Preface

This book is intended as a text for a first course on creating and analyzing computer simulation models of biological systems. The expected audience for this book are students wishing to use dynamic models to interpret real data much as they would use standard statistical techniques. It is meant to provide both the essential principles as well as the details and equations applicable to a few particular systems and subdisciplines. Biological systems, however, encompass a vast, diverse array of topics and problems. This book discusses only a select number of these that I have found to be useful and interesting to biologists just beginning their appreciation of computer simulation. The examples chosen span classical mathematical models of well-studied systems to state-of-the-art topics such as cellular automata and artificial life. I have stressed the relationship between the models and the biology over mathematical analysis in order to give the reader a sense that mathematical models really are useful to biologists. In this light, I have sought examples that address fundamental and, I think, interesting biological questions. Almost all of the models are directly compared to quantitative data to provide at least a partial demonstration that some biological models can accurately predict.

As a result, I have generally kept the mathematical manipulations and requirements to a minimum. This is not a text in theoretical or mathematical biology; several of these already exist, and, being written by bonafide mathematicians, they have much to recommend them. The minimum mathematics needed for this book are statistics to the point of simple, single-variable linear regression, a small knowledge of probability distributions, and one semester of calculus.

The book is divided into two parts. The first, *Principles*, gives the basic steps that take a modeler from a biological question to a conceptual model to a quantitative specification of the system. The conversion of vague questions and ambiguous information into precise and quantitative mathematical forms is one with which biology students have the greatest difficulty. I have found that a set of heuristic "rules-of-thumb" applied to hypothetical situations is an effective teaching approach. Once these skills are mastered, the text describes techniques for constructing computer programs to solve the equations. Following this, methods to analyze computer output to answer the initial question are presented. These include equilibrium and stability analysis, sensitivity analysis, error analysis, and validation. The concepts developed in *Principles* apply to virtually any subject or question that can be addressed or formulated such that the answer can be gleaned from the dynamics of variables that describe the system (e.g., population size). Since the majority of biological theory is formulated in terms of differential equations, I stress techniques appropriate to "continuous systems" simulation.

The second part, *Applications*, is a series of chapters in which fundamental equations and problems from various biological disciplines are presented. Here I have tried to provide students and instructors with tools that will permit them to design their own course in biological modeling. By separating the details of subdisciplines from modeling fundamentals, I hope to provide a format in which a coherent portrait of the modeling enterprise can be obtained as well as background in modeling particular biological systems. Space, interest, and expertise have limited the suite of topics considered. Since my area of interest is ecology, I have perhaps stressed this field, but as most ecologists would admit, physiology and biochemistry are relevant fields. I include some fundamental equations and examples from these areas. The intent is not to give a comprehensive review of each topic; this is well beyond my expertise. Rather, I want to whet the students' appetites, providing enough background so that the references can be used in an intelligent manner and so that meaningful exercises can be attempted.

The process of modeling biological systems is certainly not a science, but neither is it as unconstrained as the creation of a work of pure art that is evaluated solely on its esthetic content. I prefer to analogize modeling with crafting a tool useful for human problem solving. To aid in the acquisition of this craft, I have provided problems and exercises for most of the chapters. Some of these require computer programming, and I have given an example using the C programming language. I believe C is rapidly becoming required for literacy in scientific computing. The very small amount presented in this book will give the reader a taste. A discussion of simulation languages and environments also provides access to other, relatively painless methods of implementing simulation models.

For the Instructors: There seem to be two methods for teaching quantitative and mathematical methods in biology: present a large number of models from many biological disciplines and expect the commonalities and principles to emerge on their own; or, present a set of modeling fundamentals extracted from general principles with relatively few examples and hope that students learn to apply the principles to new situations. Both methods have advantages and disadvantages; I like the latter approach, as the structure of the book suggests. Nevertheless, I have tried to accomodate both and I hope those of you favoring the former teaching style will find the book useable.

For the Students: At my university, I use this book in a course for seniors and new graduate students. It really is an introduction to the subject insofar as someone, somewhere, has already written an entire book on the subject of each chapter. If you are in a considerably earlier stage in your academic career and find the book approachable, consider yourself fortunate to be smart and to have had good teachers.

While the author cannot claim to be smart, he has been fortunate to have had good teachers over the years. It seems appropriate to mention three of them here not so much as to afix blame, but to recognize their contributions. Thanks to Charles Warren, Scot Overton, and George Innis. Finally, this book in whole and in part has been examined by a number of my friends, notable among them being Linda Abbott, Susan Durham, Laura Hartt, Upmanu Lall, Alice Lindahl, Keith Mott, Darcie Neff, Jim Powell, Kirk Steinhorst, and former students in my graduate classes. While their efforts were valiant, unintentional errors remain. Remember: *Never attribute to malice anything that can be attributed to stupidity.*