

Advances in Applied Mathematics

# DYNAMICAL SYSTEMS FOR BIOLOGICAL MODELING

## AN INTRODUCTION

Fred Brauer  
Christopher Kribs



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A CHAPMAN & HALL BOOK

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**DYNAMICAL SYSTEMS  
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MODELING**  
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# Advances in Applied Mathematics

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*to our children and grandchildren*



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# *Preface*

Some understanding of difference equations and differential equations is becoming essential for students in the biological sciences. There are several recent texts providing an introduction to mathematical biology through dynamical systems, but most of these are accessible primarily to students of mathematics with some interest in applications to biology rather than to biology students who have not (yet) developed a disposition to describe real systems in mathematical terms. Many of these texts present fully developed models of biological systems ready for mathematical analysis. Such models provide students with exercises in applying mathematical techniques but little experience in the (often iterative) translation of biological concepts into mathematical terms and vice versa, which is at the heart of modeling. It is our intention to try to address both of these issues, to prepare students of biology as well as of mathematics with the understanding and techniques necessary to undertake basic modeling of biological systems through the development and analysis of dynamical systems.

We propose to present an introduction to dynamical systems, covering both discrete (difference equation) and continuous (differential equation) types, for students who have had an introduction to calculus. While we assume that students have learned basic material including differentiation, integration, and exponential and logarithmic functions, we will recall topics which may not have made sufficient impression to have been absorbed completely and will describe some topics from a slightly different perspective. Our motivation will come from biological topics, including but not confined to population biology and epidemiology. Our approach will emphasize qualitative ideas rather than explicit computations; we feel that this approach is both easier for students whose primary interests are not in mathematics and more useful in many applications. This material is not, however, intended to serve as a differential equations course for students in the physical sciences as it does omit many techniques and topics that are essential for such students.

In presenting mathematical topics, we will attempt to tell the truth and nothing but the truth, but not necessarily the whole truth. We will try to emphasize the basic truths but not to overwhelm the student with precise technical detail. Some results will be stated without proof, while others will be accompanied by outlines of the reasons why they are true. We will normally avoid detailed, rigorous proofs.

Mathematics is not a spectator sport, and can be learned only by solving



problems. We include examples of problems with solutions and some exercises which follow the examples quite closely. However, a library of solved examples used as templates will not be sufficient to meet the needs of a developing scientist. For this reason, we also include problems that go beyond the examples, both in mathematical analysis and in the development of mathematical models for biological problems, in order to encourage deeper understanding and an eagerness to use mathematics in learning about biology. We also include some problems, marked with an asterisk (\*), which are more challenging.

We recommend the introduction to modeling in Chapter 1 as a beginning of any course on biological modeling using this text. The contents of Chapters 2 through 4 overlap considerably with the material which would be covered in a unified course (probably two semesters in length) which covers calculus and some difference equations and elementary differential equations. For students who have already taken such a course, a suitable course could review these topics as needed (after starting with Chapter 1) and then continue with Chapters 5, 6, and possibly 7. For students who have had a semester of calculus without difference or differential equations, a suitable course could consist of the first four chapters.

We provide some support for helping readers use software packages to generate numerical solutions and graphs (as we ourselves have done to make some of the figures in this book), primarily in the sections dealing with numerical analysis and in the appendices. These packages and the companies that produce them are listed below.

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The figures and photos accompanying discussion of the various biological systems studied and discussed play a crucial role in bringing the models (and their motivations) to life for the reader, and many appear in this work through the kind permission of others. We therefore acknowledge here all those who generously permitted us to print their photos, or helped us obtain permission: Donna Anstey, Francine Bérubé, Daniel Bowen, John Calambokidis, Tom Chrzanowski, Patricia Ernst, Carla Flores, Tim Gerrodette, Stefano Guerrieri, Ray Hamblett, Alan M. Hughes, Duncan Jackson, Russell S. Karow, Carolyn Kribs, Joel Michaelsen, Bernard E. Picton, Dave Powell, Francis Ratnieks, Helen Sarakinos, Howard Swatland, Michael Tildesley, and S. Bradleigh Vinson.

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Part I

Elementary Topics



