Principles of
ANIMAL ECOLOGY

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"As concerns 'Relations Physiology', i.e., the study of the relations of the animal organism to the external world, this in turn falls into two segments, ecology and chorology. By ecology we mean the body of knowledge concerning the economy of nature—the investigation of the total relations of the animal both to its inorganic and to its organic environment; including, above all, its friendly and inimical relations with those animals and plants with which it comes directly or indirectly into contact—in a word, ecology is the study of all those complex interrelations referred to by Darwin as the conditions of the struggle for existence. This science of ecology, often inaccurately referred to as 'biology' in a narrow sense, has thus far formed the principal component of what is commonly referred to as 'Natural History'. As is well shown by the numerous popular natural histories of both early and modern times, this subject has developed in the most close relations with systematic zoology. The ecology of animals has been dealt with quite uncritically in natural history; but natural history has in any case had the merit of keeping alive a widespread interest in zoology."

Ernst Haeckel, 1870

PREFACE

In writing this book we hope we have a start at supplying the orientation of which ecology, a subscience of biology, is in need. The time seemed ripe for a group of ecologists, approaching the science from various points of view and with various techniques, to attempt to gather together fundamental concepts, supported in so far as possible by well-verified evidence. Others have accumulated many facts that we have drawn upon freely, from both published compilations and original research reports, but our effort has been directed primarily towards the presentation and documentation of general ecological principles. We have not been wholly successful. Many concepts and principles of a future science of ecology are only beginning to be recognized, and many important ideas that will be taught to future classes in biology have not yet been conceived by the present generation of ecologists.

We hope that, as a result of our efforts, the general biologist may more easily grasp the scope and implications of ecology and that profitable lines of investigation will be more readily apparent to interested students. We are encouraged by remembering the stimulus gained some years ago from Elton's small books, in which he emphasized ecological principles.

From our point of view there is an urgent demand for three different types of books about ecology. On the one hand we could well use an encyclopedic treatise of present-day knowledge of the subject. In distinct contrast, a brief statement of the underlying principles would also be useful. We felt that there was also a need for a study of the underlying principles together with a sampling of the evidence on which they are based. This is the task we have undertaken. So far as possible, no fact is admitted to these pages for its own sake, and although no general concept is stated without the presentation of evidence supporting it, an attempt has been made to give no more than the necessary minimum of factual support.

At one point we are immediately on the defensive. In limiting our discussion, at least in certain chapters of the book, primarily to the principles of *animal* ecology, we appear to be recognizing a logical dichotomy between ecological relations of plants and of animals where none exists. The decision not to extend our work to include the whole scope of ecology, the so-called bio-ecology of some writers, was based primarily on convenience and workability. Yet, although this book stresses animal ecology, we have felt free, in fact we have been compelled, to draw on ideas from plant ecology and to make continued use of the concepts in which plants and animals are necessarily considered together. The distinction between our "animal ecology" and ecology in the most comprehensive sense lies in our emphasis on the animal factors.

We stress ecological generalizations from two vantage points. First, there are those principles concerned with the functions or physiology of contemporary individuals and ecological assemblages of whatever rank. Second, there are those ecological principles concerned with organic evolution. We are not interested in helping to continue the separation between these two aspects of ecology. Rather, our aim is to point out their essential interrelation, and we hope we may have depicted ecology in better perspective in this connection.

In addition to attempting the correlation of the shorter-term contemporary phenomena with a longer-term evolutionary perspective, we have also been impressed by the need for an historical approach to many aspects of the subject. Besides the fairly full section on ecological history, the historical approach is frequently made elsewhere in the book. This emphasis has not necessarily affected the selection of supporting examples, since neither the older, more widely known illustrations nor the most recently discovered ones have been regularly used.

We discuss ecological principles dealing with the nonliving physical environment more or less as a unit, whether they are concerned primarily with the individual (autecology) or with the population or the community (synecology). The consideration of the biotic environment of the individual organism is less unified and perhaps less comprehensive. It is hard to avoid some duplication in dealing with the environmental relations of these different biological units, and the inherent difficulties have not been resolved formally and logically. In discussing principles dealing with the organism in its nonliving physical environment, we have anticipated many somewhat similar interrelations with the higher ecological categories. In contrast, much of the discussion of the biotic environment is given in direct connection with populations, communities, and evolution, rather than in a single part of the book.

