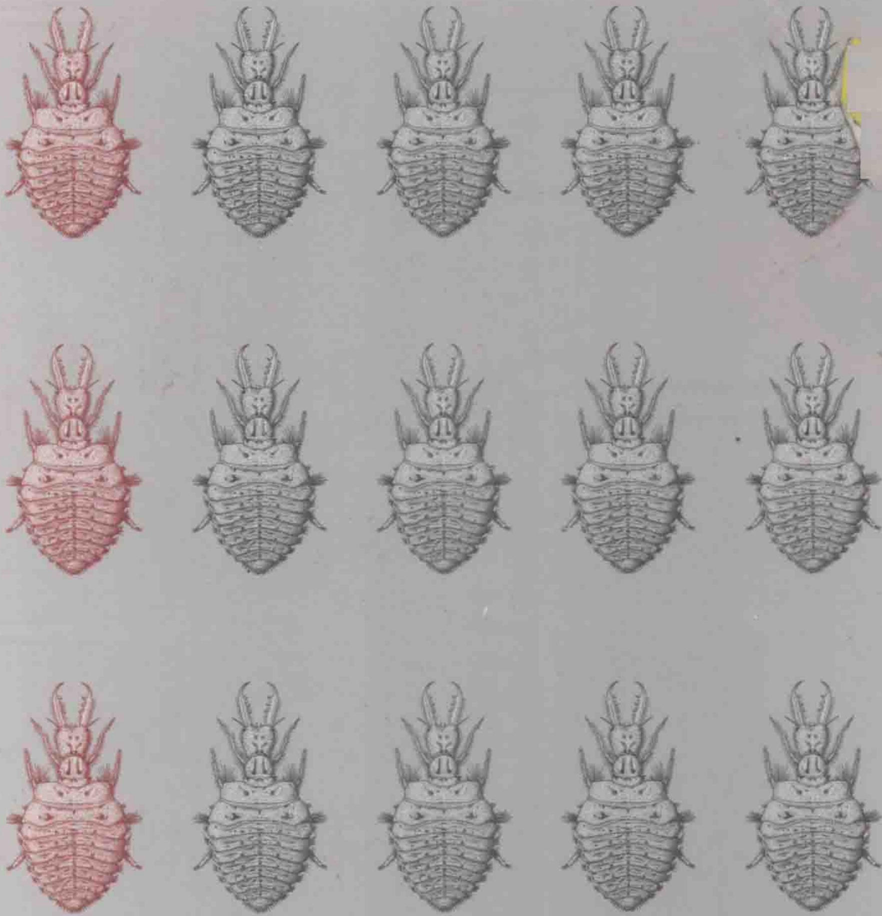
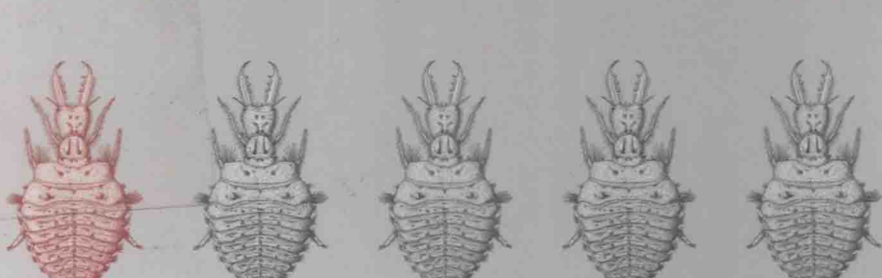


NICHOLAS J. GOTELLI

A Primer of Ecology



A Primer of Ecology

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The Cover

Third-instar larvae of the North American ant lion, *Myrmeleon immaculatus*. From *Demons of the Dust* by William Morton Wheeler (W. W. Norton, New York, 1930).

The Frontispiece

A portrayal of the complexity of ecological interactions in nature. Each chapter of the primer highlights a particular interaction from this figure. Original artwork by Shahid Naeem, University of Minnesota.

