Ecology and Field

SECOND EDITION

Robert Leo Smith

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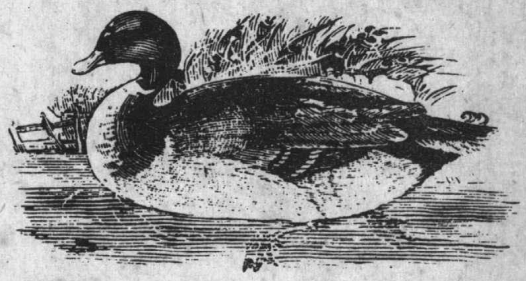

In the first edition of *Ecology and Field Biology* I wrote: "Prefaces are written to be read, although I suspect that more readers flip past them than have read them." In the eight years this text has been on the market I have received a number of letters from readers telling me that they read the preface. I still believe that in many books the preface is often the most absorbing part. In technical books and textbooks, the preface is about the only place where the author can give any real glimpse of himself and tell his reasons for writing the book, how he thinks it should be used, what problems he had, and who assisted him. So, as in the first edition, this is being written to be read before the reader ventures too far into the book.

I have retained the title *Ecology and Field Biology* for the second edition. I was tempted to drop the words *field biology* but didn't. Field biology emphasizes the field approach to ecology that is an important characteristic of this text.

A lot has happened in ecology since the appearance of the first edition. In 1966 ecology was a poor second cousin to molecular biology in academic programs. But after 1970, when the environmental problems reached home and demanded attention, ecology became almost a household word, although misused and poorly understood. Colleges that had never offered ecology courses before added them to their curricula. New ecology books began to flood the market. Many new ecology texts have appeared since 1970, as well as scores of shorter paperback texts. Lacking a choice in 1966, instructors now face a diversity of texts.

Among the current ecology texts, several approach the subject from an evolutionary viewpoint. In fact, some fall somewhat short of being ecology texts but are quite strong on population biology and population genetics. Others take an historical approach to ecology, still others a population approach. Some of the texts are strictly advanced, some elementary. Except for one text, applied ecology is largely ignored; most are devoted to theory. At least two attempts have been made to provide an adequate text for both graduate and undergraduate levels by suggesting that some chapters be utilized and others skipped, depending upon the level desired.

In *Ecology and Field Biology*, I have not attempted to write for an audience of two levels. This book is written as an introductory text to ecology at the sophomore and junior level, although graduate students and others may find it a useful reference. It is designed as a first course for majors and a terminal course for nonmajors. I believe that both should be exposed to the same material. An examination of current texts leads me to conclude that some authors believe that majors should be introduced directly into pure theory, a debatable point. Majors, I believe, should be exposed to theory early, but at the same time they should develop an appreciation of how theory can be applied to the numerous ecological problems facing us today politically, socially, and ecologically. Nonmajors should not concentrate only on the applied ecology without having some understanding of underlying ecological theory.

In this revision I have attempted to balance theoretical ecology with the applied, quantitative with descriptive and qualitative. I have tried not to be dogmatic but to point out areas where considerable controversy exists. Readers will discover that this edition contains considerably more theory and some mathematics. The math is relatively simple, and the examples can be followed easily. I have brought all sections up to date and rewritten most of the book. I have added new examples, expanded the material on populations, broken the chapter on energy and biogeochemical cycles into four new chapters. I am surprised that the subject of biogeochemical cycles so relevant to air and water pollution receives such little attention in most current ecology texts. Yet my first edition was criticized for its inadequate treatment of that subject. I have added a new chapter on ecosystem approach to resource management and one on organisms and the environment—really a chapter of physiological ecology, a topic most requested by readers.

Readers will also note a major change in organization of the text. A criticism of the first edition was its failure to integrate sufficiently the various areas of ecology discussed, ecosystem, community, population, and behavior. Some instructors failed to use the behavioral ecology material at all. To tighten the organization, I developed the revision around a central theme, the ecosystem, which is introduced in Chapter 2 and is followed throughout the text. A secondary theme is evolution and natural

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selection. This theme might not appear as obvious as it does in some evolution-oriented texts, but the theme is there; and a chapter is devoted to the subject of natural selection. The first edition of *Ecology and Field Biology* was the first general ecology text to include evolution and natural selection as a part of ecology.

