MATHEMATICS

FOR THE LIFE SCIENCES:

Calculus, Modeling, Probability, and Dynamical Systems

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Preface

“Science is built up with facts, as a house is built with stones. But a collection of facts is no more a science than a heap of stones is a house.”

Jules Henri Poincare

There are a lot of connections between mathematics and biology, yet most students---and even many mathematicians and biologists---are unaware of these connections. One reason for this is that neither the historical development nor the pedagogical introduction of either subject involves the other.

Biology grew out of natural philosophy, which was entirely descriptive. Modern biology curricula generally begin with descriptive biology, either organismal or cellular. The mathematically-rich areas of genetics, ecology, and physiology make their appearance in advanced courses, after students have come to see biology as a non-mathematical subject.

Historically, the development of calculus and calculus-based mathematics was driven by the mathematical needs of physics, and it remains standard practice to use physics to motivate calculus-based mathematics. Other areas of mathematics, such as game theory and difference equations, were motivated to some extent by biology,[[1]](#footnote-1) but these topics appear in specialized courses generally taken only by mathematics majors. Probability is another mathematical topic with strong connections to biology; however, probability is generally encountered in statistics courses, which usually emphasize social science applications.

***The basic premise of this book is that there is a lot of mathematics that is useful in some life science context and can be understood by people with a limited background in calculus, provided it is presented at an appropriate level and connected to life science ideas.*** Every topic presented in this book was suggested by biologists and/or biochemists at the University of Nebraska-Lincoln. I have consulted with mathematicians throughout the United States concerning the best ways to present what are normally thought of as higher-level topics (requiring a thorough calculus background) to readers with limited calculus background.

Of course no book on mathematics for the life sciences can be complete. Some important areas do not appear here at all because they did not fall into the broad categories of mathematical modeling, probability, and dynamical systems. Several concessions have been made in the interest of accessibility. Some topics are given only a partial treatment as compared to the treatment they would receive in a higher-level course. Others are presented in a roundabout way.

A more detailed description of the contents appears in a separate section after this preface. Here I note only the broad features.

One feature of mathematical models that causes difficulties for students is the appearance of *parameters*, which are constants whose values are not necessarily assigned. Without parameters of unspecified value, a function is merely an example to be used for routine calculations. With parameters, a function can be a model, which can serve as an environment for theoretical experimentation. Even the reader with a solid background in calculus should study the initial section of Chapter 1.

The remainder of Chapter 1 can serve as a review of calculus or a conceptually-oriented calculus primer. This chapter is not a complete treatment of calculus, which would require far more space than is available in one chapter. I present here only those aspects of calculus that provide the necessary background for the modeling, probability, and dynamical systems that make up the rest of the book. The reader who works through this chapter is well equipped for the rest of the book, but does not have a thorough understanding of calculus. The material in this book has been used successfully with life science graduate students who had no background in calculus.

After the calculus primer comes a chapter on mathematical modeling, which is the necessary focus of any study of mathematics for those whose purpose is to use mathematics to better understand science. Even the most mathematical of topics, such as probability, are best seen by scientists from a viewpoint of mathematical modeling. Unfortunately for the science student, mathematical modeling has not been granted a separate place in the standard mathematics and science curricula. In mathematics books, we generally present the mathematical ideas first and then look for applications of these ideas to science. The result is a collection of idiosyncratic examples that the reader does not remember later when studying the related science topics. In science books, the mathematics is presented as a collection of formulas, to be used as facts when required. Neither approach teaches the basic skills of mathematical modeling. If we are to use mathematics to raise our understanding of the natural and physical world, we must focus on the connections of mathematics to science. *The muscles of mathematics are connected to the bones of science by the tendons of mathematical modeling.*

Chapters 3 and 4 present the basic ideas and some applications of probability, including applications commonly classified as statistics. The treatment given here is organized differently from the treatment of this topic in statistics or probability books. Mathematicians generally use an axiomatic approach to introduce probability. My colleagues in biology helped me appreciate that the central topic of probability for scientists is that of the probability distribution, and this topic can be approached more informally by thinking of a probability distribution as a mathematical model of a dataset. My aim has been to get to probability distributions as quickly as possible while saving other topics, such as conditional probability, for later. The essentials of probability distributions form the subject of Chapter 3. Chapter 4 includes additional topics that build onto or supplement the basic material on probability distributions.

The final three chapters introduce the mathematics of dynamical systems. A dynamical system is a system consisting of one or more quantities that change in time according to prescribed rules. These rules may be in the form of difference equations, where time is taken as discrete, or differential equations, where time is taken as continuous. It is usual to make this the primary distinction within the area of dynamical systems; however, there are valuable connections to be made between the two kinds, particularly for models with only one dynamic quantity. For this reason, I have chosen to treat all dynamic models of one variable together in Chapter 5 before presenting multivariable discrete systems in Chapter 6 and multivariable continuous systems in Chapter 7.

