MODELING IN NATURAL RESOURCE MANAGEMENT

DEVELOPMENT, INTERPRETATION, AND APPLICATION

EDITED BY

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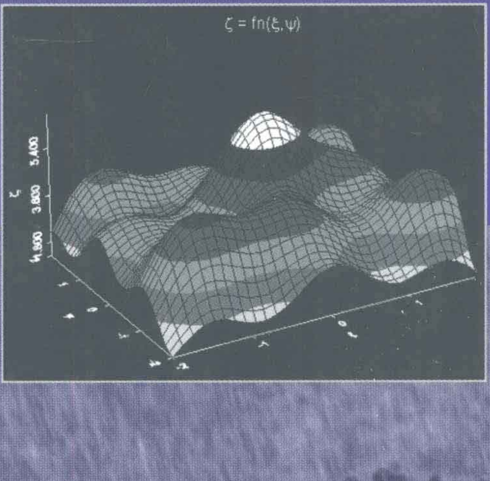

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Foreword

Every day, the men and women engaged in natural resource management use models. Indeed, nearly every decision they make concerning the management of natural resources is based on a model of one kind or another. Some of these models are mental constructs of the system in question. Others may describe statistical relationships in natural resource data. Still other models are simulations of populations or ecological systems. The natural environment is so complex that simplification through an abstraction is necessary to communicate concepts and relationships concerning different components of the ecosystem, to comprehend possible reactions of natural resources to manipulation, and to decide a course of action in conservation.

Though we all use models or abstractions in our everyday lives, learning systematically about theories and types of models can seem a formidable task. Eyes sometimes take on a zombielike glaze when viewing page after page filled with mathematical equations: chloroform in print. These equations, however, may represent the beauty of a process. They may describe how we make decisions about our finances, our social lives, and our leisure time—decisions we often take for granted.

This book presents an overview of the many facets of modeling to help natural resource managers and scientists overcome their fear of models. The book is for the nonmodeler who wants to explore this mysterious thing called modeling as well as the modeler who wants to explore model validation and the use of models in the decision process. Undergraduates just discovering models and their uses will find this book of tremendous benefit. Yet even the seasoned modeler will enjoy exploring many of the ideas. In fact, these veterans may discover in this simplified presentation basic explanations of sophisticated techniques in modeling that will help them express their ideas to others.

The book is based on an all-day symposium titled "How to Practice Safe Modeling: The Interpretation and Application of Models in Resource Management." This title must have caught the attention of many—if the large audience for this symposium in 1997 during the fourth annual conference of The Wildlife Society in Snowmass, Colorado, is any indication. The symposium was sponsored by the Biometrics Working Group of The Wildlife Society. Because one of the working group's primary goals is to communicate and promote sound use of quantitative applications in wildlife management and science, this forum had a fourfold objective: to clarify the differences among model types, to explore their strengths and weaknesses, to examine the role of modeling in making inferences for natural resource management, and to demonstrate how various models further our understanding of processes and applications for natural resource management. As a member of the audience, I learned something new from each of the speakers. I also felt that each of these four objectives was met with outstanding success.

The symposium's organizers and speakers, as well as the entire Biometrics Working Group, wanted to pass on all that we had learned. With that end in mind, everyone concerned with making this book a reality has worked diligently to synthesize the vast body of knowledge concerning models and their use in natural resource management. Each chapter has been edited carefully and reviewed by at least two outside referees. Authors and referees alike have worked to ensure that this information is usable to a broad audience. The reviewers are listed at the back of the book and deserve hearty thanks for a job well done.

The contributors were selected from the many experts in natural resource modeling and wildlife management. They have taken their work for this book seriously. The information you find here is clear and will be easily understood by managers, ecological researchers, and others interested in the application of models. Modeling can appear to be a complex, mystical, highly technical, and challenging task. Each author, however, has attempted to simplify, demystify, and paint a realistic picture of modeling and the use of models in natural resource management and science. This task was not easy, but the fruits of their labor should prove useful for natural resource professionals.

Two people at the forefront of this effort have devoted themselves wholeheartedly to the project. Without their organizational skills, tenacity, and all-around hard work, this book would never have made it into your hands. Tanya Shenk and Alan Franklin had a vision concerning the need for this body of information about modeling. They organized the symposium and edited this book. Although these tasks take only a short paragraph to mention, their efforts represent a great deal of thought and dedication. The Biometrics Working Group, The Wildlife Society, and natural resource professionals everywhere should be proud to have two such dedicated people as part of their membership.

The Biometrics Working Group hopes you will find this book useful. Through efforts like this, we foresee a promising future for the application of models to problems of natural resource management. And ultimately, through this improved application of models to research and management, our natural resources should benefit from better decisions.