One may criticize the book for being too long for a one-semester course in ecology. That was a persistent objection to the first edition. (I am happy to see that all the major ecology texts that have appeared are approximately the same number of pages.) I gave this criticism serious consideration in the revision and ended up with an even larger book in spite of deletion of considerable material. In revising the text I was faced with two alternatives. One was to reduce the book considerably to a traditional one-semester size of 450 pages. If I did that, the result would have been a book with a minimum amount of material, a skeleton of ecological principles with many areas overlooked. I would have to ignore most of the applied aspects of ecology. Then the book could be criticized as being too thin, a point made about many of the short paperback texts used in some ecology courses. The second alternative was to increase the size of the book, a necessary step if I were to maintain a balanced picture of ecology. I chose the latter alternative, although it meant some sacrifice, such as reduction in the size of some of the illustrations. The book is as large as it can grow. What will be cut in future editions is up to the readers. I would appreciate your suggestions.

In spite of it all, the book basically is not too large for a one-semester course. A text should be an aid and not a crutch for a course. It should not only provide the basic material around which lectures are built but also provide supplementary reading for the student (after all, humanities courses demand that students not only digest a text but a number of additional readings as well). *Ecology and Field Biology* is large enough to allow the instructor a great deal of flexibility. The instructor can explain theory in the lecture; the student will find sufficient material in the text to amplify the lecture material.

In some schools ecology is a lecture and discussion course. This text should fit such courses admirably. It provides the instructor and the student with necessary additional material to develop topics for discussion, as well as a key to finding new sources of informa-

tion. In other schools ecology is a lecture and laboratory course. In such a course the descriptions of the various ecosystems provide the students with an insight into the communities and ecosystems that might be involved in the laboratory. The appendixes (a popular section of the book I had considered dropping to save space) provide a guide to necessary techniques to use in the lab. (In my own course the laboratory is devoted to a study of the forest ecosystem. The various vegetational layers are sampled by different techniques, the composition and structural layers analyzed, species diversity of layer determined, populations of small mammals and forest soil invertebrates sampled, distribution of organisms analyzed, soil nutrients determined, etc., and the whole tied together in a comprehensive report.) If the instructor requires individual projects, then *Ecology and Field Biology* provides the student with the basic information and techniques needed to undertake independent field studies. This versatility would not be possible in a shorter text, nor is this versatility available in other ecology texts now on the market. In addition, the lists of journals reasonably complete at the time of compilation, general references, suggested readings, and general bibliographies provide a guide to available literature that should be invaluable to instructor and student alike.

This edition is different from other ecology texts in another important way. It recognizes that man is the dominant ecological force on earth. With one exception: Other ecology texts mention man but consider ecological theory, nature, and natural processes apart from man; yet virginal nature no longer exists. Even the most remote wilderness areas are affected by air pollution, by protection from fire, by pesticides, and by other intrusions of man. Several texts do devote the terminal chapter or so to man and ecology. In this text man is integrated into all of the discussions.

The manner in which the text is used is basically the instructor's own decision. The text approaches ecology from the ecosystem to the organisms. Some instructors may want to reverse that approach and start with the organism and work toward the ecosystem. In that event, the instructor might want to begin with Chapters 1 and 2, move to Chapter 7, then 15 and 16, and work backward through Chapters 10 through 14, and 3 through 9, and end with Chapter 20.

The book is divided into six parts. Part I is an introduction. Chapter 1 is a brief look at the history and nature of ecology, while Chapter 2 sets the stage for the material to come. Part II considers the ecosystem and man's place in it, ecosystem function, environmental influences, the nature of the community and ecosystem development. Part III considers the populations that make up the ecosystem. Chapter 10 deals with basic demographic aspects of population; Chapter 11, the interaction among members of the same population; Chapter 12 with interactions among populations of different species with special emphasis on competition, predation, and a special type of predation—exploitation by man. These chapters are followed by one on social behavior in populations and one on natural selection and evolution. Part IV looks at the individual in the ecosystem, particularly its response to its environment. Part V deals with a diversity of ecosystems, terrestrial, fresh water, and marine. Part VI and Chapter 20 look at the application of ecological principles or the lack of their application to resource management. Considered are agriculture, range management, forestry, and wildlife management. Two controversial areas, clear-cutting and hunting, are examined in some detail. The chapter ends with a short introduction to systems analysis and its application in ecology.