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Dedicated to my parents, Mary and Jim

Preface

I love to read ecology textbooks. The latest ecology texts are well-written and entertaining to read. They cover all aspects of ecology from population growth to ecosystem ecology and conservation biology. They present students with a balanced mix of theoretical, empirical, and applied topics, supported by a vast bibliography of hundreds of literature citations—everything from the "textbook classics" to the latest cutting-edge research. All this material is packaged in an attractive format, with color photographs, sophisticated graphics, and eye-pleasing type fonts. The downside is encyclopedic length and a hefty price tag for the student.

Despite their massive size, the new texts often fail in helping students with the single most difficult aspect of ecology courses: understanding mathematical models. Many texts exclude or dilute the mathematical and quantitative material, leaving students with a product that has been intellectually gutted. More traditional texts (and instructors) that do cover mathematical models also err by assuming the mathematical details are self-evident, glossing over the derivations, and failing to explicitly and concisely state the assumptions and predictions of the models.

My own pet peeve is the treatment of the exponential model of population growth. The exponential model is the basis for most population and community models, and is often used to introduce students to concepts such as continuous versus discrete population growth, population size (N), growth rate (dN/dt), and per capita growth rate $[(1/N)(dN/dt)]$. Without a firm understanding of these ideas, students cannot grasp more complex models. Yet most textbooks devote no more than a few pages, or even a few paragraphs, to the topic of exponential population growth.

THE ORGANIZATION OF THIS BOOK

This primer grew out of my dissatisfaction with existing textbooks and the fact that I could not relegate mathematical details of the models to "course readings." In this book, I have tried to present a concise but detailed exposition of the most common mathematical models in population and community ecology. Each chapter follows the same structured format:

Model Presentation and Predictions derives the models from first principles so students can see where the equations come from. Essential equations are highlighted, but a number of intermediate algebraic "expressions" are also presented so students can understand how we get from point A to point B. With the equations in hand, the predictions from the model are explained. I have relied heavily on graphical approaches, because they are often more enlightening than algebraic solutions of the equations. Although most of the models in this book are continuous differential equations, students do not need to integrate or differentiate equations to follow this material. Instead, I have emphasized the biological interpretation of the variables in the models and how the predictions change when the variables are altered. The material in this section of each chapter is covered in some form in nearly every introductory ecology course.

Model Assumptions lists the mathematical and biological assumptions behind the equations. This material is usually covered in most textbooks, but is often scattered or buried in the text.

Model Variations explains related models that can usually be derived by relaxing one or more of the critical assumptions. In this section, I have introduced topics that are suitable for advanced and graduate-level courses, including models of environmental and demographic stochasticity, stage-structured population growth, nonlinear predator–prey isoclines, intraguild predation, and passive sampling.

Empirical Examples includes two or three field studies that illustrate the utility of the models. The examples are restricted to field studies that actually measure parameters that are relevant to the models, although in many cases I was hard-pressed to find good examples. Often, the studies in which the models fail to predict patterns in nature are more enlightening than the apparent successes.

Problems give students the chance to work with the equations and understand their behavior by plugging in some numbers. The exercises are highly simplified "story problems," but they teach students how to apply the model concepts to empirical data and give them a better intuitive understanding of the equations. Fully explained solutions follow each problem set. Advanced problems that correspond to the material in "Model Variations" are marked with an asterisk.

Symbols and variable names are often a source of confusion for students. I have tried to use the symbols that are encountered in most ecology textbooks, but have made some changes for clarity and consistency. The primer includes very few literature citations, which are intended only to provide sources for the equations and examples. There is no glossary, but new terms are introduced in the text in **boldface type** to alert students to novel concepts.

THE CONTENT OF THIS BOOK

Chapters 1–4 cover models for single species, and Chapters 5–7 cover models for two or more species. In Chapter 1, the model of exponential growth is developed carefully from first principles. Advanced topics include environmental and demographic stochasticity. In Chapter 2, the logistic growth model is developed as an extension of the exponential model by incorporating density dependence in birth and death rates. Discrete growth with chaos, and random and periodic variation in carrying capacity are also described. Chapter 3 covers exponential growth for age-structured populations. Advanced topics include the derivation of the Euler equation, reproductive value, and stage-structured matrix models.

