical modeling, additional details will be presented in boxes and appendices to serve as a useful reference for more advanced modelers. In short, biologists need a book to provide them with both the necessary background to assess the power and limits of mathematical models, and the training they need to develop theory and models themselves. We want to write this book.

***THE FOCUS* —** More than any other field in biology, population biology (ecology and evolution) is suffused with theoretical models. Being familiar and comfortable with mathematical modeling thus provides a major advantage to any practicing population biologist. Although the primary aim of this book is to teach modeling techniques so that the reader can develop and analyze a model in any area of biology, examples will be tailored primarily to important questions in population biology.

***THE AUDIENCE* —** Those who will benefit most from the book will be students who are in the upper years of an undergraduate program in ecology or evolutionary biology and graduate students in these fields who have had little or no experience with mathematical modeling. We anticipate that the book will be used as a text for Biomathematics courses, and we will develop several exercises to be used in such a course. Nevertheless, we intend the book to be interesting enough to pick up and read on one's own and comprehensive enough to serve as a reference for researchers in population biology and mathematical biology.

***THE NEED* —** Currently, there is no book available whose aim is to teach how to construct and analyze mathematical models to biologists who have little prior training in mathematics. While there are several books that treat aspects of mathematical modeling in biology, many are quite advanced or cover only a small portion of the broad array of techniques used in population biology. What is lacking is a book that describes the process of modeling: how does a scientist go from a general question, to a set of equations, to answers and insights? This book will provide a much-needed resource, from which biology students can easily learn relevant mathematical skills and which can serve as a reference for established researchers.

There are a few books whose aim is to describe modeling techniques (e.g. *Mathematical Models in Biology*, 1988, by L. Edelstein-Keshet; *Mathematical Biology*, 1989, by J. Murray). These books are limited in scope, however; for example, they do not cover many of the approaches used in evolutionary biology or probabilistic models. More importantly, we have found that the mathematical content and style of these texts are advanced and are more appropriate for readers who already have a strong mathematical background. Therefore these books do not adequately serve our goal of providing a comfortable, user-friendly guide for the average biologist.

In addition, there are several books that describe some mix of evolutionary and ecological theory, including: *An Illustrated Guide to Ecological Theory*, 1999, by T. Case; *Introduction to Theoretical Ecology*, 1989 by P. Yodzis; *Population Biology: Concepts and Models*, 1997, by A. Hastings; *Theoretical Evolutionary Ecology*, 1994, by M. Bulmer; *Evolutionary Games and Population Dynamics*, 1998, and *Dynamical Systems and the Theory of Evolution*, 1988, by J. Hofbauer and K. Sigmund; and *Theory of Population Genetics and Evolutionary Ecology: An Introduction*, 1979, by J. Roughgarden. None of these books is explicitly aimed at teaching the reader how to construct and analyze their own model. The first two books by Case and Yodzis are excellent texts that are primarily focused on teaching ecological theory. Both Hasting's and Bulmer's books provide an introduction to ecological and evolutionary modeling, but both are limited in scope (e.g. probabilistic models are lacking). The books by Hofbauer and Sigmund are excellent texts from both an ecological and an evolutionary perspective, but they are written at a level of mathematical sophistication that is often too high for biology students who are looking for a user-friendly introduction to the area. Roughgarden's book presents an excellent blend of ecological and evolutionary modeling, but it is now quite old (1979), and again its focus is on teaching known theoretical results.

Finally, there are a number of more specialized books about ecological theory or evolutionary theory, with an emphasis on known results and more advanced techniques. In ecological theory, such books include: *Modelling Fluctuating Populations*, 1982, by R. Nisbet and W. Gurney; *Ecological Dynamics*, 1998, by W. Gurney and R. Nisbet; *Modelling biological populations in space and time*, 1993, E. Renshaw; and *Mathematical methods of population biology*, 1982, Frank Hoppensteadt. In evolutionary theory, such books include: *Evolution in Age-Structure Populations*, 1994, by B. Charlesworth; *Principles of Population Genetics*, 1989, by D. Hartl and A. Clark; *Theoretical Population Genetics*, 1990, by J. Gale; *Evolutionary Genetics*, 1998, by J. Maynard Smith; *An Introduction to Population Genetics Theory*, 1970, by J. Crow and M. Kimura; *Mathematical Population Genetics*, 1979, by W. Ewens; *Models of Adaptive*

Behaviour, 1999, by A. Houston and J. McNamara. Again, these books do not attempt to provide a general introduction to developing models, *per se*, but they provide a rich resource of references to which we will send the interested reader for more information concerning specific tools and topics.

