S. CHARLES KENDEIGH

ECOLOGY

with special reference to animals and man

Comprehensive treatment of the basic principles governing the ecological adjustments of animals and man...plus the problems of pollution, pest control, population growth, energy yield, and related topics.

ECOLOGY

WITH SPECIAL REFERENCE TO ANIMALS AND MAN

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PREFACE

The science of *ecology*, born at the beginning of the present century after a gestation period of several hundred years, has now not only matured into an honored and respected scholarly discipline and field of research but has also become a household word as it relates to the general condition of the environment. This book is an effort to summarize the basic concepts and principles of the subject, to present the elementary factual information with which a person to be competent in the field should be familiar, and to show how these principles and facts may be applied in a practical way to the interests and welfare of man. Although the book relates especially to animals, enough material is given concerning plants to bring out their essential place in the system of nature and to emphasize the bioecological point of view.

After a background section for orientation, local communities and habitats are discussed in some detail. It is my firm belief that a person beginning the study of ecology should first become thoroughly acquainted with the places where organisms may be found in nature, what kinds of organisms occur in different habitats, the abundance and interrelations of organisms in these habitats, the behavior and the life requirements of the principal species, and the structure and succession of communities as observed in the field. Only when he is well founded in this knowledge is he fully ready to understand the ecological processes and community dynamics that are presented in the remainder of the book.

I am also convinced that an introductory course in ecology should survey the entire field in a comprehensive and balanced manner. This I have tried to do, as shown in the table of contents, by covering basic concepts and facts in community ecology, ecosystem ecology, population ecology, evolutionary ecology, geographical ecology, and marine ecology. I am a little abashed that I do not include a section on physiological ecology, which is my major research interest at the present time, although it is dealt with sparingly throughout the book. The proper development of physiological ecology takes one extensively into laboratory experimentation, however, which is a different approach. Our emphasis here is kept on the study of the free-living organism in its natural environment. Physiological ecology as well as more advanced and detailed studies in all the various phases of ecology may best be left to advanced courses. Similarly with behavioral ecology, considerable attention is given to the behavioral responses of organisms, even though a separate section on ethology has not been organized. Although the quantitative aspect of ecology is emphasized and continually referred to, I do not believe that in an introductory book it is desirable to approach the subject from a detailed mathematical point of view. This too may well be postponed to advanced courses.

Each chapter is an independent unit, and each major topic progresses from a basic analysis of its natural relations to a discussion of how it applies and is relevant to man. This includes treatment of water, air, and soil pollution; pest control; population explosion; energy yield; cultural evolution; and how man behaves fundamentally as an animal.

This book is designed for a course at the junior-senior-graduate level, and for students who have had at least a year's background in biology. The course is best given in the autumn in order to have early contact in the field with fully developed communities. If given in the spring it would probably be best to reverse the positions of the two sections, Community Ecology and Geographical Ecology. This would provide the student with some knowledge of communities before undertaking the more theoretical sections and leave the discussion of local communities to the end of the course when it can be correlated with field work.

I gave the course during the autumn semester at the University of Illinois for 23 years. There were half-day or full-day trips every Saturday until winter weather set in and two half-day winter trips. Also included in the field work was one weekend camping trip to study communities not found locally. The students got to see at first hand a large variety of plants and animals, and to measure population sizes by quantitative methods that may have been crude but were nevertheless effective in stream riffles and pools, ponds of different ages, bogs, lakes, grassland, deciduous and coniferous forests, and seral stages as they develop on rock, sand, pond, bog, floodplain, and abandoned strip-mine areas. Some experimentation was also done in the field to analyze the manner in which both aquatic and terrestrial species respond to environmental factors. There was a small amount of laboratory work during the winter for learning quantitative methods of counting plankton, examining different kinds of respiratory systems in aquatic organisms, searching and identifying micro-organisms in the soil, and experiments in choice of habitats. Methods for measuring productivity were discussed but actual practice with these methods was left for an advanced class.

Citations to the literature in the text have been done by name and year of publication to encourage students to associate ideas with names of ecologists responsible for them and to enable the student to pursue the subject to greater depth.

Some care has been taken with taxonomic nomenclature. Common names are used throughout the text as far as possible, with the scientific nomenclature restricted to the index. Authorities followed for most scientific names are the following. Mammals: North America: Miller and Kellogg (1955); Eurasia: Ellerman and Morrison-Scott (1951). Birds: A.O.U. Check-list (1957). Reptiles and amphibians: Schmidt (1953). Fish: Bailey (1960). Invertebrates: as given by authors, not standardized. Trees: Dayton *et al.* (1953). Grasses: Hitchcock (1951); and other plants: Fernald (1950), Rydberg (1954). Common names of mammals are mostly from Hall (1957); birds, A.O.U. Checklist (1957); reptiles and amphibians, Conant (1958); and fish, Bailey (1960).

Finally I wish to acknowledge the help of Daniel I. Axelrod of the University of California at Davis; Clarence F. Clark of Ohio State University; Charles E. King of University of South Florida; Peter H. Klopfer of Duke University; James R. Karr of Purdue University; Roland R. Roth of the University of Delaware; and Glenn C. Sanderson, R. F. Labisky, and W. R. Edwards of the Illinois Natural History Survey. I am especially grateful to Robert H. Whittaker of Cornell University and Francis C. Evans of the University of Michigan who read and commented in detail on the whole manuscript. John Riina, Chester C. Lucido Jr., and Zita de Schauensee of Prentice-Hall, Inc., cooperated in every desirable way in obtaining reviews of the manuscript before publication and in efficiently seeing it through the press.

