

Preface

Imagine a field in which nearly all important theory is written in Latin, but most researchers can barely read Latin and certainly cannot speak it. Everyone cites the Latin papers, and a few even struggle through them for implications. However, most rely upon a tiny cabal of fluent Latin-speakers to develop and vet important theory.

Things aren't quite so bad as this in evolutionary biology. Like all good caricature, it exaggerates but also contains a grain of truth. Most of the important theory developed in the last 50 years is at least partly in the form of mathematics, the "Latin" of the field, yet few animal behaviorists and behavioral ecologists understand formal evolutionary models. The problem is more acute among those who take an evolutionary approach to human behavior, as students in anthropology and psychology are customarily even less numerate than their biology colleagues.

We would like to see the average student and researcher in animal behavior, behavioral ecology, and evolutionary approaches to human behavior become more fluent in the "Latin" of our fields. Increased fluency will help empiricists better appreciate the power and limits of the theory, and more sophisticated consumers will encourage theorists to address issues of empirical importance. Both of us teach courses to this end, and this book arose from our experiences teaching anxious, eager, and hard-working students the basic tools and results of theoretical evolutionary ecology.

How to use this book

While existing theory texts are generally excellent, they often assume too much mathematical background. Typical students in animal behavior, behavioral ecology, anthropology, or psychology had one semester of calculus long ago. It was hard and didn't seem to have much to do with their interests, and, as a result, they have forgotten most of it. Their algebra skills have atrophied from disuse, and even factoring a polynomial is only an ancient memory, as if from a past life. They have never had proper training in probability or dynamical systems. In our experience, these students need more hand-holding to get them started.

This book does more hand-holding than most, but ultimately learning mathematical theory is just as hard as learning a foreign language. To this end, we have some suggestions. In order to get full use of this book, the reader should:

1. Read the book in order. Each chapter builds on the last. After the first three chapters, it will be easier to jump ahead to topics of individual interest.
2. Work through examples within each chapter. Math is like karate: it must be learned by doing. If you really want to understand this stuff, you should work through every derivation and understand every step. Particularly involved derivations have been set in boxes, however, so that you can read the chapters at two levels, for general understanding and for skill development.
3. Work all the problems. At the end of each chapter, we provide a set of problems that elaborate upon the material in the chapter and allow the reader to practice the techniques we describe. The solutions to these problems are found at the end of the book. We encourage readers to attempt all the problems before looking at the solutions. We know these problems are solvable with only the tools presented in this book because our

own students have solved them. Some of the problems are subtle, however, and we encourage you to collaborate with your friends and fellow students when you attempt them.

4. Be patient, both with the material and yourself. Learning to understand and build formal evolutionary models is much like learning a language. This book is a first course, and it can help the reader understand the grammar and essential vocabulary. It is even a passable pocket dictionary. However, only practice and use of the language will build fluency. Students sometimes jump to the conclusion that they are stupid because they do not immediately understand a theoretical paper of interest. This is not justified. No one quickly learns to comprehend and produce mathematical arguments, any more than one can quickly become fluent in Latin.

The foundation of the foundations

Some reviewers of this book complained that some of the material is old fashioned. True, nearly all of Chapter 2 is 30 years old. The derivation of Hamilton's rule in Chapter 3 is hardly new either, at least to professional theorists. Most of Chapter 4 is old hat to mathematical social scientists, although biologists are unlikely to know much of it.

We think the vintage of the models is irrelevant for two reasons. One reason is that these models still have currency in important debates. But even if this material were no longer relevant to debates within the field (eventually this should be true), it would still be worth learning. Modern physicists do the bulk of their day-to-day work in mechanics using Lagrangian dynamics, a system more general and powerful than the classical Newtonian dynamics most of us learned in secondary school or college. Nonetheless, all physics programs teach Newtonian methods first because they are useful and easy to understand. In the same way, the simplest

game-theoretic and evolutionary models are worth knowing, even if, some day, they will no longer be applied in the day-to-day work of evolutionary theorists.

While this book provides a foundation for understanding the construction and analysis of formal models, it does not treat any of the topics exhaustively. At the end of each chapter, we provide a brief Guide to the Literature that directs interested readers to deeper treatments of the material.

Why so much algebra?

This book has lots of algebra. Much more, in fact, than many more-advanced texts in evolutionary theory. The reason is that beginning students need it. If you really want to learn this material, you have to follow the derivations one mathematical step at a time. Students that haven't done much math in a while often have a shaky grasp on how to do the algebra; they make lots of mistakes, and, even more important, don't have much intuition about how to get from point A to point B in a mathematical argument. All this means that they can find themselves stuck, unable to derive the next result, and unsure of whether they don't understand something fundamental or the obstacle is just a mathematical trick or algebraic error. Many years of teaching this material convinces us that the best remedy is to show lots of intermediate steps in derivations.

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The Theoretician's Laboratory

Mathematical models and the tools used to analyze them comprise the theoretician's laboratory. Since mathematical models are so intimately related to understanding the natural world, they drive important natural phenomena. The emergence of evolutionary theory and a variety of tools to study such a field, driving their growth to novel new frontiers, has taken place over long time scales, despite the evolution of theory. These models are almost always too simple to give a complete picture of even naturally occurring systems and behavior. Nonetheless, they have proven to be extremely valuable because they allow us to understand processes too complex to grasp by verbal reasoning alone.

Consequently, evolutionary biology has been greatly influenced by the use of such "experiments" in order to test the theory. The growth of evolutionary biology as a natural behavior, may have to be seen as being understood in mathematical models. Theoretical biology programs increasingly prepare new students and graduate students to read and understand mathematical theory. After which research is largely empirical, predictions are often derived from mathematical models,