Chapter 4 reflects my own interests in metapopulation models. These models relax the unrealistic assumption of no migration of individuals and represent the simplest equations for open populations. There is a close analogy between the births and deaths of individuals in a local population and the colonization and extinction of populations in a metapopulation. There is also an important conceptual link between single-species metapopulation models and the MacArthur–Wilson model of island biogeography, which is developed in Chapter 7. Although metapopulation models are only just beginning to appear in textbooks, they are an important tool for studying population dynamics in a fragmented landscape, and may have applications in conservation biology.

Chapters 5 and 6 present the standard two-species competition and predation models, and include some more complex variations with nonlinear isoclines. Chapter 5 develops a model of intraguild predation, in which species function simultaneously as predators and competitors. Chapter 6 includes a discussion of host–parasite models and briefly addresses the problem of population cycles. Both chapters stress the use of the state-space diagram as an important graphical tool for ecological modeling. Chapter 7 presents the MacArthur–Wilson equilibrium model as one possible explanation for the species–area relationship. Habitat diversity and the passive sampling model are also offered as alternative hypotheses.

PRECEDENTS FOR THIS BOOK

This book was inspired by two earlier ecology texts. The first was *A Primer of Population Biology* by E. O. Wilson and W. H. Bossert. This remarkable book, first published in 1971, has been used by thousands of students. Its concise prose, modest size, and quantitative problems introduced a generation of students to mathematical approaches in ecology and population genetics. The second was *Theoretical Ecology*, edited by R. M. May. May's overview chapters provided a concise framework for Chapters 1, 2, 5, and 6 of this primer, which cover much of the same material in a greatly expanded form.

At the risk of overstating the obvious, this primer is not a substitute for a full-length ecology text. Because of its brevity, it completely ignores many important topics in ecology that are not amenable to treatment with simple mathematical models. I hope that its concise format and modest price will justify its use as a supplementary text. If this primer helps students to understand the development, application, and limitations of mathematical models in ecology, then I will have been successful.

SOME THOUGHTS FOR THE INSTRUCTOR

I designed this primer with two sorts of courses in mind. First, the primer can serve as a supplementary text for large, introductory undergraduate courses. The material covered in "Model Presentation and Predictions" and "Model Assumptions" assumes that students have had only a single semester of calculus, and have probably forgotten most of what they learned. In my large introductory course at the University of Vermont (> 100 students), I teach all the basic material in Chapters 1, 2, 3, 5, 6, and 7. Although I do not teach the equations from Chapter 4, I do cover basic principles of metapopulations and some empirical examples. The unstarred problem sets in all the chapters are appropriate for an introductory course.

I also use the primer in my community ecology course (< 25 students), which is taught to advanced undergraduates and beginning graduate students. In this course, I treat the introductory material as a concise review, and spend more time developing the material in "Model Variations." This advanced material assumes a minimal grasp of calculus, and an exposure to basic statistical concepts of probability, means, and variances. A knowledge of matrix algebra is helpful, but not essential, for the advanced material in Chapter 3. Both the unstarred and starred problems are appropriate at this level.

My hope is that the primer will be useful to two types of instructors. Those who prefer a quantitative approach, as I do, may use the primer as a template for lectures that build ecological models from first principles. Problem-solving is essential for such a course, and most of the problems at the end of each chapter work well as exam questions.

Other instructors may not wish to devote so much lecture time to models. For these courses, the primer may serve as a tutorial to allow students to learn the details of the models on their own. In this case, instructors might wish to place more emphasis on the model assumptions and empirical examples, and perhaps eliminate the problem sets entirely.

Ecology textbooks continue to increase in size and cost, making it difficult to justify a supplemental text. However, as good as the standard textbooks are, none of them treats the mathematical models with the care and detail they deserve. I hope *A Primer of Ecology* makes your teaching easier and helps your students to better understand ecological models. For me, this has always been the most challenging and rewarding part of teaching ecology.