Illustrations come from several sources. I am most grateful to the late Victor E. Shelford for many drawings originally published in his *Animal Communities of Temperate America* (1913); to the Illinois Natural History Survey for original illustrations from several of their publications; to the U.S. Forest Service which allowed me to select what I wanted from their extensive file of photographs; to the Friez Instrument Division; to the University of Wisconsin News Service; to Dr. John W. Aldrich of the Bureau of Sport Fisheries and Wildlife of the U.S. Department of Interior for the detailed map used on the front end papers and several illustrations in the section on Geographical Ecology; to a number of other individuals for supplying photographs or other illustrative material for which acknowledgment is made in the legends of the figures; and to Colleen Nelson, Katherine Little, and Nan Brown for preparing special drawings.

Champaign, Illinois S. Charles Kendeigh

CONTENTS

Part One

BACKGROUND

Chapter 1

SCOPE AND HISTORY OF ECOLOGY

The word *ecology*, derived from the Greek words *oikos* meaning habitation, and *logos* meaning discourse or study, implies a study of the habitations of organisms.

Ecology was first described as a separate field of knowledge in 1866 by the German zoologist Ernst Haeckel, who invented the word *oekologie* for "the relation of the animal to its organic as well as its inorganic environment, particularly its friendly or hostile relations to those animals or plants with which it comes in contact."

Ecology has been variously defined by other investigators, as "scientific natural history," "the study of biotic communities," or "the science of community populations"; probably the most comprehensive definition is the simple one most often given: *a study of animals and plants in their relations to each other and to their environment.*

OBJECTIVES

Ecology is a distinct science because it is a body of knowledge not similarly organized in any other division of biology; because it uses a special set of techniques and procedures; and because it has a unique point of view. The essence of this science is a comprehensive understanding of the import of these phenomena:

1. The local and geographic distribution and abundance of organisms (habitat, niche, community, biogeography).
2. Temporal changes in the occurrence, abundance, and activities of organisms (seasonal, annual, successional, geological).
3. The interrelations between organisms in populations and communities (population ecology).
4. The structural adaptations and functional adjustments of organisms to their physical environment (physiological ecology).
5. The behavior of organisms under natural conditions (ethology).
6. The evolutionary development of all these interrelations (evolutionary ecology).
7. The biological productivity of nature and how this may best serve mankind (ecosystem ecology).
8. The development of mathematical models to relate interaction of parameters and predict effects (systems analysis).

A study of organisms in the field may bring to light problems which will be most expediently worked out in the laboratory; but field and laboratory investigations must be integrated. The investigator must often study the morphology of dead organisms in the laboratory, and there perform experiments on living animals and plants held under carefully controlled experimental conditions. But unless such studies are perspective to the normal life of an organism, as it is lived under natural conditions, they are not ecology.

The use of exact quantitative techniques is, of course, a general characteristic of all science. But special difficulties arise when such techniques are applied to free-living organisms in natural conditions. For example, size of animal populations has, in the past, often been described in such vague terms as "rare," "common," or "abundant." These are subjective terms, based largely on an impression gained by the observer of the apparent conspicuousness of the species. As James Fisher, an English naturalist, wrote in 1939, a species has usually been indicated as "rare" when actual numbers expressible in one's and two's could be recorded; "common" when the observer began to lose count; and "abundant" when he became bewildered. One of the chief problems of the ecologist is to develop methods by which to measure the absolute size of populations and the productive capacities of different habitats so that the activities of widely varying types of species may be compared. For setting up experiments and organizing and analyzing studies under natural conditions, it is becoming more and more essential that the ecologist be familiar with and employ good statistical procedures (Williams 1954). An objective of ecological research is the establishment of mathematical models or computer simulation programs for the various systems involved. Such models give proper weight to all factors so that the effect of variation of any one or combination of factors can be predicted in advance.

> As a contribution to human knowledge and understanding, ecology is in the fortunate position of being concerned with the most complicated systems of organization, apart from human societies, with which we have to deal. For this very reason it provides a constant challenge to the imagination as well as to experimental ingenuity. It is more difficult to analyze and isolate the relevant factors in a living community than in a simpler system, but the gain in significant understanding of the material world and in comprehending the beauty of its organization is perhaps better in proportion [Macfadyen 1957: 246].

RELATION TO OTHER SCIENCES

Ecology is one of the three main divisions of biology, the other two being morphology and physiology. The emphasis in morphology is on how organisms are made; in physiology, on how they function; and in ecology, on how they live. These divisions overlap broadly. To appreciate fully the structure of an organ, one needs to know how it functions, and the way it functions is clearly related to environmental conditions. The morphologist is concerned with problems of anatomy, histology, cytology, embryology, evolution, and genetics; the physiologist, with interpreting functions in terms of chemistry, physics, and mathematics; and the ecologist, with distribution, behavior, populations, and communities in relation to the environment (ecosystems). The evolution of adaptation and of species is of mutual interest to the ecologist and to the geneticist; biometeorology is a connecting link between ecology and physiology; and systems analysis interrelates ecology and mathematics. All areas, in the final analysis, are simply different approaches to an understanding of the meaning of life.