This is a mathematics book, but it is not a mathematics book for mathematicians. Mathematicians like to provide a mathematical definition for a concept and consider the meaning of the concept to be a consequence of the mathematical definition. Contrary to that plan, I prefer to begin with a functional definition and then present the corresponding mathematical definition as the solution of a problem. For example, I *define* the derivative to be the instantaneous rate of change (a functional definition rather than a mathematical definition). When we discover the mathematical formula for the derivative, I present that formula as a mathematical *result* that provides a mathematical definition equivalent to the functional definition. Mathematicians do not do this because the functional definition lacks the precision of the mathematical definition; however, I consider this to be a subtlety best left to advanced courses for mathematicians. My practice of beginning with functional definitions is particularly noticeable in the material on probability, where each distribution is defined according to its purpose rather than its mathematical representation.

Another point of disagreement between me and most other mathematicians is the extent to which mathematical results should be proved before being used. I like to joke that “a mathematician is someone who believes that you should not drive a car until after you have built one yourself.” At the risk of stern rebukes from my mathematics colleagues, I will say up front that I believe that the student should focus on how we use mathematical results to solve problems. For this goal, we need to know why mathematical results are true, but we do not need to know how we prove them to be true. An example here is the limit result needed to derive the formula for the derivative of the exponential function. The proof of this result appears in most calculus books and is indeed a beautiful piece of mathematics; however, understanding it does not help one compute derivatives or apply them to solve problems. Graphs and numerical computations strongly hint at the correct limit result; while not rigorous, these methods are more convincing to the mathematics student and use problem solving techniques that will be useful in other contexts.

Most of the sections are highly focused, often on one extended example. I have attempted to be brief, in the hope that readers will work harder to read a short presentation than a long one. I use examples as contexts in which to present ideas rather than instances where a formula is used to obtain an answer. Hence, the number of examples is limited, but each example is treated with some depth. Similarly, I include only a small number of figures. Each figure is essential to the presentation, and the reader should work hard to understand each one. Being able to explain[[2]](#footnote-2) a figure represents a high level of understanding.

Some mathematical modeling work must be done by hand, while other work is greatly facilitated by the use of computers. I view both hand methods and computational methods as tools in my modeling toolbox—I try to identify the best tool for any particular task without a bias either for or against technology. I do have a bias against using computers to do routine algebra and calculus; this stems from frequently encountering problems where valuable results can be found only with the careful use of algebraic substitution and simplification that requires a human touch.

There are a multitude of platforms for doing mathematical modeling tasks on computers. None of these is ideal, and the choice of which to use is a matter of taste. My preference is to work with one tool that, while not ideal for all uses, is reasonably good for any task (save symbolic computation) and is readily available. By these criteria, my choice is R, which runs smoothly in any standard operating system and is popular among biologists. R, like Matlab, is a programming environment. Spreadsheets provide easy access to mathematics because of their intuitive graphical interface; however, programming is limited and the details of formulas are hidden from view, making it impossible to see the overall structure of a program all at once. Compared to spreadsheets, programming environments have the enormous advantage of easy reusability. One can see an entire program at a glance and adapt prior work to a similar context with minimal changes. High-level languages, such as Java and C++, offer sophisticated programming capability, but they are difficult to learn compared to the languages used in programming environments such as R or Matlab. The choice between R and Matlab is a matter of personal taste. It is easier to get professional-quality graphics with Matlab, but R has more intuitive syntax that facilitates programming. Matlab requires an add-on toolbox for probability and statistics, while R requires supplementation for dynamical systems. R can be downloaded over the internet for free, but its help files are not as useful as the help files that come with Matlab. I use R because students can get it for free and install it seamlessly in any operating system. I maintain a collection of R scripts for various algorithms presented in the text, and these are readily available from my web page. These scripts are designed to be simple rather than robust; that is, compared to professionally written programs, they are easier to understand but less efficient and they lack error detection machinery.

There are quite a number of outstanding mathematical biology books at the advanced undergraduate and beginning graduate level, each with its own set of topics and point of view. These fine books are largely inaccessible to biologists simply because they require more mathematical background than most biologists have. My intention in this book is to help biologists to bridge the gap between the mathematics they already know and what they need to know to read these more advanced books.

Glenn Ledder, April 2012

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1. Leonardo of Pisa, more commonly known as Fibonacci, developed his famous sequence as the solution of a difference equation model of population growth. [↑](#footnote-ref-1)
2. An *explanation* includes context and analysis as well as mere *description*. [↑](#footnote-ref-2)