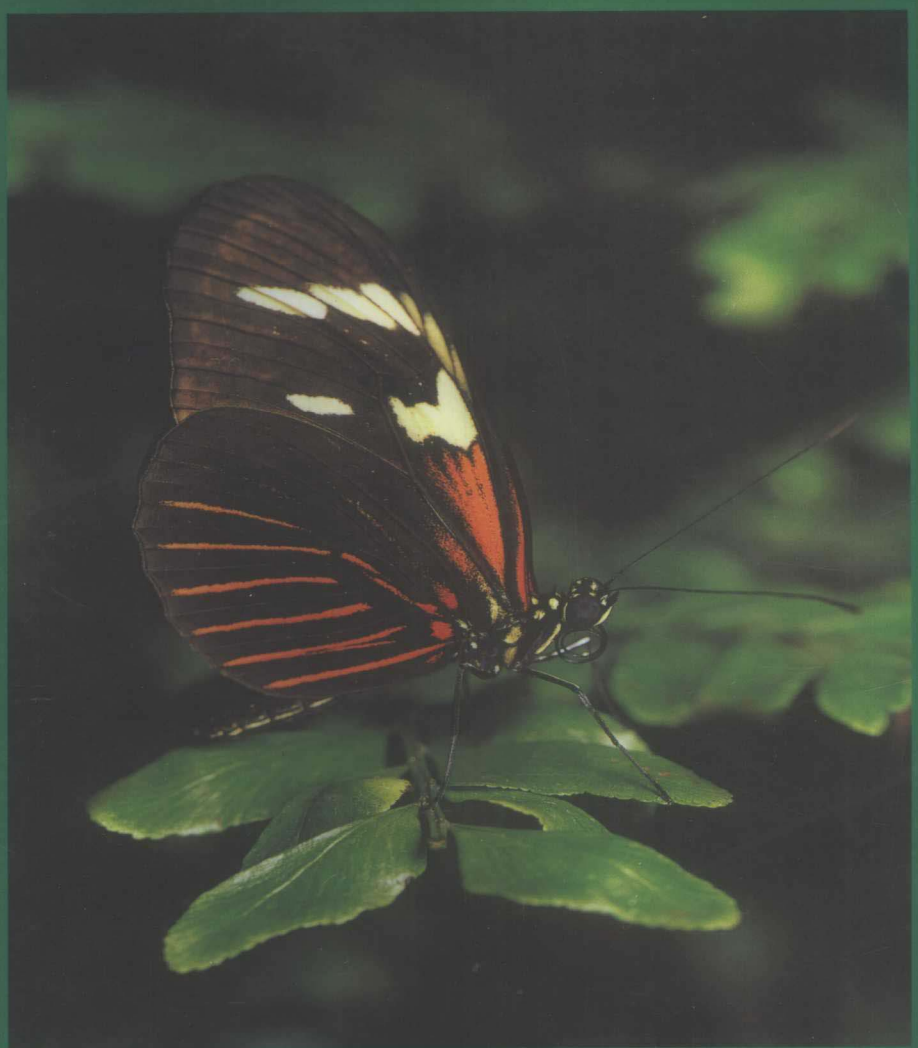
国外生命科学优秀教材

ECOLOGY

生态学（第五版）

（影印版）

Charles J. Krebs



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生 态 学

（第五版 影印版）

Ecology: The Experimental Analysis of Distribution and Abundance

(Fifth Edition)

Charles J. Krebs

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内 容 简 介

本书是生态学领域颇享赞誉的教材，目前已出版到第五版。在生物种群和生物群落水平上探讨了生物的分布和多样性，并在涉及生态学的基础知识和研究方法的基础上，讨论了生态学中许多有关生物分布和多样性还具有争论性的问题。该书的编排体例更易于理解，较同类书具有更多的有关数量、分析和统计上的生态学信息，重点论述了生态学实验的目的，使学生对生态学有更深入的认识。其基础知识较全面，知识量较大，较适合高等院校相关专业的师生以及致力于环境保护和自然规划人员使用。

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Charles J. Krebs

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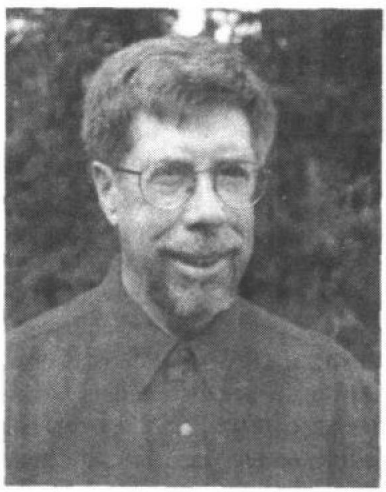
To the Unknown Ecologist

who works without recognition to preserve the
ecological integrity of the Earth for our grandchildren
and who measures riches not in stocks and bonds
but in biodiversity