In our treatment of the ecological principles that emerge with the population as the unit of study, our attention centers first on the population in both laboratory and field and, later, on aggregations and on certain aspects of societies. The analysis of functional contemporary principles leads naturally to the examination of interspecies groups. Here our primary concern is with the underlying structure, organization, successional development, and distribution of the ecological community. In this section our emphasis is on terminology only in those instances in which the term itself is a well-authenticated index of the principle. The multiplication of terms represents a juvenile stage of the science as a whole, and it is hoped that a critical definition and sifting of the concepts that support the terminology may lead to a reduction of their complexity and to an advance toward maturity.

Finally, in examining the problems of evolution we attempt to bring out those ecological aspects that are particularly significant, such as isolation, selection, adaptation, distribution, regressive evolution, and others, insofar as they contribute to ecological principles or as the ecological approach aids in their solution.

The book was planned jointly. Each author undertook primary responsibility for preparing the first draft of sections or chapters for the handling of which he showed particular competence so far as our group membership was concerned. Early working outlines and successive copies of each chapter or section were distributed to the other authors and received criticism concerning both manner and matter, particularly with regard to possible omissions. Eventually all parts of the manuscript were read aloud to the other authors, and there was much discussion of questioned points. We feel that in the main we have reached a truly remarkable degree of agreement both on the major and minor principles of ecology, though some generalizations, emphases, and conclusions are not shared with equal enthusiasm by every author. Fortunately, these are usually matters of relatively minor significance.

Many parts of the manuscript were read critically by persons outside our circle, and the revised version was again distributed to the other authors. Finally there was a period of collation between pairs of authors. Near the end of the writing each author was instructed to use his own judgment in the final polishing of the chapters for which he prepared the first draft.* Chapters from various sections were also read to the

* We had originally hoped that many traces of personal origin of chapters would disappear during this extended and detailed critical treatment and that final responsibility would rest entirely with the group. This hope has been realized in large part, but, as was to be expected, each author feels decidedly more responsibility for the selection, organization, presentation and interpretation of the material he has himself written than he does for other chapters, or even for the book as a whole. Particular responsibility for the different chapters was distributed as follows:

Preface and Introduction (Chapter 1): K.P.S. (based on drafts by W.C.A. and T.P.).

Chapters 2, 4 to 16, inclusive, and 23: W.C.A.

Chapters 3 and 18 to 22, inclusive: T.P.

Chapter 17: W.C.A. and K.P.S.

Chapters 24 and 31 to 35, inclusive: A.E.E.

Chapters 25 to 29, inclusive: O.P.

Chapter 30: K.P.S. and O.P.

General editing of the manuscript: K.P.S.

The four junior authors here acknowledge the leadership of Dr. Warder Clyde Allee and their indebtedness to him throughout the preparation of the present work.

Chicago Ecology Club, and the resulting discussions were stimulating and profitable.

We take this opportunity to thank many people for their help in this enterprise. Of course, final responsibility for all remaining errors rests with the authors.

Dr. Theodor Just (Chicago Natural History Museum) and the late Dr. Chancey Juday (University of Wisconsin) read all of Section I, and the latter also criticized the material on limnology in Section IV. The late Dr. F. R. Lillie, Dr. Elizabeth A. Beeman (University of Chicago), and Dr. Ruth M. Merwin (National Cancer Institute, Bethesda, Maryland) read Chapter 2, and the last mentioned checked its bibliography. Dr. Garrett J. Hardin (Santa Barbara College) criticized Chapters 4 to 18, inclusive. Mr. Peter W. Frank and Mr. Gerson Rosenthal (University of Chicago) each read certain of those chapters. Among others from the same University, Dr. T. F. W. Barth (Geology) checked over the paragraphs on earthquakes, Dr. Ralph W. Gerard (Physiology) and Dr. Clay G Huff (Parasitology) gave similar advice and aid concerning other matters in Section II, and Dr. Charles E. Olmsted (Botany) gave helpful botanical aid. Dr. Fritz Haas (Chicago Natural History Museum) was helpful on various sections.