The Appendixes, too, have been reorganized. Appendix A provides an annotated bibliography on the use of statistics in ecology. Appendix B is devoted to the sampling of animal and plant populations. Appendix C is concerned with sampling community attributes, including primary and secondary productivity, species diversity, association between species, and population dispersion. Appendix D includes techniques for measuring a number of environmental variables.

I have written this book to be read and used. I hope that I have been able to infuse into *Ecology and Field Biology* some enthusiasm for the subject and some feeling for the natural world and man's place in it. By necessity the reader will find in these pages some of the dull textbook stuff; but in it, too, I hope the user will find a feeling for the world outdoors. If that too can become as much a part of ecology as theory, mathematics and computers, then perhaps posterity also will be able to study ecology.

Robert Leo Smith

Acknowledgments

The author of a textbook depends upon a number of people, mostly those researchers whose long hours in the laboratory and field have provided the raw material out of which textbooks are fashioned. Aside from these, there are a number of people who must be singled out individually. The idea and the encouragement for writing the book in the first place must go to Dr. F. Reese Nevin, State University of New York at Plattsburgh. Among those whose comments and criticisms were important in the development of the first edition were Professor Arnold Benson, Dr. Willem van Eck, Dr. Warren Chase, Dr. David E. Davis, Drs. Robert and Millicent Ficken, Dr. Henry Tompson, Dr. Harold A. Mooney, Dr. J. T. Enright, and Dr. Monte Lloyd.

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Between the publication of the first edition and the writing of the second I received many helpful comments from readers, most of whom will have to go unnamed. I particularly appreciate the comments of those who responded to a questionnaire. Suggestions were passed along by Dr. Thomas Pauley, Salem College; Dr. Paul Hafer, State University of New York

at Potsdam; Dr. Richard Hartman, University of Pittsburgh; and Dr. Richard W. Coleman, Upper Iowa College. Dr. James Monro, New South Wales Institute, Australia, clarified the *Cactoblastis* story and provided additional information.

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The majority of drawings (graphics excluded) were done by Ned Smith, a nationally known wildlife artist who did a superb job for the first edition. New drawings were done by my son, Robert Leo, Jr., a student of graphic design and a developing outdoors and wildlife illustrator. He did the task well under heavy pressure of deadlines and classes.

The book would not have arrived at the present stage without the constant encouragement, advice, and prodding from Al Abbott, Carol Dempster, and Holly Detgen of Harper & Row. Dan Cooper, field representative of Harper & Row, did a great job of passing along suggestions from users of the text and of acting as a liaison between the Clarion State College reviewers and me. Drs. Dave Samuel and Ed Michael of the wildlife biology section of the Division of Forestry, West Virginia University, took over some of my work with students when time was closing in. Finally, I wish to acknowledge the assistance and encouragement of my wife, Alice, and children who had to endure my many hours of preoccupation with the revision and all that it involved.

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Introduction

This is an age of ferment and change. A little more than two-score years ago Charles Lindberg bravely crossed the Atlantic alone in a single-engine plane. Today we have landed upon and explored the surface of the moon and have sent photographic probes to Mars. In the early 1920s radio was just beginning to get its feet on the ground; today pictures along with voices are being transmitted around the world by way of communication satellites. We have probed the secrets of the atom and unleashed its awesome power. In so doing we have changed the direction of world history and the destiny of mankind. A ferment also has developed in biology. The probing of the secrets of the cell, the discovery of DNA, and advances in biochemistry and genetics have revolutionized biology and have produced profound implications for the future of man.

