The Theoretical Biologist's Toolbox
Quantitative Methods for Ecology and Evolutionary Biology

Mathematical modeling is widely used in ecology and evolutionary biology and it is a topic that many biologists find difficult to grasp. In this new textbook Marc Mangel provides a no-nonsense introduction to the skills needed to understand the principles of theoretical and mathematical biology. Fundamental theories and applications are introduced using numerous examples from current biological research, complete with illustrations to highlight key points. Exercises are also included throughout the text to show how theory can be applied and to test knowledge gained so far. Suitable for advanced undergraduate or introductory graduate courses in theoretical and mathematical biology, this book forms an essential resource for anyone wanting to gain an understanding of theoretical ecology and evolution.

MARC MANGEL is Professor of Mathematical Biology and Fellow of Stevenson College at the University of California, Santa Cruz campus.

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Marc Mangel
Department of Applied Mathematics and Statistics
University of California, Santa Cruz

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To all of my teachers, but especially Susan Mangel.

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Preface: Bill Mote, Youngblood Hawke, and Mel Brooks

I conceived of the courses that led to this book on sabbatical in 1999–2000, during my time as the Mote Eminent Scholar at Florida State University and the Mote Marine Laboratory (a chair generously funded by William R. Mote, who was a good friend of science). While at FSU, I worked on a problem of life histories in fluctuating environments with Joe Travis and we needed to construct log-normal random variables of specified means and variances. I did the calculation during my time spent at Mote Marine Laboratory in Sarasota and, while doing the calculation, realized that although this was something pretty easy and important in ecology and evolutionary biology, it was also something difficult to find in the standard textbooks on probability or statistics. It was then that I decided to offer a six-quarter graduate sequence in quantitative methods, starting the following fall. I advertised the course initially as "Quantitative tricks that I've learned which can help you" but mainly as "The Voyage of Quantitative Methods," "The Voyage Continues," etc. This book is the result of that course.

There is an approximate "Part I" and "Part II" structure. In the first three chapters, I develop some basic ideas about modeling (Chapter 1), differential equations (Chapter 2), and probability (Chapter 3). The remainder of the book involves the particular applications that interested me and the students at the time of the course: the evolutionary ecology of parasitoids (Chapter 4), the population biology of disease (Chapter 5), some problems of sustainable fisheries (Chapter 6), and the basics and application of stochastic population theory in ecology, evolutionary biology and biodemography (Chapters 7 and 8).

Herman Wouk's character Youngblood Hawke (Wouk 1962) bursts on the writing scene and produces masterful stories until he literally has nothing left to tell and burns himself out. The stories were somewhere between the ether and the inside of his head and he had to get them out. Much the same is true for music. Bill Monroe (Smith 2000) and Bob Dylan (Sounes 2001) reported that their songs were already present, either in the air or in their heads and that they could not rest until the songs were on paper. Mozart said that he was more transcribing music that was in his head than composing it. In other words, they all had a

story to tell and could not rest until it was told. Mel Brooks, the American director and producer, once wrote "I do what I do because I have to get it out. I'm just lucky it wasn't an urge to be a pickpocket."

I too have a story to get out, but mine is about theoretical biology, and once I began writing this book, I could not rest until it was down on paper. Unlike a novel, however, you'll not likely read this book in a weekend or before bed. But I hope that you will read it. Indeed, it took me two years of once a week meetings plus one quarter of twice a week meetings with classes to tell the story (in Chapter 1, I offer some guidelines on how to use the book), so I expect that this volume will be a long-term companion rather than a quick read. And I hope that you will make it so. Like my other books (Mangel 1985, Mangel and Clark 1988, Hilborn and Mangel 1997, Clark and Mangel 2000), my goal is to bring people – keen undergraduates, graduate students, post-docs, and perhaps even a faculty colleague or two – to a skill level in theoretical biology where they will be able to read the primary literature and conduct their own research. I do this by developing tools and showing how they can be used. Suzanne Alonzo, a student of Bob Warner's, post-doc with me and now on the faculty at Yale University, once told me that she carried Mangel and Clark (1988) everywhere she went for the first two years of graduate school. In large part, I write this book for the future Suzannes.