Dr. L. C. Birch (University of Sidney) read Chapters 3 and 18 to 22, inclusive. Of the staff of Northwestern University, Dr. William Powers aided with Chapter 28, Dr. Orrie J. Eigsti read the material on bacteria, Dr. L. H. Tiffany was consulted with respect to photosynthesis, and Dr. Albert Wolfson was helpful on the subject of bird migration (Section IV).

The following men, all from the University of Chicago, helped in the section on Evolution. Dr. Sewall Wright read the whole section. Dr. Herluf H. Strandskov read parts, especially the matters dealing with population genetics. Dr. Clay G Huff and Dr. W. H. Taliaferro criticized and made suggestions concerning parasitism. Dr. O. H. Robertson helped similarly with the treatment of *Pneumococcus,* as did Dr. E. J. Kraus with the portion on rusts and with plant ecology, and Dr. John M. Beal with botanical names, evolution of chromosomes, rusts, and at various other places. Dr. Ernst Mayr (American Museum of Natural History) read Chapter 32. Mr. Robert F. Inger was extremely helpful in checking bibliographic references, and our few references to the Russian literature were put in correct form by Mr. D. Dwight Davis (Chicago Natural History Museum).

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THE AUTHORS

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INDICES

1. INTRODUCTION

Ecology may be defined broadly as the science of the interrelation between living organisms and their environment, including both the physical and the biotic environments, and emphasizing interspecies as well as intraspecies relations. The *living organism* may be defined, though somewhat incompletely, as a physicochemical mechanism that is self-regulating and self-perpetuating, and is in process of equilibration with its environment. The *environment* of any organism consists, in final analysis, of everything in the universe external to that particular organism. Those parts of the total environment that are evidently of direct importance to the organism are regarded as constituting the *effective environment*. The relations of any organism or community of organisms with the environment are, in the language of Raymond Pearl (p. 266), (1) particular: specific for every organism; (2) continuous: the organism living in its environment for its total life; (3) reciprocal: the environment affecting the organism, and *vice versa;* and (4) indissoluble: dissociation of an organism from its environment being impossible. The organism and groups of organisms are the essential biological units in ecology, and we exclude the intraorganismal or cellular environment except as special cases demand its examination.

The reciprocal relations require especial attention. The interaction of the environment and the organism is obvious in almost every field of biology. Physiological processes are correlated primarily or secondarily with environmental fluctuations: energy for life is derived from the environment; growth and development show relationship to environmental factors; environmental forces and substances impinge upon the sense organs of animals and the reactive systems of plants; behavior patterns in large part are responses to environmental patterns; distribution of plants and animals is determined by variations in the environmental complex; isolation through environmental factors has profoundly influenced genetic systems of organisms, and the environment has acted as a selective agent in determining the survival of organisms and populations, thus leading to the evolutionary development of living systems.

In its more scientific aspects, ecology is intrinsically a difficult subject. In its relations it depends on many other phases of biology, and it is built directly, as well as indirectly, on the physical sciences. The subsciences of biology and the physical sciences are in turn dependent upon and affected by ecology. Yet in its close relationship to natural history, ecology is near the stolon from which all biology has developed. As such it sometimes seems deceptively simple, and under many conditions ecology may really be simple. Almost any good, precise observation within its extended borders makes a useful contribution to the mass of needed ecological information. Its wide range of subject matter, open to exploration by diverse techniques, is a major reason for the lack of ready integration of the field of ecology as a whole. It is at any rate obvious that the development of generalizations and principles in ecology and the orientation of its subject matter with respect to such principles, have been slow.

Workers in ecology, like those in any other broad field, face reproach from more narrow specialists. Physiologists, for example, are hard pressed to meet the rigorous standards of biophysics or biochemistry, to say nothing of those of physics or chemistry proper. In part this particular difficulty is not directly related to subject matter, as evidenced by the relative precision gained by specialists as contrasted with generalizers in any field. In part the difficulty in biology is associated with the intrinsic complexity of the materials to be analyzed or synthesized.

Biologists working with the social life of insects, or of other animals, are frequently tempted to regard their own work as more precise than that done by equally competent students of human sociology; and those dealing with human material often feel compelled to explore subjective psychological aspects of sociology that are almost or completely closed to the student of social insects.