SUBDIVISIONS OF ECOLOGY

Ecology may be studied with particular reference to animals or to plants, hence *animal ecology* and *plant ecology*. Animal ecology, however, cannot be adequately understood except against a considerable background of plant ecology. When animals and plants are given equal emphasis, the term *bioecology* is often used. Courses in plant ecology usually dismiss animals as but one of many factors in the environment. *Synecology* is the study of communities, and *autecology* the study of species. There is some confusion in these terms since Europeans commonly use "ecology" in a narrower sense—meaning the environmental relations of organisms or of communities. The broader study of communities, including species interrelations and community structure and function as well as environmental relations (synecology), is generally termed "biocenology" or "biosociology" by Europeans.

In this book we shall survey the fundamentals and basic facts of ecology as they relate to animals and have application to man. We will study *community ecology*, the local distribution of animals in various habitats, the recognition and composition of community units, and succession; *ecosystem dynamics*, the processes of soil formation, nutrient cycling, energy flow, and productivity; *population ecology*, the manner of population growth, structure, and regulation; *evolutionary ecology*, the problems of niche segregation and speciation; and *geographic ecology*, concerned with distribution, paleoecology, and biomes. We will be interested throughout the text with how organisms respond and adjust physiologically to the physical factors of their environment, but a full study of *physiological ecology* must be left to another time and place. We will also be concerned throughout with *systems ecology*, that is, the possibility of translating ecological concepts into mathematical models, although we will not go deeply into the actual statistical manipulations involved (Dale 1970, Lieth 1971). This new field is becoming very important in ecological philosophy, changing the emphasis of research from the empirical to the theoretical (Ashby 1956, Margalef 1968). This has potential value in rendering ecology a more exact science so that future events may be predicted when any of several inherent parameters vary. Finally, in several parts of the book we will deal with *human ecology*, involving the population ecology of man and man's relation to the environment, especially man's effects on the biosphere and the implication of these effects for man.

When special consideration of their ecology is given to one or another taxonomic group, we speak of *mammalian ecology, avian ecology, insect ecology, parasitology, human ecology*. When emphasis is placed on habitat, we speak of *oceanography*, the study of marine ecology; *limnology*, the study of fresh-water ecology; *terrestrial ecology*; and so on. *Ethology* is the interpretation of animal behavior under natural conditions; often, detailed life history studies of particular species are amassed. *Sociology* is really the ecology and ethology of Mankind.

Ecological concepts, which may be grouped together as *applied ecology*, have many practical applications; notably *wildlife management, range management, forestry, conservation, insect control, epidemiology, animal husbandry*, and even *agriculture*.

This preview of ecology indicates the great breadth and unique character of the subject material, which justifies the view of ecology as one of the three basic divisions of general biological philosophy.

HISTORY

That certain species of plants and animals ordinarily occur together and are characteristic of certain habitats has doubtless been common knowledge since intelligent man first evolved. This knowledge was essential to him for procuring food, avoiding enemies, and finding shelter. However, it was not until the fourth century B.C. that Theophrastus, a friend and associate of Aristotle, first described interrelations between organisms and between organisms and their environment. He has, therefore, been called the first ecologist (Ramaley 1940).

The modern concept that plants and animals occur in closely integrated communities began with the studies of August Grisebach, a German botanist, in 1838; K. Möbius, a German investigator of oyster banks, in 1877; Stephen A. Forbes, an American, who described the lake community as a microcosm in 1887; and J. E. B. Warming, a Danish botanist, who emphasized the unity of plant communities in 1895 (see Kendeigh 1954 for further details and literature citations). C. C. Adams recognized and described many animal communities in his ecological surveys of northern Michigan and of Isle Royale in Lake Superior, published in 1906 and 1909. V. E. Shelford presented a classic study of animal communities in temperate America in 1913, and Charles Elton published an outstanding analysis of community dynamics in 1927. Although an appreciation that the whole community is one biotic unit, rather than one unit of plants and another of animals, may be discerned in the writings of some early investigators (for example, J. G. Cooper in 1859), the fact has been brought to modern emphasis in the work of F. E. Clements and V. E. Shelford, especially in their *Bio-ecology*, published in 1939. Much interest has been stimulated in recent years by D. Ramon Margalef, Robert MacArthur, and others for analyzing the structure of these biotic communities, particularly in respect to such phenomena as species diversity, niches, and how they came about through evolution.

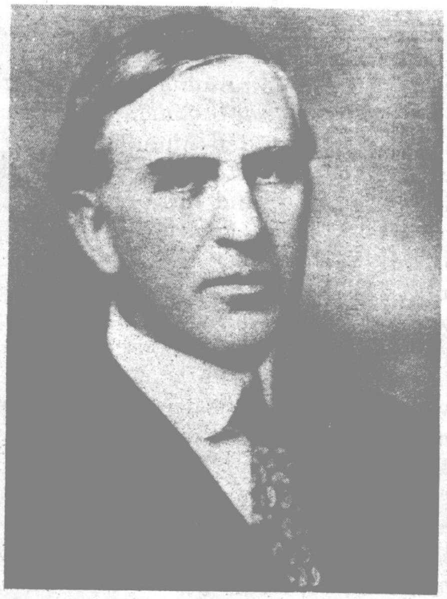
Succession of plant species after burns and in bogs has been known in a general way since about 1685, and European ecologists have studied succession since the late nineteenth century. The present-day interest

(Left) C. C. Adams, 1873–1955, animal ecologist (courtesy Dorothy Kehaya).