ABOUT THE AUTHOR



While growing up in St. Louis, I became interested in polar exploration and read every book in the library about the arctic. I was fortunate to get a summer job working on the Pribilof Islands in the Bering Sea, and have been a northern ecologist ever since. I began my studies in wildlife management at the University of Minnesota, and moved to Canada to do graduate work at the University of British Columbia in 1957. After a Ph.D. on lemming populations in the Canadian arctic, I moved to Berkeley to do a Miller Postdoctoral Fellowship with Frank Pitelka. I finally got a proper job at Indiana University in Bloomington in 1964 and began teaching ecology to undergraduates. It was clear to me that there was a shortage of teaching material in ecology, and in particular there was no text that captured the Eltonian approach to ecology through population and community dynamics. I began writing this book in 1967 and the first edition appeared in 1972. One of the great joys of writing a textbook is meeting people all over the world who used my text during their education. Through five editions I have tried to track the progress of ecological science, and it is a sign of progress that ecologists are now recognized all over the world for their contributions to wise management of our natural heritage.

I am currently Professor of Zoology at the University of British Columbia in Vancouver. In addition to teaching ecology, I have worked extensively on the population of rodents in northern Canada, the United States, and Australia, trying to understand the mechanisms behind population fluctuations. I have written three ecology textbooks including *Ecology: The Experimental Analysis of Distribution* and *Abundance, Fifth Edition* and *Ecological Methodology, Second Edition* both published by Benjamin Cummings

PREFACE

YOU ARE LIVING IN THE AGE OF ECOLOGY, and as a citizen you ought to learn something about this subject. There has been a revolution of human thinking in the last 30 years that has centered on the relationship between humans and their environment. The broader policy problems this revolution has brought forward are the focus of the environment movement, the applied scientific problems, and the focus of environmental science. The basic science behind it all is the science of ecology. Sustainability is the mantra of all our politicians, and environmental problems are now a common subject in the daily newspapers.

Just as it is useful to know something about physics if you wish to be an engineer, it is useful to learn something about ecology if you wish to understand the problems humans face with sustaining their environment. This text is dedicated to presenting to you the outlines of the science of ecology. If you understand how the natural world works, you will be better poised to understand the Age of Ecology as it unfolds, to think with an ecological conscience.

Two dilemmas face the textbook writer. First, the writer must plot a course that will place the book serenely between the pitfalls of the past and the bandwagons of the present. We all recognize the pitfalls of the past, and any text has an obligation to point out some of these lest history repeat itself. We do not do as well at recognizing the pitfalls of the present-at recognizing which of the current bandwagons in ecology are enduring and which are ephemeral. Science, like most subjects of human endeavor, is subject to bandwagons, only some of which are useful for our long-term understanding. Second, the writer must create a textbook that pleases not only the students but also their instructors. I have strived to make this book readable, and the greatest compliment any text can get is that students think it readable and interesting.

Each chapter in this book attempts to raise a question about how populations and communities operate in nature, and to give you enough information that you can think about it intelligently. If you need more information, a list of suggested readings is a good starting point. Each chapter ends with a series of questions and problems that are devised to stimulate thought. I have not provided answers to these questions. For many of them the answer is not yet known. An overview question at the end of each chapter is a still more general question that may be the focus of a class discussion. Many overview questions are action-oriented. A key focus of much ecological thought ought to be "What are the practical consequences of this idea?"

In this edition I have added chapters on the population dynamics of disease and parasitism, and on ecosystem health and human impacts. I have tried to emphasize the historical development of ecology by adding photos of famous ecologists in each chapter. Science is a human activity and the scientists who have built ecology and are building it today are themselves interesting characters worthy of more recognition. I have extensively revised many of the chapters, particularly those on conservation biology, community organization, and primary production, and strengthened the integration of evolutionary and functional ecology. Conservation biology is a focus for practical problems that cry out for ecological understanding and is one of the strong growth points of ecological science. Many of the attempts to converse biodiversity hinge on concepts of community organization that need careful thought and analysis. Many chapters deal with ecological attributes and their evolutionary background. Ecologists can benefit by stepping back and looking at ecological systems in a revolutionary perspective, and students of evolution can benefit from knowing how ecological systems function, for they cannot otherwise understand natural selection. I have added essays in many chapters to illustrate some of the kinds of problems and ques-

tions ecologists deal with in their attempt to understand nature.