Much of human sociology is an integral part of ecology. There are reciprocal influences between these two sciences, influences that are especially apparent in such practical matters as the development of the Canal Zone in Panama, with the details and outreach of the Tennessee Valley Authority, with stream pollution, and with the whole set of problems centering about the potential or actual dust bowls of semiarid regions of the world. Much that is now being done in such projects is recognized as ecology.

A major difference between human relationships and those of other animals is the role played by the symbolic language of man, and by ideas, as contrasted with the restricted use of both among nonhuman populations. The extent to which animals other than primates communicate with each other, and the means employed, are still matters for investigation. We know much about the importance of odors as signals, particularly among such animals as dogs, ants, and moths. We also know about various cries, songs, and visual displays that reveal sexual receptivity, or nonreceptivity, that facilitate aggregation or warn of danger. We have evidence that the complex activities within the ant colony are integrated primarily by touch and odor; to regard such manifestations as language emphasizes the distinctiveness of human speech. The demonstration of ideas—particularly of abstract ideas—among the mental processes of nonhuman animals is still more difficult.

We have purposely avoided emphasis on human sociology, but we hope that in time a maturing ecology will be properly fused with that field.

The line between ecology and physiology is equally difficult and perhaps equally impossible to draw with exactness. One of the most helpful distinctions concerns the working units in the respective subject matter. The physiologist seldom gets beyond considering an individual as his upper limit; often he is content with some organ or even with an individual nerve fiber; his research may focus finally at the molecular level. In contrast, the ecologist usually regards an individual organism as his smallest unit, except as he needs information about the functioning of the liver, pancreas, muscles, or other organs in order to understand the general environmental relations of the whole organism, or of the community. The kidneys give a remarkably good illustration of the close correlation that may exist between an inner organ of the body and the general environment. For ecology, the supra-individualistic units are real entities. Aggregations, populations, societies, and various units at or near the community level present problems rarely recognized by physiologists working as physiologists. Yet the problems of this level are real and lie so near the center of ecology that Shelford (1929, p. 2) makes the statement that ecology is the science of animal communities.

A single *Asellus* moving upstream in a small brook has an ecology of its own, even though it is not at the moment in direct association with any organisms other than the bacteria and other nannoplankton of the water or those minute forms residing on its own surface or acting as its parasites. We have no reason to believe that this particular isopod remembers or anticipates contacts with another living creature. It is essentially alone, a creature of the moment, responding to an innate urge to move upstream against the current of water. The positive reaction is not free from environmental influences; it is dependent on such external relations as the amount of oxygen and of carbon dioxide present, and on the ionic content of the surrounding water. The isopod is also, without knowing it, a member of the community of the brook and so is related to the ground water that feeds the stream and, to some extent, to the body of water into which the brook flows. At a different level, the single, isolated isopod may well have been and may soon become again a member of an isopod aggregation with which other animals are also associated.

The physical environment impinges directly on the individual as it does on populations or on a whole community, and it initiates and directs the course of action of innumerable small-scale events. Phenomena on the largest scale may likewise depend directly on the physical environment, as exemplified by isostasy, the condition of equilibrium in which the heavier portions of the earth's crust sink to form the ocean basins, while the lighter parts are pushed up as the continental platforms.

The definition of ecology as the science of communities may be valid in its total implications. The isopod illustration presents a phase of a much larger problem. In another example, is the cell, the tissue, or the organism as a whole the unit? The cell may itself be broken into parts, and in genetics we hear much about chromosomes, chromomeres, and genes. So in ecology there may be ecological relations of parts of organisms—the nephridial system, for example—of the whole animal, of populations, whether aggregated or dispersed, of associations and communities, and of biomes. At whatever level one begins, and whatever the point of view, one must study all possible unitary levels before coming to a full understanding of the ecology of either an isolated isopod moving slowly upstream in a small brook, or of the vast biome in which the brook itself is a minor and almost negligible incident.