(Right) Victor E. Shelford, 1877–1968, animal ecologist.

(Left) F. E. Clements, 1874–1945, plant ecologist.

(Right) Henry C. Cowles, 1869–1939, plant ecologist (courtesy R. J. Pool).



in succession, however, especially in North America, dates from the plant studies of Henry C. Cowles in 1899 on the sand dunes at the south end of Lake Michigan, and the work of Frederic E. Clements, 1916. C. C. Adams and V. E. Shelford, in the citations noted, were among the first to apply the concept to animals.

Geographic ecology, in the modern sense, dates from the generalizations on the worldwide distribution of animals made by the French naturalist Georges L. L. Buffon (1707–1788), and the explorations of the German naturalist Alexander von Humboldt (1769–1859). There was lively interest and many important contributions in this general field during the nineteenth century; notably, the life-zone concept of C. Hart Merriam (1890–1910) needs special mention. During the present century the concept of biotic provinces is identified with L. R. Dice (1943) and the biome concept with F. E. Clements and V. E. Shelford (1939). The broad survey of ecological animal geography made by R. Hesse in 1924 exerted considerable influence, and this treatise was later translated into English and revised by W. C. Allee and Karl P. Schmidt (1951).

The study of population dynamics, so important in modern ecology, dates back at least to Malthus, who pointed out in 1798 the limitation to population growth exerted by available food. Darwin, in 1859, recognized the importance of competition and predation in developing his theory of evolution. Pearl, 1925, analyzed mathematically the characteristics of population growth, and Lotka, 1925, and Volterra, 1931, developed theoretical mathematical equations to show the manner in which populations of different species interact. These studies led to the classic experiments of Gause, 1935, with interacting populations of predators and prey. Nicholson's publication in 1933 stimulated much thinking concerning the factors that stabilize populations at particular levels. Andrewartha and Birch, 1954, emphasized the importance of climate and other factors on determining the size of populations.

The measurement and analysis of energy use by organisms for existence and growth is now of very great interest in ecology. Attention to biological productivity began in the 1930's in connection with practical pond-fish culturing and the limnological studies of Thienemann in Europe and of Birge and Juday at the University of Wisconsin, but the modern crystallization of the subject came with the fresh-water and marine investigations of Lindeman, Hutchinson, and Riley at Yale University (Ivlev 1945) and of Eugene and Howard Odum. An early study of energy relations within terrestrial communities is that of Stanchinsky (1931).

Physiological ecology had its historical beginnings in the correlation of biological phenomena with variations in temperature stimulated by Galileo's invention of a hermetically sealed thermometer about 1612 A.D. The French naturalist Reaumur summed the mean daily temperatures for April, May, and June in 1734 and again in 1735, and correlated the earlier maturing of fruit and grain during the first year with the greater accumulation of heat. A discovery of parallel significance was of oxygen in 1774 by the English clergyman, Priestley, and the finding by Lavoisier, a Frenchman, in 1777 that it was an essential part of air. Claude Bernard, another French physiologist, enunciated the principle of homeostasis in 1876. This concept originally referred to regulatory mechanisms which maintained the "internal environment" of the body constant in the face of changing external conditions. Later, the concept came to be applied also to maintenance of community interrelations. Van't Hoff, a Dutch scientist, contributed to physiological ecology in 1884 in describing how the speed of chemical reactions increased two- or threefold with each rise of 10°C. K. G. Semper and Charles B. Davenport clearly established physiological ecology in bringing together pertinent information in 1881 and 1897–99, respectively. More recent summaries of knowledge and methods in this general field have been made by V. E.

Shelford in *Laboratory and Field Ecology* (1929) and by Samuel Brody in *Bioenergetics and Growth* (1945).

The development of animal behavior or ethology may be traced back through the natural history of ancient times. More recently the 13 volumes of *Thierleben*, prepared by A. E. Brehm during the period 1911–18, are noteworthy. H. S. Jennings, 1906, and Jacques Loeb, 1918, made valuable contributions to the understanding of the behavior of invertebrates. Precise modern techniques and concepts as applied to vertebrates began to take form about 1920 with the development of banding and marking of individual animals by S. Prentiss Baldwin (1919) and the recognition of territories in the nesting of birds by H. E. Howard (1920). The formulation of the concept of releasers as controlling instinctive behavior by Wallace Craig (1908), K. Lorenz (1935), and N. Tinbergen (1951) has produced a profound effect on present-day thinking.