ABOUT THE AUTHORS —

SARAH P. OTTO is an evolutionary biologists interested in the forces shaping the structure of the genome (e.g. chromosome number, gene copy number, recombination rate). Using mathematical models, she has shown that genome evolution often depends on particular aspects of a species and its environment, thus helping to explain the remarkable diversity of life at the genomic level. Dr. Otto has published 45 articles, including several influential reviews. She has received numerous awards, including the prestigious Steacie Fellowship from the Natural Sciences and Engineering Research Council (Canada), the Young Investigator Prize from the American Society of Naturalists, the Poste Rouge from the Centre National de la Recherche Scientifique (France), and a Distinguished Scholar in Residence at the Peter Wall Institute (UBC). Dr. Otto is currently an associate professor in the Department of Zoology at the University of British Columbia and is a member of the Institute of Applied Mathematics. She developed and taught a course in Biomathematics aimed at teaching modeling techniques to upper-level undergraduates in biology.

TROY DAY is a mathematical biologist working at the interface between ecology and evolutionary biology. He has a B.Sc. and an M.Sc. in Zoology and a Ph.D. in Mathematics. His research has focused on two broad themes: (1) exploring how life history and morphological characters evolve in response to ecological interactions, and (2) exploring how population structure and limited individual dispersal result in interactions between genetically related individuals that consequently affect the evolution of life history characters. Dr. Day has published numerous scientific articles and has been awarded the prestigious American Naturalist's Young Investigator's Prize, the Doctoral Prize from the Natural Sciences and Engineering Research Council (Canada), and the Canadian Applied and Industrial Mathematics Society Doctoral Dissertation Award. Dr. Day is currently an assistant professor and Canada Research Chair in Mathematical Biology in the Departments of Mathematics and Biology at Queen's University. He has developed and taught Biomathematics courses at the undergraduate and graduate level, as well as courses in introductory calculus and differential equations.

SOFTWARE — Biologists can tackle much more sophisticated mathematical models with the aid of symbolic-manipulation software (e.g. Mathematica, Maple, Matlab). These software packages remember the rules of calculus that most biologists have forgotten or never learned, they can simplify equations that would not otherwise be interpretable, and they can simulate dynamics and generate graphs to help guide and check mathematical analyses. We will teach the reader how to use the symbolic-manipulation software, Mathematica, to perform all of the techniques described in the book. A fold-out key will be supplied that describes the most useful commands in Mathematica. A CD will contain Mathematica packages containing the source code used in the book as well as several tutorials, which guide the reader through all of the steps of a model. Since not everybody has access to Mathematica, we will translate these instructions and tutorials into Maple and Matlab, which will also be available on the CD.

[QUESTION: Any copyright issues?]

OUTLINE —

Chapter 1: Mathematical Modeling in Biology.

Chapter 2: How to Construct a Model.

Chapter 3: Understanding Dynamics using Graphical Techniques.

Chapter 4: Understanding Dynamics using Mathematical Techniques: Equilibria and Their Stability for One Variable Models

Chapter 5: Approximations and Tricks of the Trade

Chapter 6: Understanding Dynamics using Mathematical Techniques: Equilibria and Their Stability for Multi-Variable Models. I. Linear Systems.

Chapter 7: Understanding Dynamics using Mathematical Techniques: Equilibria and Their Stability for Multi-Variable Models. II. Nonlinear Systems.

Chapter 8: Understanding Dynamics using Mathematical Techniques: Cycling Behavior

Chapter 9: Understanding Dynamics using Mathematical Techniques: Analytical Solutions

Specialized Modeling Techniques in Ecology and Evolutionary Biology

Chapter 10: Models of Structured Populations

Chapter 11: Population-Genetic Models for Quantitative Traits

Chapter 12: Modifier models in Population Genetics

Chapter 13: Optimality Models for Quantitative Characters

Chapter 14: Game Theory and “Adaptive Dynamic” Models for Quantitative Characters

Stochastic Models in Ecology and Evolutionary Biology

Chapter 15: An Introduction to Probability Theory

Chapter 16: Markov-chain Models, Birth/Death, Branching Processes

Chapter 17: Diffusion Equation Approximations in Population Genetics

Chapter 18: Additional Techniques for Stochastic Modeling (tracking moments, transforms, etc.)