

Manuel C. Molles Jr.

second edition



# ECOLOGY

Concepts and Applications

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Manuel C. Molles, Jr.

University of New Mexico



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# ABOUT THE AUTHOR

**Dr. Manuel Molles** is Professor of Biology at the University of New Mexico, where he has been a member of the faculty and curator in the Museum of Southwestern Biology since 1975. He received his B.S. from Humboldt State University in 1971 and his Ph.D. from the Department of Ecology and Evolutionary Biology at the University of Arizona in 1976. The author has sought to broaden his geographic perspective by teaching and conducting ecological research in Latin America, the Caribbean, and Europe. He was awarded a Fulbright Research Fellowship to conduct research on river ecology in Portugal and has held visiting professor appointments in the Department of Zoology at the University of Coimbra, Portugal, in the Laboratory of Hydrology at the Polytechnic University of Madrid, Spain, and at the University of Montana's Flathead Lake Biological Station.

Originally trained as a marine ecologist and fisheries biologist, the author has worked mainly on river and riparian ecology at the University of New Mexico. His research has concerned a wide range of ecological levels, including behavioral ecology, population biology, community ecology, eco-

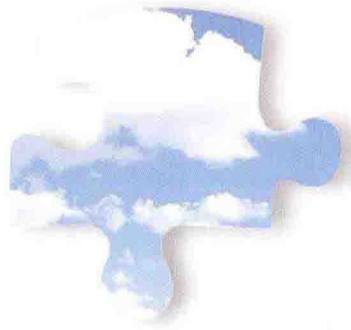
system ecology, biogeography of stream insects, and the influence of a large-scale climate system (El Niño) on the dynamics of southwestern river and riparian ecosystems. His current research concerns the effects of flooding and exotic vegetation on the structure and dynamics of the Rio Grande riparian ecosystem.

Throughout his career, the author has attempted to combine research, teaching, and service, involving undergraduate as well as graduate students in his ongoing projects. At the University of New Mexico, he has taught a broad range of lower division, upper division, and graduate courses, including Principles of Biology, Evolution and Ecology, Stream Ecology, Limnology and Oceanography, Marine Biology, and Community and Ecosystem Ecology. He has also taught courses in Global Change and River Ecology at the University of Coimbra, Portugal, and Groundwater and Riparian Ecology at the Flathead Lake Biological Station. Dr. Manuel Molles was named Teacher of the Year by the University of New Mexico for 1995–96 and Potter Chair in Plant Ecology in 2000.



*To Bobbie,  
Hani, and  
Anders*





# PREFACE

About 2,500 years ago, the Greek philosopher Zeno proposed a paradox that captures the challenge faced by ecology instructors and their students. In the tale of Achilles and the Tortoise, Zeno argued that if a fast runner, such as the mythical Achilles, gave a tortoise a head start in a race, he could never overtake it. Zeno proposed that since there are an infinite number of points between him and the tortoise, Achilles never catches up. Modern mathematics has solved this paradox and we can take comfort that, even in Zeno's theoretical universe, Olympic runners can overtake tortoises. However, there is a place where Zeno's arguments appear to hold, and that is in the world of teaching dynamic scientific disciplines such as ecology.

The challenge to ecology instructors and their students is much greater than that faced by Achilles—greater because instructors and students are matched against a much swifter opponent with a longer head start. As they attempt to cover the space between the beginning and end of this subject, the rapid pace of discovery moves the limits of the discipline ahead, not at the speed of a tortoise but at that of a hare. Zeno would be very happy in this universe because here, the instructor and students can never catch up. However, with careful organization and modern tools, such as the World Wide Web, they can come close.

In an address at the 1991 meeting of the Ecological Society of America in San Antonio, Texas, eminent ecologist Paul Risser challenged ecology instructors to focus their attention on the major concepts of the field. If we subdivide a large and dynamic subject, such as ecology, too finely, we can not cover it in one or two academic terms. Risser proposed that by focusing on major concepts, however, we may provide students with a robust framework of the discipline upon which they can build.