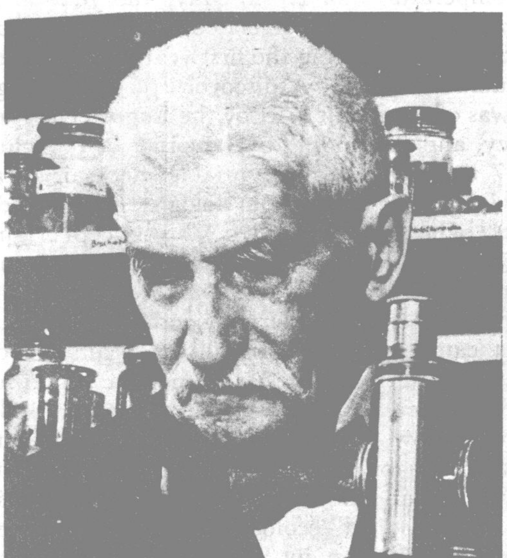
In regard to other divisions of ecology, the crystallization of studies in oceanography may be credited to Edward Forbes 1843, Maury 1855, Alexander Agassiz 1888, Petersen and his colleagues 1911, and Murray and Hjort 1912; limnology to Forel 1869, Birge 1893, Juday 1896, Ward and Whipple 1918, Thienemann 1913–35, and Naumann 1918–32; and wildlife management to Aldo Leopold 1933.

Ecology, then, is of comparatively recent development as a distinct science, but its roots extend well back into the past. An early comprehensive treatment of the subject is *Principles of Animal Ecology* by Allee, Emerson, Park, Park, and Schmidt, published in 1949 (for citations of historic interest in this chapter, see this reference). Since ecology is a young science, it should be emphasized that its concepts and techniques have not become standardized and that there is opportunity and stimulus here for many new investigators.

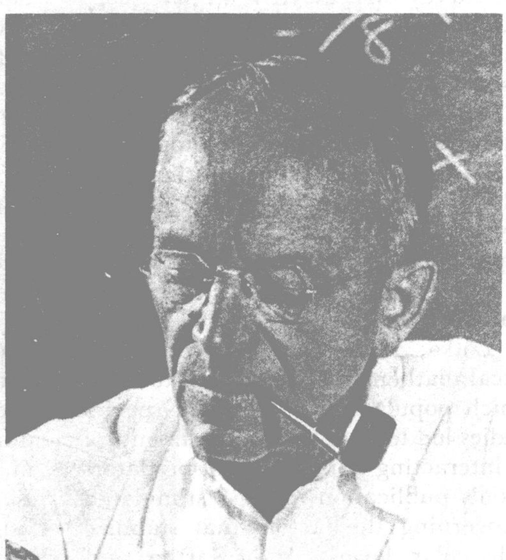
The Ecological Society of America was founded in 1915, and in 1971 had a membership of 4700. The British Ecological Society, organized in 1913, has a membership of about 2000. The society in America has given birth to several offspring: The Wildlife Society, Society of Limnologists and Oceanographers, the Nature Conservancy, and the Animal Behavior Society. Each of these daughter organizations has its own journal. Also resulting from promotion by the Society, the Inter-American Institute of Ecology became established in 1971. The Institute, supported by both private and government funds, is designed to conduct and promote research, provide analytical and other services, and relate ecological information to the development of far-reaching public policies and to solving environmental problems.

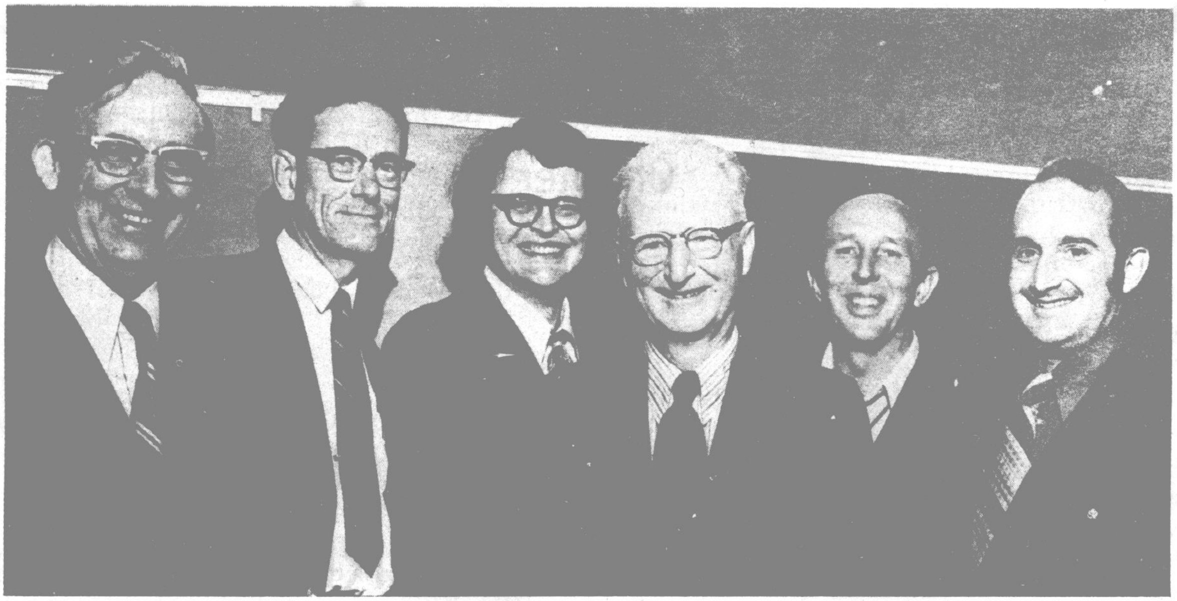
The Ecological Society of America publishes three periodicals: *Bulletin* for general articles and Society business, *Ecology* for short scientific papers, and *Ecological Monographs* for long papers. The British Ecological Society also publishes three periodicals: *Journal of Ecology* for papers on plants, *Journal of Animal Ecology* for papers on animals, and the *Journal of Applied Ecology*. *Oikos* began publication in 1949 to represent ecologists in Denmark, Finland, Iceland, Norway, and Sweden. The Polish Academy of Science has been publishing *Ekologia Polska* since 1953. *Oecologia*, a German periodical derived from *Zeitschrift für Morphologie und Ökolgie der Tiere*, began in 1968. The U.S.S.R. Academy of Sciences initiated the periodical *Ekologiya* in 1970, and an English translation of it appears under