February 28th, 1994
5° 33′ 20″ N, 87° 02′ 35″ W
Cocos Island, Costa Rica

Acknowledgments

First and foremost, I thank my students. Undergraduate and graduate students at the Universities of Oklahoma and Vermont forced me to slow down, speak plainly, and avoid jargon in my lectures. Their questions taught me what needed to be included in a primer of ecology. Andy Sinauer and his staff enthusiastically supported this project, transforming my text and rough drawings into a polished product. I thank Bobbie Lewis for copyediting the manuscript, and Shahid Naeem for his artwork, which graces the frontispiece and chapter headings. Janice Moore and Bob May encouraged me to accept the challenge of writing a primer, and Joe Schall taught me to keep the perspective of the average student while I wrote.

Each chapter benefitted from detailed reviews by a number of colleagues: Bob May, Janice Moore, Bob Ricklefs, and Joe Schall (1), Peter Stiling and Guiyun Yan (2), Hal Caswell (3), Bob Holt (4), Rob Colwell (5), Andy Dobson (6), and Mark Lomolino (7). Stewart Berlocher and Carol Boggs read the entire manuscript, and provided feedback from their undergraduates as well. Bob Ricklefs' critical review of Chapter 1 forced me to sharpen my prose throughout. The treatment of demography in many textbooks is confused and incorrect, and my initial draft of Chapter 3 was no exception. I thank Hal Caswell for reviewing this chapter twice and for setting me straight on a number of major and minor points.

Chapter 5 owes a special debt to Rob Colwell. The organization of this chapter, the restatement of the competitive exclusion principle, and the "milkshake analogy" were all taken from my undergraduate lecture notes from Colwell's community ecology course at the University of California, Berkeley (winter 1980). Andy Dobson encouraged me to include more quantitative material on predator–prey isoclines and provided me with a derivation of the disk equation from his own course lecture notes.

Chris Taylor double-checked all the problem sets and detected several typos and errors that would have frustrated students. Neil Buckley corrected my prose throughout and patiently helped me to read galley proofs. The National Science Foundation and the Fulbright Foundation supported my research while I wrote, and my graduate students cheerfully tolerated my preoccupation. Finally, I thank my wife and best friend, Maryanne Kampmann. She forced me to put down the guitar and get back to work, so that this primer was actually finished on schedule.

To the Student

The most common question beginning ecology students ask me is, "Why do we have to use so much mathematics to study ecology?" Many students enroll in my ecology course expecting to hear about whales, global warming, and the destruction of tropical rain forests. Instead they are confronted with exponential growth, doubling times, and per capita rates of increase. The two lists of topics are not unrelated. But before we can begin to solve complex environmental problems, we have to understand the basics. Just as a mechanical engineer must learn the principles of physics to build a dam, a conservation biologist must learn the principles of ecology to save a species.

The science of ecology is the study of distribution and abundance. In other words, we are interested in predicting where organisms occur (distribution), and the sizes of their populations (abundance). Ecological studies rely on measurements of distribution and abundance in nature, so we need the tools of mathematics and statistics to summarize and interpret these measurements.

But why do we need the mathematical models? One answer is that we need models because nature is so complex. We could spend a lifetime measuring different components of distribution and abundance and still not have a very clear understanding of ecology. The mathematical models act as simplified road maps, giving us some direction and idea of exactly what things we should be trying to measure in nature.

The models also generate testable predictions. By trying to verify or refute these predictions, we will make much faster progress in understanding nature than if we try to go out and measure everything without a plan. The models highlight the distinction between the *patterns* we see in nature and the different *mechanisms* that might cause those patterns.

There are two dangers inherent in the use of mathematical models in ecology. The first danger is that we build models that are too complex. When this happens, the models may contain many variables that we can never measure in nature, and the mathematical solutions may be too complex. Consequently, the most useful ecological models are often the simplest ones, and these have been emphasized throughout this primer.

The second danger is that we forget that the models are abstract representations of nature. However logical a model might appear, nothing says that nature must follow its rules. By carefully focusing on the assumptions of the model, we may be able to pinpoint the places where it departs from reality. As you will see from the examples in this primer, the models often tell us more about nature when their predictions do not match our field observations.

The purpose of this primer is to de-mystify the mathematical models used in ecology. Many of the equations in this primer can also be found in your textbook. However, your textbook may provide little or no explanation for where these equations come from, whereas the primer develops them step by step. I hope this primer will help you to understand the mathematical models and to appreciate their strengths and limitations.

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CHAPTER 1

Exponential Population Growth