STEVEN L. SHERIFF
1997 Chair of the Biometrics Working Group
The Wildlife Society

Acknowledgments

This book was developed from a symposium given at the fourth annual conference of The Wildlife Society. We thank the participants of that symposium for their excellent presentations that stimulated the development of this book. We also thank the officers and members of the Biometrics Working Group of the Wildlife Society, especially Christine Bunck and Steve Sheriff, who actively supported the project from its inception.

Thanks are extended as well to the contributors. We invited these authors to contribute chapters because of their expertise in natural resource modeling. Each chapter, therefore, represents their expert summation of ideas, viewpoints, and supporting evidence for the development, interpretation, and use of models in natural resource management.

We also wish to thank the many reviewers who contributed their time and expertise to this project (see "Reviewers" at the end of this volume). Each chapter was reviewed by two referees and was further enhanced by their comments.

As novices to the process of publishing, we especially thank Barbara Dean of Island Press for her guidance in bringing this book to fruition. Barbara spent many extra hours helping us through each step. We are also grateful to Barbara Youngblood and Cecilia González at Island Press for their careful work in preparing the manuscript for production.

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Chapter 1

Models in Natural Resource Management: An Introduction

Tanya M. Shenk and Alan B. Franklin

We began our careers as field biologists who were primarily interested in natural history. Although we still consider ourselves field biologists, at some point in our careers we recognized the importance of modeling—not only for understanding the natural world but also for guiding natural resource management and developing conservation strategies. There are many types of models, modeling approaches, and actual models being used in natural resource management. We found it a challenge to learn the roles of various models in science and management as well as explore the strengths and weaknesses of these models and modeling approaches. Remembering how we ourselves struggled to integrate modeling into our work, we felt the need for an introductory overview of the critical components of modeling—an overview that would explain how models are developed and used appropriately in natural resource management. Recognizing the potential for capturing such a wealth of knowledge in a single printed volume, we pursued the development of a book that would concentrate the best and most current information about modeling.

This book focuses on the fundamental components of development, interpretation, and application of models in natural resource management.

It is not a blueprint for how to develop specific models. Rather, it presents the basic principles for understanding and evaluating models. Above all, we view this book as a primer designed to demystify models. Each chapter emphasizes how models should be constructed and interpreted and highlights how models can be used and misused. For those already familiar with modeling, the book is a refresher course because many of the principles presented here include recent progress in developing and interpreting models—such as model selection and evaluation—and approaches to individual and spatially explicit modeling. We have divided the book into three parts. Part I, "Overview of Models," provides a conceptual framework for the book by defining what models are and how the different classes of models fit into the process of science. Part II, "Developing and Interpreting Models," discusses the key components necessary for addressing the question "Is this model appropriate and useful for the question at hand?" Here we build on the first part of the book by presenting chapters that discuss different modeling paradigms and explain how models can be evaluated. Part III, "Applying Models," shows how models are used in natural resource management and looks ahead to the future use of modeling in both the science and management of natural resources.

When talking about models, it is impossible to avoid the use of mathematics. Thus a number of the chapters include mathematical equations. For many in our profession, mathematical equations cause frustration and disinterest. We hope these readers will focus first on the philosophy and approaches espoused by the various authors and then on the details to become more informed about the mathematics of modeling. As the science of modeling progresses, so too will its application to natural resource management problems. Application of models requires the same understanding we need to develop the model: we have to comprehend models in order to use them appropriately. Most important, managers who are presented with a model that proposes solutions must be able to evaluate whether the model is appropriate for the problem at hand. Decisions based on biological knowledge and caution, for example, may be more appropriate than those that rely on a complex model replete with untested assumptions and based on sparse data. While such a complex model may appear more like "science," it cannot provide reliable knowledge (see Romesburg 1981).

Our primary goal is to communicate to two very different groups of readers: scientists involved with natural resource management and managers who apply models to real-world problems. These groups often speak different "languages," and communication between them is usually less than ideal. In developing each chapter, we asked authors to present their material in a manner that would be clear to the general reader but would also be acceptable to their own peers.

THE ROLE OF MODELS

As natural resource professionals, we meet the term *model* everywhere in the scientific literature and planning documents. And as models are frequently developed to guide management decisions, natural resource professionals must understand what models are and learn their strengths and weaknesses. A common misconception is that a model is a complex, computer-driven set of rules and equations that mysteriously produces a result. Indeed, the term *model* has often become synonymous with models that are computer-intensive, yet there are many types of models that serve different purposes. Models range from the very simple—a simple linear regression equation is a model—to the very complex.