E. A. Birge, 1851–1950, limnologist.



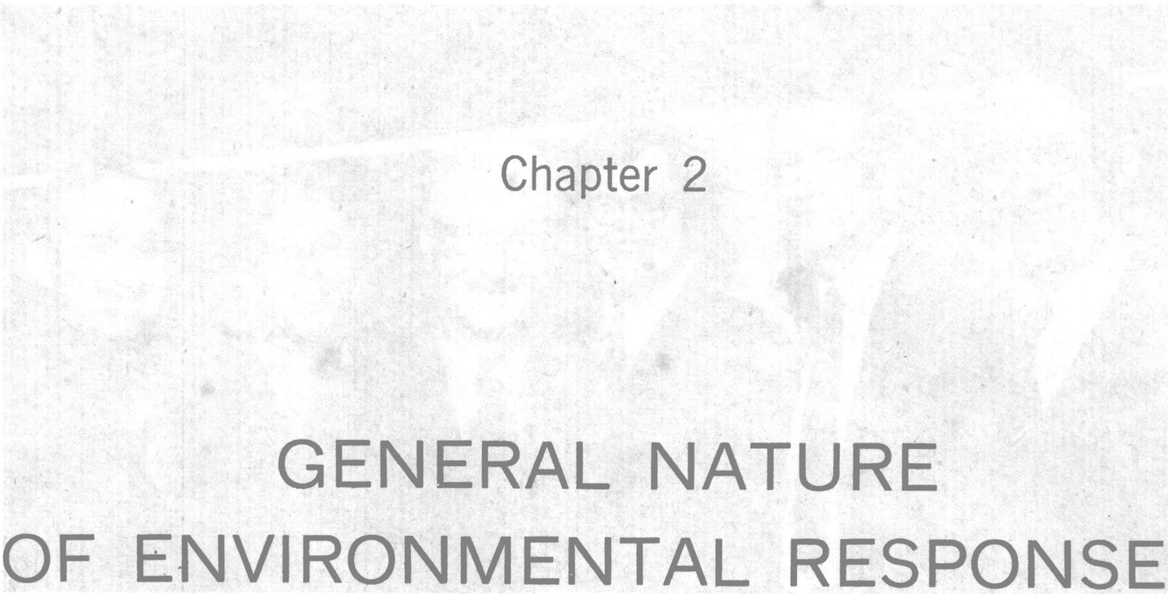
Aldo Leopold, 1886–1948, wildlife manager.





Some well-known ecologists at the present time (*see* Bibliography), all Ph. D. graduates from the University of Illinois. The photograph was taken on May 26, 1973, on the occasion of Dr. Kendeigh's retirement from teaching (Robert K. O'Daniell, *The News-Gazette*). From left to right: Dr. Eugene P. Odum, University of Georgia; Dr. Robert H. Whittaker, Cornell University; Dr. Robert V. O'Neill, Oak Ridge National Laboratory; Dr. S. Charles Kendeigh, University of Illinois; Dr. Robert M. Chew, University of Southern California; and Dr. James R. Karr, Purdue University.

the title *Soviet Journal of Ecology*. The International Society for Tropical Ecology, including India and adjacent countries, was founded in 1960 and publishes *Tropical Ecology*. The New Zealand Ecological Society came into existence in 1952 and the Ecological Society of Australia in 1960. *Proceedings* of the New Zealand annual conventions are published. *The Japanese Journal of Ecology*, begun in 1954, is the official publication of the Ecological Society of Japan. Many of its articles are in Japanese, but there are summaries in a European language. *Researches on Population Ecology*, started in 1959, is published by the Japanese Society of Population Ecology. In 1968, an International Association for Ecology was formed within the International Union of Biological Sciences to coordinate ecological work in various countries. It began publishing the *Intecol Bulletin* in 1969. No attempt will here be made to list the new journals dealing with pollution and environmental problems of practical or economic importance. Finally, many papers of interest to ecologists appear in biological journals of various sorts that do not carry the word "ecology" in their titles.



Chapter 2

GENERAL NATURE OF ENVIRONMENTAL RESPONSES

Ecology, by definition, deals with the interrelations of organisms with each other and with their environment. These interrelations become established as organisms respond in various ways to contacts with one another and with the ever-changing environment.