This book attempts to address Risser's challenge. Each chapter is organized around two to four major concepts to present the student with a manageable and memorable synthesis of the subject. I have found that while beginning ecology students can absorb a few central concepts well, they can easily get lost in a sea of details. Each concept is supported by case histories that provide evidence for the concept and introduce students to the research approaches used in the various areas of ecology. Wherever possible, the original research and the scientists who did the research are presented. Allowing the scientists who created this field to emerge from the background and lead students through the discipline breaths life into the subject and helps students retain information.

## AUDIENCE

I have written this book for students taking their first undergraduate course in ecology. I have assumed that students in this one-semester course have some knowledge of basic chemistry and mathematics and that they have had a course in general biology that included introductions to physiology, biological diversity, and evolution. An evolutionary perspective forms the foundation of the entire discussion. Evolution is brought to center stage throughout the book, as it is needed to support understanding of major concepts. My choices about coverage and depth of study are based on the past 20 years of teaching ecology to undergraduate students. With these students in mind, I organized the book as follows.

## ORGANIZATION

The discussion begins with a brief introduction to the nature and history of the discipline of ecology, followed by section I, which includes two chapters on natural history—life on land and life in water. My intent is to establish a common foundation of natural history upon which to base the later discussions of ecological concepts. The introduction and natural history chapters can stand on their own and should be readily accessible to most students. They may be assigned as background reading, leaving 20 chapters to cover in a one-semester course. Sections II through VI build a hierarchical perspective; section II concerns the ecology of individuals; section III focuses on population ecology; section IV presents the ecology of interactions; section V summarizes community and ecosystem ecology; and finally, section VI discusses large-scale ecology and includes chapters on landscape, geographic, and global ecology. These topics were first introduced in section I within a natural history context. In summary, the book begins with the natural history of the planet, considers portions of the whole in the middle chapters, and ends with another perspective of the entire planet in the concluding chapter.

## NEW FEATURES IN THIS EDITION

The three new chapters, 7, 8, and 12, written for this edition, are intended to strengthen coverage of behavioral and evolutionary ecology. Chapter 7, "Social Relations," concludes

section II of the book and introduces behavioral ecology. This chapter extends the discussion of the ecology of individuals in section II to interactions between individuals within the social environment. Chapter 7 focuses on mate choice and sexual selection and the evolution of sociality. Case histories demonstrating mating ecology are drawn from studies of guppies, scorpionflies, and wild radish. The discussion of sociality draws from extensive studies on cooperation among woodhoopoes and African lions, emphasizing the concepts of inclusive fitness and kin selection. The Applications and Tools section continues the discussion of sociality through a comparison of eusocial species as a way of introducing the comparative method.

Section III is introduced by a new chapter 8, titled "Population Genetics and Natural Selection." Chapter 8 presents the conceptual basis for evolutionary ecology through case histories concerning genetic and phenotypic variation in populations, the Hardy-Weinberg equilibrium model, changes in the genetic structure of populations due to random processes, and natural selection. The case histories, as in all parts of the book, attempt to include a wide variety of plant and animal studies and to balance vertebrate with invertebrate animal coverage. The coverage also emphasizes a historical perspective that spans the beginnings of evolutionary ecology through very recent work, employing modern tools and perspectives.

Chapter 12, titled "Life Histories," is the third new chapter. This chapter concludes the section on population ecology and provides additional evolutionary perspective. The case histories in chapter 12 begin with a discussion of the trade-off between offspring size and number, further developing the "principle of allocation" introduced in chapter 6, while the second set of case histories concerns the relationship between adult survival and age at first reproduction. The case histories in chapter 12 conclude with a classification of life histories, beginning with *r* versus *K* selection and ending with a classification of life histories that proposes opportunistic (*r*), equilibrium (*K*), and periodic life histories as alternative evolutionary trajectories. Again, the chapter develops parallel discussions of plants and animals throughout. It ends with an Applications and Tools section showing how knowledge of plant life histories is being used to restore riparian forests in western North America.

## Learning Aids

All chapters beyond chapter I feature the following learning system:

**Introduction** The introduction to each chapter presents the student with the flavor of the subject at hand and important background information. Some introductions include historical events related to the subject and present an example of an ecological process. All attempt to engage students and draw them into the discussion that follows.

**Concepts** The goal of this book is to build a foundation of ecological knowledge around key concepts. The concepts are listed after the chapter introduction to alert the student to the

major topics to follow, and to provide a place where the student can go to find a list of the important points of each chapter.