Close interaction exists between genes and the general environment, both in development and in evolution. A gene may be helpfully regarded as a reagent in the process of development; the environment also enters intimately into the developmental processes. Aside from supplying continuity under suitable conditions, much that is produced by the gene system can be duplicated by appropriate surroundings, either as a result of shock furnished by an environmental insult or from the more steady pressure of a steadily continuing physical or biotic induction. Such subjects are treated in some detail in any modern work on physiological genetics (Goldschmidt, 1938), in more specialized books such as Hogben (1933) or Newman, Freeman and Holzinger (1937), and even in more popular accounts, as in the small book by Dunn and Dobzhansky (1946).

Animals do not develop without an environment; contrariwise, even given optimum environment, organisms do not start to grow without the presence of a spore or zygote or of a group of cells from a preceding organism. Both a bearer of heredity and a suitable environment are necessary for development. After much discussion, lasting from the time of Darwin, Galton, and Weismann, we can now ask fairly exact questions in this field and expect to find fairly exact answers. Some pertinent data are available at various evolutionary levels such as those of the micro-organisms, the insects, and man. The relation between heredity and environment is frequently called the problem of nature versus nurture. In its present dress the discussion does not center about environment versus heredity in general, but rather concerns the functions of these two necessary components with regard to some particular characteristic, such as the color of the shanks in hens, the width of the bar in bar-eyed *Drosophila*, coat color in certain mammals, or intelligence or stature in man.

Concrete examples may clarify what is meant by the ecological relations of such characters. Yellow fat in rabbits or yellow shanks in hens require a source of yellow coloring matter, such as is furnished by yellow corn or by the xanthophyll from green foliage or other similar foodstuffs; but, for yellow to be developed, the enzyme that breaks down xanthophyll must be absent, and this lack in the hen or rabbit is associated with gene action. Absence of xanthophyll from the food yields equally white fat or white shanks, and one cannot know whether the absence of yellow is primarily environmental or genetic, or both, without more direct knowledge of both the heredity and the feeding routine. The effect of temperature on the width of the bar in bar-eyed *Drosophila*, of heat on the production of feathers in young frizzle fowl, or of the absence of iodine in water containing frog tadpoles fed on an iodine-free diet, all demonstrate significant effects of the environment on the development of characters that are also definitely related to the gene complex (Hogben, 1933).

In man, the best assay of nature in association with or in contrast to nurture has come from studies of identical twins reared apart compared with those of others reared together, and further compared with similar qualities in fraternal twins. Identical twins have an identical gene pattern, fraternal twins do not. A good study of this kind is that of Newman, Freeman, and Holzinger

(1937), which shows that "physical characters are least affected by the environment, that intelligence is affected more; educational achievement still more; and personality or temperament, if our tests are to be relied upon, the most."

Reasons for the slow development of ecology can be found in the general state of nonecological science, in the relative inability of ecologists to work with intellectual and physical tools of precision, and especially in the scope and innate complexity of the subject.

There are few good reasons other than the convenience of authors and readers for not treating ecology as a whole. Plant ecologists can make a strong case for focussing on plant relations and largely neglecting animal life, since the plants are primary producers and play a highly important role in providing shelter for many types of animals. Even so, the neglect of animal activities omits or minimizes such phenomena as grazing and browsing, working of the soil, seed scattering, and the pollination of many important flowering plants. Students of animal ecology must give due attention to plants if for no other reason than that animals live in an environment largely conditioned and controlled by the plant matrix. Acknowledging the failure of the present work to develop a unified ecology, we fully recognize the need for a future work on the Principles of Ecology which will make the logical synthesis of the two fields.

Plant ecology presents two aspects, vegetational and floristic. Animal ecology largely lacks the vegetational phase so far as land animals are concerned. It is true that forest animals differ in general appearance from those of grasslands, but the differences in body proportions by no means approach the contrast in growth forms between grasses and trees. The general aspect of aquatic animals stands in marked contrast with that of land forms, and various convergences exist among both series that approach what we understand when a vegetational type is mentioned. Thus the fishlike form of whales, seals, walruses, fossil sea reptiles, tadpoles, certain larvae of lower chordates, and of the whole galaxy of fishes stands in distinct contrast with typical terrestrial structures. The sessile animals of coral reefs and oyster banks approach the terrestrial vegetational concept even more closely. Contrary to first impression, the fact that animal ecology is based primarily on faunistic considerations tends to simplify its study, since the student of animal relations is not so much tempted to pursue the superficial types of inspection that make the carwindow approach one of the charms and also one of the pitfalls of plant ecology.