James D. Nichols (Chapter 2) defines three classes of models: theoretical, empirical (statistical), and decision-theoretical. Each class functions at different stages of the scientific method. The management objective determines which class should be developed. Theoretical models, for example, are developed to suggest mechanisms and thus lead to predictions even before data are collected (see Mangel et al. in Chapter 4). Popper (1962) proposed that advances in science come from the rejection of hypotheses. Given the time constraints imposed on natural resource managers, it may be frustrating to see the ever increasing production of theory that appears to impede the process of science in an endless cycle of hypothesis generation. Yet theorists contribute to the scientific method by suggesting new ways of looking at problems—a worthy attribute in scientific investigation. The concept of a suite of alternative hypotheses must always be given a high priority in inductive scientific process (see Franklin et al. in Chapter 5). And it is theoretical models that formulate these alternative hypotheses.

Statistical models, by contrast, are used to make inferences from data (see White in Chapter 3). If estimating a parameter such as survival or recruitment is the objective, for example, a statistical model is the most appropriate approach to meeting it. Statistical models may also be used to test hypotheses. Maurer (1998) suggests that statistical analysis of several complex hypotheses requires the complementary skills of theoreticians and empiricists. Theoreticians must develop models that are empirically testable—models with parameters for which rigorous empirical estimates can be obtained. Field ecologists must know the relevant theory and be prepared to design sophisticated experiments and observational studies that provide data to analyze the models developed by theoreticians. Model selection (see Franklin et al. in Chapter 5) can be used to evaluate the plausibility of each theoretical hypothesis within a suite of hypotheses to explain the data—thus merging the use of theoretical and statistical models.

The third class is decision-theoretical models. Too often we hear that research does not address the concerns of natural resource managers. This complaint is often justified. Researchers and managers must collaborate more effectively in addressing key problems. But natural resource managers must frequently develop management plans before hypotheses are tested or research is complete. Decision-theoretical models can be used to indicate which decisions are likely to meet management objectives in light of uncertainty and dynamic systems. Models based on adaptive management results (see Kendall in Chapter 10) or on optimizing decisions (see Conroy and Moore in Chapter 6) can be used in such situations.

Using models to address specific issues in natural resource management has led to the development of various disciplines. Population viability analysis is one such modeling discipline (see Boyce in Chapter 8); wildlife resource selection is another (see McDonald and Manly in Chapter 9). Investigating the effect of individual heterogeneity on population demography has led to the development of individual-based models (see DeAngelis et al. in Chapter 11). With the proliferation of models has come a parallel concern about their validity. Douglas Johnson (Chapter 7) outlines the problems associated with validating models and suggests approaches to model evaluation. Since the utility of a modeling procedure is hampered when biological input is ignored, a collaboration among managers, field biologists, and modelers is the most efficient means for solving natural resource problems. (See Clark and Schmitz in Chapter 12; Anderson et al. 1999.)

HOW MODELS ARE USED: AN EXAMPLE

Early attempts to predict population growth stemmed from specific concerns about human population growth and economically important species (see Cole 1957). Before the eighteenth century, however, no modeling or formulation of any general concepts other than the balance of nature was inferred from studies on population growth (McIntosh 1985). In his *Essay on the Principle of Population,* Thomas Malthus (1798) recognized that population abundances were constrained within bounds set by the availability of the space and resources required by individuals. The implications of this essay stimulated both Charles Darwin and Alfred Russel Wallace to formulate their concepts of natural selection and the idea that environment limits populations, which then led to the concept of population regulation.

Howard and Fiske (1911) were the first to propose the role of *density* to explain changes in population abundance. In their work on the control of pest insect populations by parasites, they distinguished between "facultative" and "catastrophic" mortality factors. Catastrophic factors, such as storms, were defined as those that destroyed a fixed percentage of a population without regard to population density. Facultative factors, such as predators or parasites, destroy a greater proportion of individuals within a population as the population increases. These facultative factors later became part of the theory of density-dependent population regulation. Replacement of the terms *catastrophic* and *facultative* with *density-independent* and *density-dependent,* respectively, followed the work of Smith (1935).

Parallel to the development of the theory of density-dependent populations, mathematical descriptions—that is, models—of population growth with respect to some equilibrium density were suggested. The most successful attempt, the logistic equation, was proposed by Verhulst in 1838 (Kingsland 1985), but the equation was not widely acknowledged at the time. Later, however, Pearl (1927) developed and successfully promoted the same population growth equation. Several laboratory experiments supported the logistic equation as an accurate model of population growth (Pearl and Parker 1922; Gause 1934). Field data, however, were equivocal in their support of density-dependent population growth. Although Lack (1954) provided evidence of logistic population growth in many bird populations, Andrewartha and Birch (1954) concluded that population growth of Australian thrips was related more to weather than to density. They argued that most populations, insects and small invertebrates in particular, are influenced primarily by density-independent factors.

