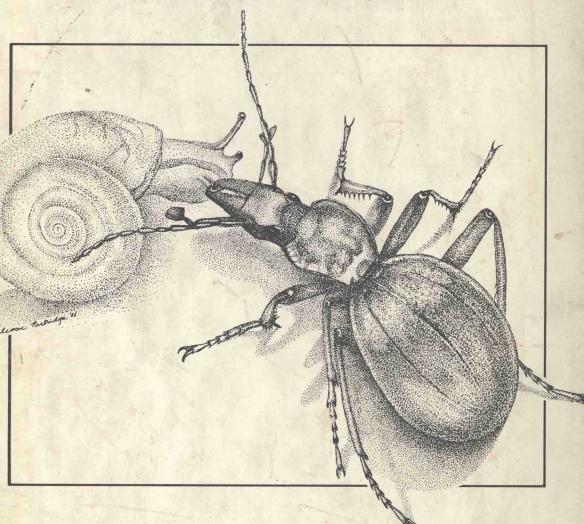
# INSECT ECOLOGY

Second Edition



Peter W. Price

## INSECT ECOLOGY

**Second Edition** 

PETER W. PRICE

Department of Biological Sciences Northern Arizona University Flagstaff

A WILEY-INTERSCIENCE PUBLICATION

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## INSECT ECOLOGY

#### **PREFACE**

This book is intended as a text for courses relating to the general area of insect ecology at the advanced undergraduate and graduate student levels. Central concepts in ecology are developed throughout and related to insect ecology. All ideas are illustrated with examples from the insects and other organisms, so that a tangible link is made between concept, theory, and the real world. Mathematical treatments are kept simple. Emphasis throughout the book is on understanding insects in nature and how conceptual ecology can enrich our enjoyment of these fascinating animals. A guiding principle has been to familiarize the reader with the general ecological literature while emphasizing the important role that studies on insects have played in developing ecological thought; the significance of insects as members of communities and ecosystems; and their value in resolving many debates in ecology.

My intention in each chapter has been to develop a subject as far as space will allow, but not to allow space to limit the reader's developing interest. Therefore, I have provided many references to literature that develops areas in more depth, enabling the reader almost limitless exploration of the subject.

The potential for rapid evolution in insects is well known, so it would be unrealistic to consider ecology as a subject isolated from evolution. Insects also relate to each other and their environments through their behavior. As a result ecology must integrate evolutionary and behavioral aspects of the organism's life, so that it meshes almost imperceptibly into the subject of evolutionary biology. These themes and links will be seen throughout the book.

Another level of integration that the study of insect ecology forces is between plant and animal ecology. Insects are extremely important as herbivores, and in order to understand the plant-herbivore interaction, plants as resources need to be studied in much more detail than in the past. This interaction is discussed in many chapters.

I have also emphasized in this second edition some areas of ecology that have not received enough attention in the past from ecologists. Size and scaling in insect design offer a link between ecological physiology and vi Preface

ecology and define many aspects of the way in which insects relate to their environment. Chapters on insect parasites and insect mutualists have been added because these kinds of interactions are just as important as predation in nature. This coverage is not usually seen in modern ecology textbooks.

In the second edition I have also included a chapter on modeling insect population dynamics. I consider this an important addition because progress in this area is rapid and real breakthroughs in understanding natural populations are likely to emerge in the near future; emphasis on modeling is common in insect pest management programs; and there are few sources where a student can find an introductory treatment of the subject.

Major additions in the second edition are necessarily compromised by deletions, to keep the book from growing outrageously. I have had to keep to central issues in general ecology, restraining the subject matter to the area between ecological physiology on the lower end of levels of integration and more applied areas of ecology, such as agricultural ecology, and biological control of weeds and insect pests.

My major objective has been to make the subject of insect ecology as interesting and exciting for the reader, as it is for me.

PETER W. PRICE

Flagstaff, Arizona March 1984

### PREFACE TO THE FIRST EDITION

This book is written as a text for a course for advanced undergraduates and graduate students in entomology. In selecting material for this book it has been difficult to decide how much general ecology and how much entomological material to incorporate. A guiding principle has been to familiarize the reader with the general ecological literature while emphasizing the important role that studies on insects have played in ecological thought, the significance of insects as members of communities, and their potential value in resolving many debates in ecology. Since insects have been herbivores probably longer than any other terrestrial animals, and since they are the most important herbivores in many communities, they offer an ideal opportunity for integration of plant and animal ecology. I have attempted this integration in various chapters, since the ecology of plants, as a food source for many insects, is necessarily involved in the understanding of insect ecology.

The content of each chapter has been determined to some extent by the availability of other texts. Because methods in insect ecology have been expertly covered by Southwood (1966), these are not emphasized in this text. Andrewartha and Birch (1954), Clark et al. (1967), and Varley et al. (1973) provide good introductions to studies on insect population dynamics. The experimental approach to insect ecology is treated by Lewis and Taylor (1967). Several excellent books on biological control of insects and weeds are mentioned in Chapter 12, and pest management is covered in Metcalf and Luckmann (1975), therefore applied aspects of insect ecology are not treated in detail in this book. Apart from the deemphasis on areas of insect ecology mentioned above I have aimed at a comprehensive treatment of the subject. Such a treatment has not been attempted since Chapman's (1931) Animal ecology with special reference to insects, and Andrewartha and Birch's (1954) The distribution and abundance of animals. I hope that the contents of this text will offer some measure of the extent to which the subject has grown since these two books were published. This text also diverges from those mentioned above in using in several chapters an evolutionary approach to ecology. This approach seems appropriate for dealing with a group of animals that, because of their large numbers, high mortality per generation, and short generation time, evolve very rapidly.

PETER W. PRICE

Urbana, Illinois March 1975

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P. W. P

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## Part I INTRODUCTION

The subject of ecology covers a wide range of topics, from molecular properties such as enzyme systems adapted to function well under certain environmental conditions, to organismal, population, community, and ecosystem structure and function. The two introductory chapters of this book deal with the ends of this continuum of relationships, discussing major components and processes in ecosystems (Chapter 1), and how small organisms such as insects relate individually to an environment that inevitably constrains their design and activity in nature (Chapter 2).

Much of ecology is devoted to identifying and understanding patterns in nature. Ecology could be defined as the science devoted to the development and study of theories of natural history of organisms. Such theories can relate to cellular processes in relation to environmental factors, all the way up to global patterns. A framework for considering theories and concepts in ecology is provided by discussing major processes in ecosystems.

Ecology can be defined also as the science of relationships of organisms to their environment. How they relate depends on their structure. Thus a chapter dealing with aspects of insect design seems fundamental to understanding their ecological relationships. Ideally, one would enter the field of insect ecology with a detailed knowledge of insect body form and function obtained, perhaps in a course on insect physiology, including environmental physiology, or in a course on the physiological ecology of insects. To cover such material in this book would double its size, making it unreasonably large. Therefore only the link is provided in Chapter 2 between central aspects of ecology and those of physiology.

These chapters set the stage for considering intermediate levels of interaction involving trophic relationships (Part II), populations (Part III), and communities (Part IV).