This book is my own attempt to present modern ecology as an interesting and dynamic subject. Beneath the variety of approaches that characterize modern ecology lie a few basic problems that I have attempted to sketch. I have placed special emphasis on problems and have illustrated them by examples chosen as diversely as possible from the plant and animal kingdoms. This book is not an encyclopedia of ecology but an introduction to its problems. It is not descriptive ecology and will not tell students about the ecology of the seashore or the ecology of the alpine tundra. It approaches ecology as a series of problems, problems that confined neither to the seashore nor to the alpine tundra but are sufficiently general to be studied in either area.

To understand the problems of ecology, students must have some background in biology and mathematics. Students will find that they can understand ecology without knowing any mathematics but that mathematics is necessary for those who wish to proceed beyond the simplest level of analysis. Ecology is not a haven for people who cannot do mathematics, and in this respect it is no different from chemistry and physics. Statistics and calculus are useful but not essential for an understanding of this book. I present mathematical analyses step by step and illustrate them with graphs. Students who cannot follow the mathematics should be able to get the essence of the arguments from the graphs.

The problems of ecology are "biological" problems and will be solved not by mathematicians but by biologists. Students will find that, contrary to the impression they get from other sources, the problems of ecology have not all been solved. A start has been made in solving many ecological problems, and I cannot give the "answer" to many of the problems I discuss. Controversies are common in ecology, and an important part of ecological training is appreciating the controversies and trying to understand why people may look at the same data and yet reach opposite conclusions.

Students can learn much about the science of ecology by analyzing one of its controversies. If you think that ecologists have the answer to most of our environmental questions, you will be surprised when you look into the variety of ecological controversies. Controversy is not a sign of weak science, and to appreciate controversies you should try to find out the scope of the controversy and what kinds of observations are needed to solve it. Many of the environmental controversies of our day, like climate change, involve a mixture of scientific facts and policy decisions. Scientific facts alone do not determine policy, but policy without a solid scientific grounding is doomed. The relevant scientific facts are never completely known for many environmental problems, and we must decide what to do in the face of uncertainty. Interim policy decisions always point out the need for more scientific analysis, and there must be a continuous feedback loop between policy and all the environmental sciences, including ecology.

Good ecology is quantitative. At the end of many of the quantitative chapters, problems are included because no one can appreciate the quantitative aspects of ecology without going through some of the calculations. Most of the calculations are simple, but I have tried to leave some of them open-ended so that interested students can carry on under their own steam.

If there is a message in this book, it is a simple one: Progress is answering ecological questions comes when experimental techniques are used. The habit of asking, "What experiment could answer this question?" is the most basic aspect of scientific method that students should learn to cultivate. When there is controversy, asking this question can cut to the heart of the matter.

Technical terms in this book are kept to a minimum; labeling with words should not be confused with understanding. The glossary of technical words, together with the indexes, should be adequate to cover technical definitions.

I thank my many friends and colleagues who have contributed to formulating and clarifying the material presented here. In particular I thank my colleagues Dennis Chitty, Judy Myers, Jamie Smith, Carl Walters, and Tony Sinclair for their assistance, and Brian Walker and the many ecologists at CSIRO Wildlife and Ecology in Canberra who answered endless queries during this version. For a detailed critique of the revision I am indebted to John C. Horn, St. Ambrose University, Davenport, IA; Alan Stam, Capital University, Columbus, OH; Merrill Sweet, Texas A&M University, College Station, TX; John Baccus, Southwest Texas State University, San Marcos, TX; Ralph J. Larson, San Francisco State University, San Francisco, CA; Mary Wicksten, Texas A&M University, College Statuibm TX; Stephen G. Tilley, Smith College, Northampton, MA; Robert Bailey, Central

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Thanks to Elizabeth Fogerty, Heather Dutton, and Chriscelle Merquillo at Addison Wesley who did more than their share of editorial work to help improve this edition. Finally I want to thank the real authors of this book, the hundreds of ecologists who have toiled in the field and laboratory to extract from the study of organisms the concepts discussed here. A person's life work may be boiled down to a few sentences in a book, and we ecologists owe a debt that we cannot pay to our intellectual ancestors.

Charley Krebs

CONTENTS IN BRIEF

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(continued)

(Chapter 6, continued)