Strong opposition followed the claims made by Andrewartha and Birch. Nicholson (1954) in particular argued that within a balance-of-nature framework, population densities continually move toward a stable level in relation to fluctuating environmental conditions. He suggested that a regulating mechanism must limit populations by operating with greater severity as population abundances approach stability. Nicholson (1954) proposed that interspecific competition was the density-dependent controlling factor. The Cold Spring Harbor Symposium on Quantitative Biology held in 1957 addressed the controversy over these competing models of population regulation. Eventually, the theoretical model of density-dependent regulation became widely accepted. Interest then turned to the detection of density dependence in natural populations using empirical (statistical) models. This focus on statistical models sparked a minor controversy of its own, however, centered on the form of the statistical model to use and what data were appropriate for testing density dependence in a natural population. (See the review in Shenk et al. 1998.) Given the controversy at the time over the existence of density dependence, a natural resource manager responsible for developing conservation strategies would have benefited from decision-theoretical models designed to predict the outcomes of various management strategies (that is, models that incorporated density dependence and models that did not).

HOW MODELS ARE MISUSED: AN EXAMPLE

Models are misused when invalid inferences are made from their results. Invalid inferences are made when poor data or incorrect estimation procedures are used in the model or when an inappropriate model is used. A 13-year controversy between C. H. T. Townsend, an entomologist, and I. Langmuir, a Nobel Prize–winning physicist, over the flight speed of male deerflies provides an example of invalid inferences stemming from the misuse of models (see Wenner 1989).

Townsend (1926) claimed that male deerflies were capable of flying 818 mph. His velocity calculations were based on poorly estimated times and distances, which he observed traveled by a deerfly. Townsend published his findings, ignoring the inaccuracies of the data used to calculate his estimate and without fully exploring or understanding the implications such a flight speed would have for an insect. In his publication he noted that a flight speed of 818 mph would allow the fly to go around the world in a "daylight day" [*sic*], a world flight record. After publication, the record, but not the flight speed, was challenged. Townsend took this as support for the flight speed and went on to model the wing structure of the fly that would allow for such speed.

With the publication of the wing structure model, the flight speed was finally challenged by Langmuir (1938) based on the biological infeasibility of a fly attaining such speed. Using a series of established mathematical models relating velocity, resistance, power, and force, he established that a flight speed of 818 mph traveled by an object the size of a deerfly would have resulted in (1) pressure high enough to crush the insect, (2) greater energy requirements than could be met by the fly, (3) a force on impact that would penetrate human flesh, and (4) rendering the fly invisible in flight. Thus, using appropriate theoretical models, Langmuir refuted Townsend's flight speed and proposed his own flight speed of 25 mph. Despite Langmuir's strong evidence against the probability of his published flight speed, Townsend (1939) continued to support his own estimated flight speed of 818 mph and wing structure that would allow it.

This example highlights how models can be misused. First, Townsend used poor data to model flight speed and, secondly, he did not fully explore the implications of his results. Had he worked with someone more familiar with the mathematics of flight, such as Langmuir, he might have avoided making the invalid inference of an impossible flight speed for the deerfly. Ignoring both of these flaws, however, he continued to build on his estimate of flight speed to develop a model of the design of the fly wing to support such speeds, a model that would clearly be wrong. Lastly, despite strong evidence to the contrary, he continued to support his single, pet hypothesis and avoided altogether any notion of competing hypotheses and model selection. Although Langmuir did not misuse models, he never evaluated his own model. He could have contributed more had he worked with a field biologist to collect data on observed flight speeds to evaluate his own proposed flight speed of 25 mph.

In natural resource management, an analogous situation would be the use of poor or sparse data in a model whose results are then incorporated into a management plan that is implemented but never evaluated in terms of its success or failure to meet its objective. Such scenarios could be avoided if all the professionals involved (managers, researchers, model developers) had a better understanding of the development, interpretation, and application of models to ensure that both the biology and the mathematics are sound (see Clark and Schmitz in Chapter 12).

We designed this book to help the reader understand the kinds of models available and how to interpret and evaluate them for use in natural resource management. The book is directed to natural resource managers, who must make decisions based on models, and to researchers who use models to improve their understanding of scientific and management questions. While the scientific literature has addressed specific topics, there is no single source compiling the multitude of issues and viewpoints relevant to the development, interpretation, and application of natural resource models. This book begins to fill the gap.

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