The application of even a well-formulated generalization to a given situation may require further research. Thus in the control of mosquito-borne diseases of man, the mosquitoes that transmit epidemic yellow fever behave according to rule. A trained executive can sit at his desk in New York, after he has fully learned the principles involved, and give directions which, if faithfully carried out, will lead to the control of the disease. It is not so with the anopheline mosquitoes that carry malarial parasites. Each type of malarial vector is a special case, and, without further knowledge, the general principles may seem inapplicable to the given situation. In the southeastern United States, malaria is transmitted by a marsh-dwelling mosquito characteristic of sluggish water; in Italy, by a form that lives in the cold running water of the uplands; in Puerto Rico, by a brackish-water mosquito. Under such varied conditions the needed local detail is of equal value with knowledge of the underlying general principles.

An example of the benefits to be derived from an approach to ecology through general principles is given in the summarizing paragraph of ocean currents by Sverdrup, Johnson, and Fleming (1942, p. 399), who conclude:

> "From this brief summary it is evident that it is virtually impossible to obtain knowledge of the ocean currents on an entirely empirical basis. If this were to be accomplished, it would be necessary to conduct measurements from anchored vessels at numerous localities for long periods and at many depths."

A word is in order about "principles." We do not wish, nor are we competent, to enter into a philosophical evaluation and definition of "laws," "concepts," and "principles." Ecology proceeds, as does any empirical science, (1) by the collection of relevant facts; (2) by the arrangement of these facts into ordered series according to their relations and patterns; and (3) by the development of higher-category knowledge or principles that synthesize and correlate the material at hand. Thus the "principles" we shall attempt to formulate and interrelate are simply those generalizations inductively derived from the data of ecology. We regard the so-called "laws of nature" as empirical, derived from the facts, and not the facts from the laws. In this view, a principle is a means of description of nature in succinct and compressed form. This is true in the relatively well-organized physical sciences, in which the principles frequently can be reduced by mathematical statement to the extreme of simplification. In the vastly more complex biological sciences, mathematical formulation of generalizations is more difficult, and possible only in limited segments of the complex. The process of inductive generalization is useful at every stage. The principles derived from the compression of a mass of data into a science form the main basis for deductive thinking and for hypotheses which ask new questions and make possible new advances, on the one hand by opening up new fields of inquiry and on the other hand by progressive correction of the older generalizations in the light of additional data.

We subscribe to the general principle of scientific parsimony ("William of Occam's razor"), which may be stated as follows: "Neither more, nor more onerous, causes are to be assumed than are necessary to account for the phenomena" (Pearson, 1937, p. 340). For ecology in particular, the number of entities should not be unnecessarily increased. Furthermore, Morgan's canon (1894) concerning animal behavior is essentially a quantitative development of "Occam's razor" and an application of the law of parsimony: "In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of one which stands lower in the psychological scale."

There is an understandable tendency in any synthesizing discussion to review chiefly the progress made in recent years or decades. This is sound practice in many ways, but one result is that work, often excellent work, of previous decades or even centuries may be neglected. A false idea of rapidity of progress is thereby encouraged, and the concept of the relatively complete modernity of subject matter tends to be built up in the thinking of younger readers, although the minds of authors and editors may have been entirely free from such a misconception. We have accordingly made a serious effort throughout this book to supply historical perspective and regard the history of ecology and of its antecedent sciences as an integral and significant part of our treatment.

Ecological history, like that of zoology in general, can be summed up briefly as follows: In the Greek period—either because such was the case, or because Aristotle did not cite sources—it was the apparent rule to study nature directly and to think over the implications of observations made at first hand. During the long scholastic period in the Middle Ages, the influence of which unhappily lingers on here and there, the fashion changed to a study of books, or at least a part of those available. The spirit of the scientific awakening was at length summarized by the dictum of Louis Agassiz: "Study nature, not books."* Too often this became perverted, by practice rather than by precept, to the study of preserved specimens, and some books. A gradual change occurred until in the early decades of the present century the tacit advice became: Study living and preserved organisms in the laboratory together with the pertinent books.