- Uneven heating of the earth's spherical surface by the sun and the tilt of the earth on its axis combine to produce predictable latitudinal variation in climate.
- The geographic distribution of terrestrial biomes corresponds closely to variation in climate, especially prevailing temperature and precipitation.

**Case Histories** Illustrating concepts with case histories provides a narrative that reinforces the concepts, supports them with evidence, and introduces students to the methods and people that have created the discipline of ecology. My presentation approximates the case-studies approach that has worked well for my former students who have gone on to schools of law and medicine.

**Applications and Tools** Many undergraduate students want to know how abstract ideas and general relationships can be applied to the ecological problems facing us all. They are concerned with the practical side of ecology and want to know more about the tools of science. It is for these students that I have included a chapter section called Applications and Tools. It is clear to professional ecologists that addressing the practical side of ecology is aided by a knowledge of the abstract and theoretical sides of the field. However, many undergraduates have not yet reached this stage of development. I have found that including a few applications in my courses motivates students to learn more of the underlying principles. In addition, it seems that environmental problems are now so numerous and so pressing that they have erased a once easy distinction between general and applied ecology.

**Summary** The chapter summary reviews the main points of the content. The concepts around which each chapter is organized are boldfaced in the summary to reemphasize the main points of the chapter.

**Review Questions** The review questions are designed to help students think more deeply about each concept and to reflect on alternative views. They also provide a place to fill in any remaining gaps in the information presented and take students beyond the foundation established in the main body of the chapter.

**Suggested Readings** Each chapter ends with a list of suggested readings. Though all of the readings take the student beyond the coverage in the chapter, they have been chosen to serve a variety of purposes. Some are books that provide a broad overview; others are papers that trace the development of particular concepts or controversies in ecology. I have provided a brief description and rationale for each.



**On the Net** The World Wide Web provides one of the most powerful tools to help keep abreast of changes in ecology. A broad range of applicable Internet sites are just a click away on the Online Learning Center that accompanies this edition. Practice quizzing, articles on current ecological and environmental issues, and a variety of teaching aids are also available online at <http://www.mhhe.com/ecology>.

**References** are an important part of any scientific work. However, I have found that many undergraduates are distracted by a large number of references within the text. Undergraduates in a general ecology course are usually in a state of transition. Their scholarship has advanced beyond a general biology course, but they are not yet accomplished researchers. One of the goals of a general ecology course should be to introduce these students to the primary literature without burying them in citations. With this goal in mind, I have reduced the number of citations to those necessary to support detailed discussions of particular research projects. References cited are listed at the end of the book.

## Illustrations

Finally, a great deal of effort has been put into the development of illustrations, both photographs and line art. The

goal has been to create more effective pedagogical tools through skillful design and use of color and to rearrange the traditional presentation of information in figures and captions. Much explanatory material has been moved from captions to illustrations to provide students with key information where they need it most. The explanatory boxes used in this text are unique and not available in any other ecology textbook.

