AN INTRODUCTION TO METHODS & MODELS IN Ecology, Evolution, & Conservation Biology

STANTON BRAUDE &
BOBBI S. LOW
Editors

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Preface

Many biology courses are offered with laboratory sections that teach the techniques specific to that discipline as well as the broader tools of how we do science. While this text cannot replace the hands-on experience of an ecology lab, it does introduce many of the theoretical and quantitative tools of ecology, conservation biology, and environmental science, and often shows how they intersect.

The exercises in this text were written and piloted by a group of teachers committed to helping students experience the intellectual excitement of ecology and environmental science, even when their courses may not give them the opportunity to gather their own data out in the field. These exercises have transformed our discussion sections into "brains-on" thinking labs rather than "hands-on" technique labs.

You will see that every exercise asks you not only to read, think, and "digest" the content, but also to analyze the information in specific ways, both alone (before class) and with others (in class). This is deliberate—we too have fallen asleep in class when all we had to do was listen! And we have assigned some of the most difficult tasks to be solved in small groups of students so that collaborative learning can take place.

You will also notice that we choose very simple techniques, often using paper and dice, for example, when there exist computer programs that can do the same task in a fraction of the time. This, too, is deliberate. For almost all of us, what is actually done in a computer is a mystery, a Black Box of methodology, if you will. We think it is *essential* to understand the process first, especially in simulation modeling. In part, you can explain better to others what you have done, if you have actually performed the process, rather than simply entering data. It is also true that if you understand the process thoroughly, you will be better at catching problems in later computer runs—you will have an intuition about the approximate answer, so that if you have mis-entered a data point (e.g., 20 rather than 2.0), you won't slavishly copy the computer's answer. And, finally, you will be better prepared to explain computer simulations to others.

One of our aims is to show how, even though we do not typically recognize it, ecology (section I), demography and population biology (section II), and population genetics (section III) are all closely related. Further, all these fields require that you be able to do some forms of quantitative analysis (section IV), and to synthesize what others have done leading to our present understanding, and to think about the current state of affairs (section V). It is not intended that any one course would use all of the chapters you find here. But the subset chapters used in different courses will overlap very differently depending on the approach and interests of your instructor. You may have this book as a supplemental text in more than one course—in fact, even if you do not, we hope that you will find some unassigned sections useful in other courses.

Acknowledgments

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Special thanks go to James Robertson. In addition to authoring many of these chapters, James worked with many other contributors to design and develop their own chapters. He taught these exercises for five years; he is both an original biologist and a dedicated and creative teacher.

We would also like to thank Nancy Berg, Carl Simon, and Michael Low, who have read various chapters and provided extensive editorial help. Kate Malinowski taught herself *In-Design* and laid out the first draft of this text. Leah Corey, Carole Shadley, and Rebecca Martin very patiently compiled, edited, and formatted revisions.

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Introduction

WELCOME TO *An Introduction to Methods and Models in Ecology, Evolution, and Conservation Biology*. We hope you will enjoy using it. The fields of ecology, evolution, behavior, and conservation, although treated as separate topics, in fact are aspects of a large interdisciplinary core of knowledge with a common theoretical foundation—we hope you will find that the skills you acquire are useful in many contexts. The best work in all of these fields begins with hypotheses about "how things work" and proceeds to devise experiments or collect data to test clear predictions that are derived from the hypotheses. The point, of course, is to devise tests so that the answers will distinguish among *alternative hypotheses*—different explanations that cannot simultaneously be true.

You will also find that we do something that may strike you as a step backward: we ask you to do a lot of pencil-and-paper work, plotting things as you think them through, for example. This is actually deliberate. We have found (as we bet you have, too) that it's altogether too easy to "cookbook" a process such as a statistical test without actually understanding just what we are doing. Only if you really understand just what each equation, each process *does,* will you be able to know when to use each in new situations, and how to apply each to new data.

Just how you use this text will depend on the particular course(s) in which you are using it, so you may not begin at the beginning, or go through the chapters in a linear fashion. In fact, if this text has been assigned in one of your courses, you may find it useful (we hope so) in others. Do, please, browse through!

Section I focuses on the foundations of evolutionary ecology: natural selection, adaptation, phylogeny, and life history analysis. In section II, we examine more traditional ecological models, from the Lotka-Volterra competition and predator/prey models to MacArthur and Wilson's island biogeography model. In section III, we deal with the basic population genetic parameters so frequently involved in making conservation decisions, but which are rarely well understood. You will use these to design conservation programs, for example. Section IV is a bit different. These chapters are organized around quantitative tools that we need to examine a wide array of ecological systems. You may find that you return to the statistics chapters for years, as you work to understand statistical language in scientific papers or when you choose statistical tests for your own independent projects. Finally, section V has synthetic exercises we hope will help you pull together a variety of skills you have learned this semester in the service of making broad applied or theoretical arguments.

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Section I

Evolutionary Biology

1 Evolution and Pesticide Resistance: Examining Quantitative Trends Visually

Stanton Braude and John Gaskin

Introduction and Background

Evolution and natural selection have always been central concepts in the study of ecology. When German biologist Ernst Haekel coined the term "ecology" in the 1860s, he envisioned studying the forces of nature that were selective forces in the Darwinian sense. Darwin is popularly associated with the rise of evolutionary thought in biology; his major contribution was explaining natural selection—and the concept is so rich that we still find it fascinating to explore today.

Evolution is the term we use for changes in gene frequencies in populations or species over time. It is not the same as natural selection; in fact, evolution results from mutation, recombination, and drift, which generate variation but are not predictable, as well as from natural selection. So what is natural selection? It is the mechanism that drives adaptive evolution; the result of the simple fact that in any environment, depending on the conditions of that environment, some variants—individuals with specified genetic traits—survive and reproduce better than others. If we understand how any environment shapes traits, favoring some and disfavoring other individuals who possess those traits, we can predict how traits should match environmental conditions—and how populations will change over time. We will see this throughout this book, especially in this chapter, and in chapters 2, 4, 5, 18, and 19.

Ecology is a very empirical science, so it is not surprising that much ecology of the early twentieth century was descriptive. Ecologists today know that understanding natural selection and evolution is central to understanding important "why" hypotheses—especially today, when we humans change environments (and thus selective pressures) rapidly without necessarily understanding our impacts.

"Why" hypotheses can be of several sorts (Tinbergen, 1963). Hypotheses that explain why phenomena exist in nature are ultimate hypotheses, and those that explain how things work are proximate hypotheses. Both are important, but it is especially crucial not to confuse the two; it is confusing and wrong to offer a proximate answer to an ultimate question. For example: why do birds fly south for the winter? "Because individuals in this species in this region that migrate seasonally survive and reproduce better than those that do not" is an ultimate answer (and you can see all sorts of testable predictions: whether hummingbirds will migrate when seed-eating species will not; whether migration will be associated with seasonal changes, etc.). "Because changing day length causes shifting hormone levels" is a