One constant effort of the modern ecological movement has been to take the study of nature again out under the sky. This could not entirely succeed, in part because of the difficulties in doing accurate analytical work in the field. A partial compromise is attained by our turning to the greenhouse and breeding cage, where experimentally-minded ecologists have been met by workers moving out of orthodox laboratories into these substitutes for field conditions. Some ecologists have remained stubbornly in the field, where they are being joined by a trickle of the more orthodox indoor students. Laboratory and field ecology are interdependent, and both are essential. At the same time, the check of knowledge gained directly against printed accounts, both as to empirical content and

* An amusing and even paradoxical commentary on this famous aphorism may be derived from the fact that Agassiz prepared the first comprehensive bibliography of zoology—the four volume *Bibliographia Zoologiae*, published by the Ray Society (1848–1854).

philosophical implications, is being given more balanced consideration.

The reality and usefulness of the population as an ecological unit were apparent to us when we outlined the present book, and our subsequent work has reinforced our conviction of the importance of the principles that center on the population. We view the population system, whether intraspecies or interspecies, as a biological entity of fundamental importance. This entity can be studied with some measure of precision, and the emergent principles are significant throughout the field of ecology. The population is forged by strong bonds with autecology through the physiology and behavior of individuals; communities are composed of recognizable population elements; and evolutionary ecology depends directly upon population systems, since selection acts upon populations that evolve and become adapted to their environments, to a more important degree than upon individuals. The study of populations as such, as operational systems, yields principles that clarify the nature of group interactions, interactions that do not exist at the level of the single organism, and that are too complex at the community level to be analyzed in a quantitative way.

The major relations of animals center around nourishment, reproduction and protection. The reaction to these needs may be summarized by the concept of a "drive" towards favorable ecological position. This usually implies a drive for security of one kind or another, or of all kinds. The partially mystical idea of a "drive" hides the nonmystical one of the survival values furnished by the attainment of nourishment, protection and sufficient reproduction, or even by the attempt to secure them.

The situation can be clarified somewhat by attending to only one of the three fundamental needs—protection, for example. The given animal, or population, may orient and move actively toward protected places as a generalized reaction that may become much more marked in times of particular stress. Or the individual or population may wander about, apparently at random, and come to rest under favorable conditions. Animals may invade a more stable physical environment such as that furnished by a pond or a forest, or in winter there may be a movement down to the forest floor or an active invasion of its superficial carpet of leaves and of the soil beneath them. Security may be gained by attaining control of a portion of the environment through the slow processes of ecological succession leading toward the establishment of an ecological climax or through the more active animals moving into natural safe niches or building their own shelters. A third mode of progress toward ecological security, or more assured ecological position, is found in societal evolution. These are all aspects of the tendency toward ecological homeostasis, and this sort of homeostasy is one of the major inclusive principles of ecology and, with a different emphasis, of physiology as well.

The tendency towards homeostasy extends through the diverse phases of ecology, whether the subdivisions are based on habitat differences such as those characteristic of oceanography, of limnology, or of the land, or of the living habitats of parasites. Such tendencies are found under primarily physical relations with nonliving environments and also when all the relations are primarily biotic.

The physical universe is indifferent to life in general and resistant to the influence of living organisms even in slow-working long-time trends. For that matter, organisms are largely indifferent to each other. Dramatic incidents occur, and there is a strong tendency to record and to overemphasize these. Animals, under many conditions, and plants as well, may merely persist; it is then needful to search out the undramatic relations that allow them to continue to live when little or nothing beyond mere existence is involved. Often only a saving few individuals survive in a given habitat, and these may spend much of their time apparently doing nothing at all except remaining alive. Hibernation, aestivation, "resting" cysts, and resistant or so-called winter eggs represent periods of marked quiescence. The quiet retirement of animals capable of extreme activity is often a fundamental part of living. Hens fight and actively establish social orders based on dominance and subordinance, yet they spend much more time in which no activity is evident. Chimpanzees exhibit a strong drive for status in a social group, and yet they too pass only a small percentage of their time in active social tension. Outdoor nature is a place where there is much inactivity. Even in the teeming tropics an observer frequently has nothing to do except wait and watch. In fact, patience is one of the prime prerequisites for naturalistic study of undisturbed wild life, even when attention is limited to selected birds or mammals. The essential impatience of observers is one of the dominant reasons for the growth of experimentation in ecology; but great patience is required for any adequate long-term program of experimentation, the ramifications of which may seem endless.