## SUPPLEMENTARY MATERIALS

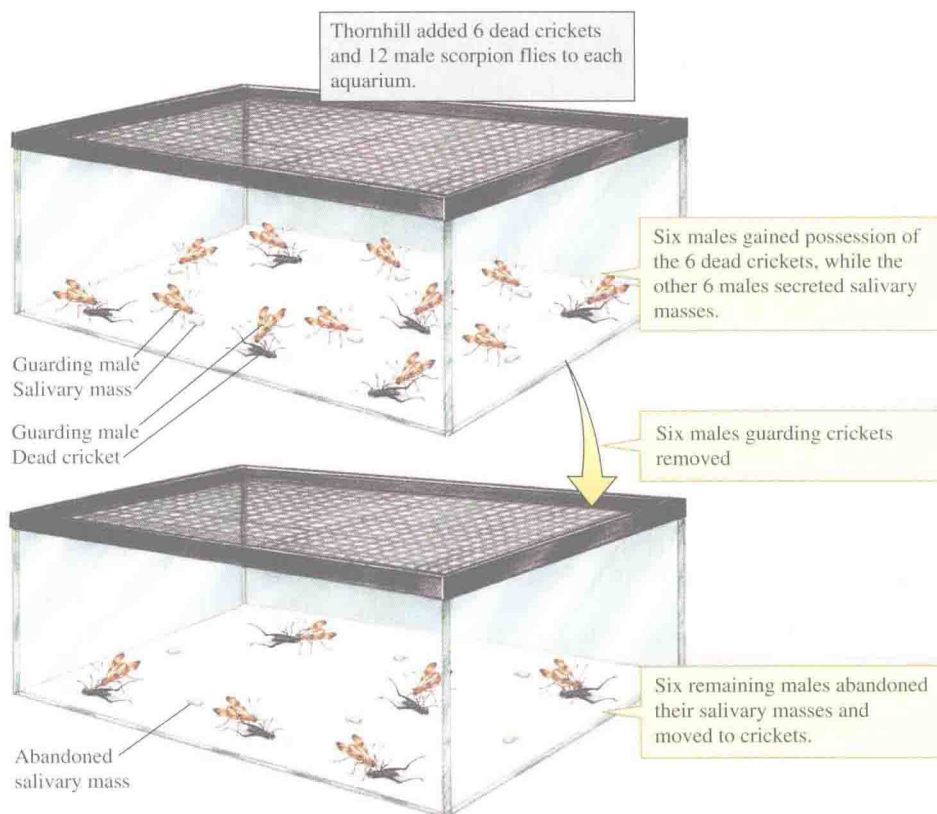
### Instructor's Manual and Test Item File

The complimentary Instructor's Manual and Test Item File is designed to assist instructors as they plan and prepare for classes using *Ecology: Concepts, and Applications*. Relevant films, videotapes, and computer programs are included in the manual, as well as a listing of the transparencies that supplement the text. The Test Item File offers 40 to 50 questions per chapter, including multiple-choice, fill-in-the-blank, and true/false questions.

## ON THE NET

Visit our website at <http://www.mhhe.com/ecology> for links to the following topics:

- Biomes and Environmental Habitats
- Tropical Rainforests
- Temperate Forests
- Savannah
- Grasslands
- Deserts
- Tundra
- Taiga
- Land Use: Forests and Rangelands
- Tropical Rain Forests and Land Use Issues
- Nontropical Forests and Land Use Issues
- Rangelands and Land Use Issues
- Atmosphere, Climate, and Weather



**FIGURE 7.11** Experimental test of the influence of nuptial offerings on mating success by male scorpionflies (information from Thornhill 1981).



## Classroom Testing Software

This helpful, easy-to-use, computerized test-generating software is available at no charge to instructors for testing and grading.

## Transparencies

A set of transparencies of 100 key figures from the text are available free to instructors.

## Laboratory Manuals

*Laboratory manual for General Ecology*, 8th ed., by Cox. This lab manual has been revised to correlate with *Ecology: Concepts and Applications*, 2nd ed.

*Field and Laboratory Methods for General Ecology*, 4th ed., by Brower, Zar and Von Ende.

## Titles of Related Interest

*Conservation Biology*, 2nd ed., by Cox.

*Connections in Environmental Science*, by Mayer.

*Environmental Science: The Study of Interrelationships*, 7th ed., by Enger and Smith.

*Environmental Science: A Global Concern*, 6th ed., by Cunningham and Saigo.

*Principles of Environmental Science*, by Cunningham and Cunningham.

*Environmental Problem Solving Wordbook: A Case Study Approach*, by Heathcote.

*Annual Editions: Environment 00/01*. Editor: John L. Allen.

*Taking Sides: Clashing Views on Controversial Environmental Issues*, 8th ed. Editor: Theodore D. Goldfarb.

*Sources: Notable Selections in Environmental Studies*. Editor: Theodore D. Goldfarb.

*The Dushkin Student Atlas of Environmental Issues*. Editor: John Allen.

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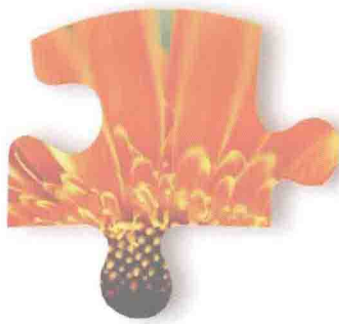
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