The term *environment* describes the sum total of physical and biotic conditions influencing the responses of organisms. More specifically, the sum of those portions of the hydrosphere, lithosphere, and atmosphere into which life penetrates is the *biosphere.* There are no characteristic or permanent inhabitants of the atmosphere, although the air is traversed by many kinds of animals and plant propagules. Of the hydrosphere, there are two major *biocycles*, marine and fresh water; of the lithosphere there is one, land (Hesse *et al.* 1951).

A *habitat* is a specific set of physical and chemical conditions (for example, space, substratum, climate) that surrounds a single species, a group of species, or a large community (Clements and Shelford 1939). The ultimate division of the biosphere is the *microhabitat*, the most intimately local and immediate set of conditions surrounding an organism: the burrow of a rodent, for instance, or a decaying log. Other individuals or species are considered as part of the community to which the organism belongs and not part of its habitat. The term *biotope* defines a spatial or topographic unit with a characteristic set both of physical and chemical conditions and of plant and animal life.

In order for organisms to exist they must respond or adjust to the conditions of their environment. The first living organisms probably evolved in the sea and must have possessed very generalized adjustments to this relatively uniform and favorable habitat. However, these early organisms had inherent in them the potential for expansion, as they later spread into other and more rigorous habitats, particularly fresh-water and land. As evolution proceeded, organisms became more and more limited in the range of their ability to respond as they became specialized in their adjustments to particular habitats. This led to the great diversification of species that we see at the present time, with each species restricted to its particular microhabitat and place in the community.

Organisms respond to differences or changes in their environment in four principal ways: morphological adaptations, physiological adjustments, behavior patterns, and community relations. Chapters 2 and 3 are a resumé of these responses, the general fundamentals of which must be understood before the subtle relations of an organism to its environment that are the substance of ecology can be appreciated.

Probably the most important of distinctions between organisms in a consideration of their morphological responses to the environment is whether they are sessile or motile (Shelford 1914). Most plants are, of course, sessile; most animals, motile. There are, however, some motile plants among unicellular forms and male gametes, and there are many sessile or slow-moving animals in aquatic habitats. Sessile organisms respond to variations of the environment primarily by changes in form; motile animals, primarily by changes in behavior.

MORPHOLOGICAL ADAPTATIONS

Changes in Form and Structure

Consider a sessile organism, the tree. It is essential to the tree that its foliage be exposed to sunlight. As it grows within a forest, it is usually tall and slender, and little branched except at the top, where the cap of foliage reaches into the full sunlight. Growing on the forest's edge, the tree is shorter, and branching and foliage are dense both at the cap and on that side exposed to full sunlight. The tree which grows solitary in an open place is short, but branching and foliage are dense and uniformly distributed, often starting close to the ground. In similar manner, the variations in form assumed by sessile colonial animals, such as sponges and corals (Fig. 2-1), reflect vicissitudes imposed by habitat (Wells 1954).

Morphological variations induced by peculiarities of habitat do occur in motile animals: thickening of the shells of clams subjected to strenuous wave action; variation in number of vertebrae, scales, and fin rays among fish subjected to different temperatures at critical periods in their growth (Barlow 1961); changes in the number of facets in the bar-eye of the fly *Drosophila* as a correlative of temperature variations during a short critical period in larval growth (Krafka 1920); the many variations in form and size of internal parasites, depending on crowding and other environmental conditions (Baer 1951); pointed tails in certain flatworms crawling over a substratum during growth, contrasted with rounded tails occurring in the same species when individuals are experimentally prevented from crawling (Child 1903).

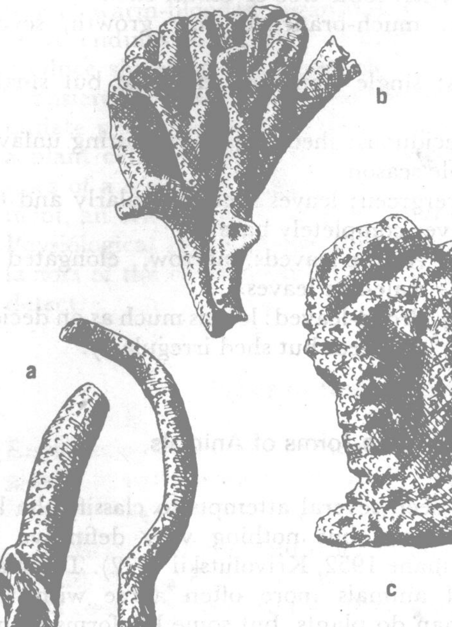
That individuals of the same species are so much alike attests the great extent to which the course and outcome of morphological development are genetically determined. But that there are variations between individuals, and between groups of individuals, of the same species shows that morphological development is also responsive to environmental influences. Modifications induced by the environment emerge as the individual develops and are not specifically inherited by the succeeding generation. These modifications are called *growth-forms* or *ecophenes*. If the generation following is similar in growth-form to the parent generation, it is a similar morphological response to a similar environment (Schmalhausen 1949). If and when the growth-form becomes inherited as the result of evolutionary processes, it then becomes an *ecotype*. *Life-form* is a general term referring to the shape or appearance of an organism irrespective of how formed (Daubenmire 1947). The prevalence of particular life-forms among the important organisms helps to separate and characterize biotic communities, as we will see repeatedly in later discussions.