Before writing this story, I told most of it as a six quarter graduate seminar on quantitative methods in ecology and evolutionary biology. These students, much like the reader for whom I write, were keen to learn quantitative methods and wanted to get to the heart of the matter – applying such methods to interesting questions in ecology and evolutionary biology – as quickly as possible. I promised the students that if they stuck with it, they would be able to read and understand almost anything in the literature of theoretical biology. And a number of them did stick through it: Katriona Dlugosch, Will Satterthwaite, Angie Shelton, Chris Wilcox, and Nick Wolf (who, although not a student earned a special certificate of quantitude). Other students were able to attend only part of the series: Nick Bader, Joan Brunkard, Ammon Corl, Eric Danner, EJ Dick, Bret Eldred, Samantha Forde, Cindy Hartway, Cynthia Hays, Becky Hufft, Teresa Ish, Rachel Johnson, Matt Kauffman, Suzanne Langridge, Doug Plante, Jacob Pollock, and Amy Ritter. Faculty and NMFS/SCL colleagues Brent Haddad, Karen Holl, Alec MacCall, Ingrid Parker, and Steve Ralston attended part of the series too (Brent made five of the six terms!). To everyone, I am very thankful for quizzical looks and good questions that helped me to clarify the exposition of generally difficult material.

Over the years, theoretical biology has taken various hits (see, for example, Lander (2004)), but writing at the turn of the millennium,

Sidney Brenner (Brenner 1999) said that there is simply no better description and we should use it. Today, of course, computational biology is much in vogue (I sometimes succumb to calling myself a computational biologist, rather than a theoretical or mathematical biologist) and usually refers to bioinformatics, genomics, etc. Although these are not the motivational material for this book, readers interested in such subjects will profit from reading it. The power of mathematical methods is that they let us approach apparently disparate problems with the same kind of machinery, and many of the tools for ecology and evolutionary biology are the same ones as for bioinformatics, genomics, and systems biology.

I have tried to make this book fun to read, motivated by Mike Rosenzweig's writing in his wonderful book on species diversity (Rosenzweig 1995). There he asserted – and I concur – that because a book deals with a scientific topic in a technical (rather than popular) way, it does not have to be thick and hard to read (not everyone agrees with this, by the way). I have also tried to make it relatively short, by pointing out connections to the literature, rather than going into more detail on additional topics. I apologize to colleagues whose work should have been listed in the Connections section at the end of each chapter, but is not.

For the use of various photos, I thank Luke Baton, Paulette Bierzychudek, Kathy Beverton, Leon Blaustein, Ian Fleming, James Gathany, Peter Hudson, Jay Rosenheim, Bob Lalonde, and Lisa Ranford-Cartwright. Their contributions make the book both more interesting to read and more fun to look at. Permissions to reprint figures were kindly granted by a number of presses and individuals; thank you.

Nicole Rager, a graduate of the Science Illustration Program at UC Santa Cruz and now at the NSF, helped with many of the figures, and Katy Doctor, now in graduate school at the University of Washington, aided in preparation of the final draft, particularly with the bibliography and key words for indexing.

Alan Crowden commissioned this book for Cambridge University Press. His continued enthusiasm for the project helped spur me on. For comments on the entire manuscript, I thank Emma Ådahl, Anders Brodin, Tracy S. Feldman, Helen Ivarsson, Lena Månsson, Jacob Johansson, Niclas Jonzen, Herbie Lee, Jörgen Ripa, Joshua Uebelherr, and Eric Ward. For comments on particular chapters, I thank Per Lundberg and Kate Siegfried (Chapter 1), Leah Johnson (Chapter 2), Dan Merl (Chapter 3), Nick Wolf (Chapter 4), Hamish McCallum, Aand Patil, Andi Stephens (Chapter 5), Yasmin Lucero (Chapter 6), and Steve Munch (Chapters 7 and 8). The members of my research group (Kate, Leah, Dan, Nick, Anand, Andi, Yasmin, and Steve)

undertook to check all of the equations and do all of the exercises, thus finding bloopers of various sizes, which I have corrected. Beverley Lawrence is the best copy-editor with whom I have ever worked; she deserves great thanks for helping to clarify matters in a number of places. I shall miss her early morning email messages.

In our kind of science, it is generally difficult to separate graduate instruction and research, since every time one returns to old material, one sees it in new ways. I thank the National Science Foundation, National Marine Fisheries Service, and US Department of Agriculture, which together have continuously supported my research efforts in a 26 year career at the University of California, which is a great place to work.

At the end of *The Glory* (Wouk 1994), the fifth of five novels about his generation of destruction and resurgence, Herman Wouk wrote "The task is done, and I turn with a lightened spirit to fresh beckoning tasks" (p. 685). I feel much the same way.

Have a good voyage.

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