While all these advances were taking place, other changes were also at work. Man's environment was deteriorating, and although warnings had been sounded, few paid any attention. Population was increasing explosively. Technological advances were destroying the environment at an accelerating rate. Nitrogenous wastes and excessive phosphorus were draining from farmlands and urban areas, causing eutrophication of natural waters and lowering water quality. DDT and other hydrocarbons, PCB, and mercury and other heavy metals were accumulating in some species of animals, impairing their reproduction or making them unfit as human food. The nonreturnable bottle, nonbiodegradable plastic, and forced obsolescence of appliances and automobiles were creating massive solid-waste problems and littering the countryside. Demand for increased electricity brought about by industry and the public acceptance of air conditioning and all-electric homes increased sulphur dioxide and particulate pollution of the air. It upturned midwest farmland and Appalachian Mountains for cheap strip-mined coal. A rapid multiplication of automobiles poured increasing amounts of nitrous oxides and lead into the atmosphere, which under proper conditions produce choking photochemical smog. Roads slashed through open country, and urban and suburban expansion ate into the hinterlands and farmlands. Wilderness areas and wild places were disappearing at an accelerating pace, and the increased interest in outdoor recreation placed intolerable pressures on state and national parks. Even the oceans were not spared, as man's debris and chemicals were deadening the seas. Suddenly the public began to awaken to the fact that planet earth was in trouble, and suddenly they became aware of ecology.

In the late 1960s the general public was hardly aware of the term *ecology*. As a topic of interest ecology stirred little public discussion, and as a science it had none of the glamor of molecular biology. By 1970 ecology had become a household word, but it was misunderstood, misused, and equated with environmental science. Too many failed to understand that ecology refers to the interrelations of an organism with its environment and that this includes man. They only vaguely realized that the relationship is two-way, that just as the environment has an impact on an organism, so an organism has an impact on its environment. But at least a great majority became aware of the environment. And the shattering view of earth from outer space forced on us the realization that the earth is finite and that what it is and what it contains are all we have.

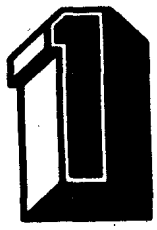
Because it deals with life, ecology has been considered a part of biology. A quarter of a century ago and earlier the major introductory path to biology was through natural history, or as it was more popularly known, nature study. This was a time when people were just awakening to the world about them. Nature had ceased to be an enemy. The fields were cleared, the forest subdued, and there was even becoming a danger that many common animals—gray squirrels, beaver, deer, wild turkeys, and ducks—were on the border of extinction. The conservation movement was building up full steam in the 1930s, and nature study was a part of nearly every school curriculum, even though more often than not it was poorly taught. Too often it consisted only of coloring bird pictures and writing paragraphs about them. But at least youngsters became aware that birds existed, that they were colorful and interesting, and that they were something more than living targets for BB guns. It was a time when John Burroughs was popular, the Reed *Bird Guides*

were the last word in field guides, and the Comstock *Handbook of Nature Study* was the bible of natural history.

Out of this background of close contact with nature and an interest in life, the biologists developed. But as the country became more urbanized and less rural, people lost this contact with nature. Interest in biology from a field approach declined, and research biologists became more concerned about the functioning of an organism than about its relationship to its environment. Modern biologists appeared at the doorways of chemistry, physics, and mathematics—disciplines not immediately related to the living environment. They looked upon biology as beginning and ending with a group of chemical compounds, and they thought that the answer to life lay within the realm of the physical sciences.

Part of the reason for the swing away from natural history lies in biology itself. For a long time traditional biology started and ended with the naming of organisms. Biology as taught in schools and colleges was an endless repetition of the study of types of organisms. It was largely descriptive, weak in quantitative data, and it lacked the strong conceptual foundation that so marked physics, chemistry, and mathematics. Even at the popular level, the mass of amateur naturalists who started out watching birds or collecting insects rarely got beyond the identification stage. They made little or no attempt to understand the organism, to find how it really lived or what its function was in nature. Even professionals fell into this trap, or at least they confined their work to descriptive biology. As a result natural history, once a rigorous subject, lost its position among the sciences and became equated with emotionalism and superficiality. But the ecological revolution of 1970 ended all that.