Life-forms of Plants

The life-form of a plant is characterized by its vegetative form, its length of life, the arrangement and character of its leaves, whether its stem is herbaceous or woody, its manner of growth, and its means of overwintering. Life-form categories sometimes agree with large taxonomic units, such as ferns or mosses. On the other hand some taxonomic groups contain species exhibiting a variety of life-forms, and some life-forms include species only remotely related taxonomically.

There have been many systems proposed for the classification and terminology of the life-forms of plants. One widely used system (Raunkiaer 1934) is based primarily on position of buds or other meristematic tissues in relation to the soil surface. A most useful system for both plant and animal ecologists is one emphasizing differences in plant forms responsible for the structure, or physiognomy, of plant communities,

Fig. 2-1 Form assumed by the coral *Madrepora* as it develops in (a) deep water; (b) barrier pools; (c) rough water (from Wood-Jones 1912).



such as the following based on Pound and Clements (1900):

1. Annuals: Passing the winter or dry season in seed or spore form alone, no propagation or accumulation of aerial shoots; living one year.
2. Biennials: Passing one unfavorable season in the seed or spore form and the next in a vegetative stage; no accumulation of aerial shoots; living two years or parts of two years.
3. Herbaceous perennials: Passing each unfavorable season in both seed or spore and vegetative form; no accumulation of aerial shoots; living several to many years.
   a. Broad-leaved herbs: mostly terrestrial
   b. Sod grasses: a continuous turf
   c. Bunch grasses: scattered clumps
   d. Succulents: some broad-stemmed cacti
   e. Water plants:
      (1) Submerged: vegetative body entirely underwater.
      (2) Floating: leaves floating on water surface; water lilies, duckweed.
      (3) Emerging: leaves extending above water surface; cattails, sedges, rushes.
   f. Ferns
   g. Mosses
   h. Liverworts
   i. Lichens
   j. Fungi
   k. Algae
4. Woody perennials: Passing the unfavorable season as aerial shoots or masses, often as seeds also; living many years as a rule.
   a. Lianas: vines
   b. Succulents: some tree or barrel cacti
   c. Bushes: much-branched, low growth, several stems
   d. Shrubs: single stem and tree-like but smaller
   e. Trees:
      (1) Deciduous: shedding leaves during unfavorable season.
      (2) Evergreen: leaves shed irregularly and tree never completely bare.
         (a) Needle-leaved: narrow, elongated or scale-like leaves.
         (b) Broad-leaved: leaves much as on deciduous trees but shed irregularly.

Life-forms of Animals

There have been several attempts to classify the life-forms of animals, but nothing very definitive has resulted (Remane 1952, Krivolutskii 1972). The major life-forms of animals more often agree with their taxonomy than do plants, but some life-forms include representatives from several different taxonomic groups. There can be recognized encrusting forms such as the fresh-water bryozoan *Plumatella* and some sponges; coral forms, including grass, leaf, or shrub forms; radiate forms, such as coelenterates and echinoderms generally; bivalve forms; snail forms; slug forms; worm forms; crustacean forms; insect forms; fish, snake, bird, and four-footed forms. Each of these major types may be divided into narrower structural or behavioral types, for example among the four-footed form of mammals (Osburn *et al.* 1903):

Aquatic (swimming): Seal, whale, walrus
Fossorial (burrowing): Mole, shrew, pocket gopher
Cursorial (running): Deer, antelope, zebra
Saltatorial (leaping): Rabbit, kangaroo, jumping mouse
Scansorial (climbing): Squirrel, opossum, monkey
Aerial (flying): Bat

Adaptations

Specific life-forms are adaptations of plants and animals to live in particular habitats and to behave in particular ways (Klaauw 1948). The life-forms listed for mammals are largely adaptations to particular strata (water, subterranean, ground, tree, air) within a community rather than to the habitat as a whole; for instance, the subterranean adaptations of mammals living in the Arctic tundra are similar to the subterranean adaptations of mammals in the tropics. In communities lacking one or more strata (for instance, the tree stratum in grassland), animals specifically adapted to the missing strata are also absent. In communities in which all strata are present, a catholic variety of life-forms occurs.

In addition to adaptations to stratum and habitat, there occur ecologically significant adaptations for food-getting and metabolism, protection, and reproduction. The variety of teeth found in mammals and lizards, the variation in shape and size of bills of birds, the different mouth parts of insects, the siphons of clams, the suckers of leeches, the water canal systems of sponges are but a few special anatomical features especially designed for food-getting. Associated with food-getting is a great diversity in structural adaptations for the digestion of the food, for respiration, for circulating food materials and gases through the body, for excreting wastes, for support and movement, and for nervous and hormonal regulation. All these internal organs and structures are necessary to the animal for utilizing the energy resources of the environment.

All animals are subject to predation or competition and must have means of protecting themselves or offsetting losses in the struggle for existence. Such adaptations take a variety of forms such as body armor, concealing coloration, attack weapons, or behavior patterns of escape. High rates of mortality are offset by high rates of reproduction or, in some lower organisms, by considerable power of regenerating whole organisms from fragmented parts.