With the environmental awareness of the 1970s, interest in natural science began to revive. Suburban man has become acutely aware of his environment, and there is a new impetus to study the natural world. Books on natural history and ecology have become popular sellers; even the Reed *Bird Guides* and Comstock and Burroughs are back in vogue. Environmental study has returned to some classrooms; interest in wildlife and forestry has increased. Public outcries, wise or unwise, have been voiced against hunting and against environmental destruction by timber-cutting



Ecology: its meaning and scope

practices, highways, dams, power plants, and strip mining. Many people are seeking a closer contact with the natural world. Some, especially the young, seek to return to the earth by establishing rural communes and attempting a subsistence agricultural way of life. Industry for the first time is finding itself on the defensive. Its uncontested right to pollute the air and water and to destroy the landscape for profit is being challenged.

Thus natural history evolved into ecology and ecology into a science that has entered the public consciousness. Where the old focal point was kinds of organisms, the new focal point is the nature of living systems. Just as molecular biology attempted to probe the secrets of living systems at the cellular level, so ecology probes the secrets of living systems at the levels of the organism, the populations, and the ecosystem.

The term *ecology* was coined by the German zoologist Ernst Haeckel, who called the "relation of the animal to its organic as well as its inorganic environment" *ökologie*. The origin of the word is the Greek *oikos*, meaning "household" or "home" or "place to live." Thus ecology deals with the organism and its place to live. Basically this is the organism's environment; so ecology might well be called environmental biology. That word *environment*, like sin, covers a multitude of things. For one thing the environment includes the organism's surroundings. It also includes for the individual organism those of its own kind, as well as organisms of other kinds. There are relationships between individuals within a population and with individuals of different populations. Animals react in a social sort of way, in various behavior patterns. Because all organisms have become adapted to the environment and are always adjusting to a changing environment, natural selection and evolution become a part of ecology.

Because of its far-flung involvements with so many fields, ecology, call it what you will, is often regarded as a generality rather than a speciality. Indeed one ecologist, A. MacFadyen, in his book *Animal Ecology: Aims and Methods* (1963)* wrote:

> The ecologist is something of a chartered libertine. He roams at will over the legitimate preserves of the plant and animal biologist, the taxonomist, the physiologist, the behaviourist, the meteorologist, the geologist, the physicist, the chemist, and even the sociologist; he poaches from all these and from other established and respected disciplines. It is indeed a major problem for the ecologist, in his own interest, to set bounds to his divagations.

This statement nicely emphasizes that ecology is a multidisciplinary science. It has to be to reach the heart of the problems of environmental biology.

It is difficult to trace ecology back to any clear beginnings. The Greek scholar Theophrastus, a friend and associate of Aristotle, wrote of the interrelation between organisms and their environment. But modern impetus to the subject probably came from the plant geographers Humboldt, De Candolle, Engler, Gray, and Kerner. They described the distribution of plants, and in so doing raised some questions that have not been answered yet.

Out of the roots of plant geography developed another subject of study, the plant community, which became *community ecology*. The study of the plant community developed in two regions, western Europe and the United States. In Europe Braun-Blanquet (1932) and others concerned themselves with the composition, structure, and distribution of plant communities. In America, such plant ecologists as Cowles (1899), Clements (1916, 1939), and Gleason (1926) studied the development and dynamics of plant communities. While these investigators were studying plants, Shelford (1913, 1937), Adams (1909), and Dice (1943) in America and Elton (1927) in England were investigating the interrelations of plants and animals.

At the same time an interest in dynamics of populations was developing. The theoretical approaches of Lotka (1925) and Volterra (1926) stimulated the experimental approaches by biologists. In 1935 Gause investigated the interactions of predators and prey and the competitive relationships between species. At the same time Nicholson studied intraspecific competition. Later the work of Andrewartha and Birch (1954) and the field studies of Lack (1954) provided a broader foundation for the study of the regulation of populations. The discovery of the role of territory in bird life by H. E. Howard in 1920 led to further studies by Nice in the 1930s and 1940s. Out of such studies came

* Full information for sources can be found in the Bibliography.