Such considerations lead naturally to thinking about the interrelations between ecology and animal behavior, since the active behavior of animals both in field and laboratory may be striking, and behavior studies can yield important indications of current environmental effects. This does not imply that all studies of animal behavior as developed at present are directly or even indirectly ecological (except in a quite remote sense). Students of behavior are much concerned with psychological problems, which in turn may lead into physiology and into philosophy rather than into ecology proper.

Many of the ecological phases of animal behavior cluster about the central problems of distribution, being concerned with the closely related matter of so-called habitat selection or, objectively expressed, of modality. Gradients of important environmental factors exist in nature both on small and on large or even gigantic scales. Gradients of concentration of oxygen, carbon dioxide, and other chemicals, including food, heat, moisture, light and pressure, to mention no more, give stimuli to which animals react. The responses may be fairly direct and oriented, amounting at times to forced movements, or there may be random reactions of the trial-and-error variety. The results may either be apparent immediately or they may be deferred for days, weeks, seasons, years, centuries or millenia; or finally they may be discoverable only in the vast perspective of geological time. Migrations such as those of birds and butterflies are frequently large-scale spectacles; in contrast, important emigrations may be inconspicuous events, the effects of which have not become fully apparent during recorded history.

Emigrations may have evolutionary as well as contemporaneous importance. These time scales sometimes blend, as they do in illustrations of what is known as the host-selection principle (p. 615). In theory, it is only a short step from the host selection shown by wood-boring beetle larvae that tend to live in and feed upon a particular species of tree, to the more crystallized behavior shown by solitary wasps that catch, sting, and oviposit on a particular kind of caterpillar, grasshopper or spider. (The implied evolution can be explained by modern assumptions centering about natural selection.) This brings up also the problem of search for the right animal to be captured, stung and parasitized, in which the innate behavior patterns, commonly and somewhat roughly called instincts, have real and far-reaching ecological implications. (The interested reader is referred to Tinbergen, 1942, for a behavioristic approach to the subject.)

Some behavior patterns of higher vertebrates appear to resemble innate, instinctive behavior, and yet have been demonstrated for certain birds to result from a specialized type of early learning, called "imprinting" by Lorenz (1935). Imprinting results when a young animal at an impressionistic age, when the learning threshold is low, is exposed to a meaningful stimulus or to some suitable substitute. Normally at such times the stimulus that becomes imprinted, so to speak, initiates persisting behavior that may dominate the animal's activities for the rest of its life. A common example concerns the following of an adult of the species, often the female parent. This behavior results from a few contacts, or even from a single contact at the proper age. In the absence of the parent, the tendency to follow a given individual may be imprinted by exposure to some other animal at the crucial time, with amusing and incongruous results. The tendency is important in the normal building of family or flock integration; the interesting psychological mechanisms and implications lead beyond our scope.

Other types of integrations with the biological or physical environment are also apparent, as are many fundamental questions. How does an animal find and settle in a given habitat? How much so-called search is involved? Is there an element of active preferential choice, or, more simply, is there a reaction to the relative absence of disturbing stimuli? To what extent is the behavior innate, and how much is reestablished each generation? This leads to curiosity concerning the possible presence of tradition among nonhuman animals. How much learning, if any, is involved? To what extent, if at all, are animals conscious of their actions or surroundings?

These are troublesome questions concerning which it is difficult to collect exact and pertinent information, whether from existing literature, directly from outdoor nature, or by means of planned experiments. Elton (1933) recognized the existence of such problems and suggested some conclusions that depart from current trends of thought in scientific circles. Apparently speaking primarily of birds and mammals, he says (p. 46):

"Changes in habitat are frequent, and we do not yet know precisely what relative importance to attach to psychological factors (new ideas, or broken traditions or accumulative fatigue with old habits) and how much to organic changes in the form of mutations affecting behaviour. Finally it is of great interest to inquire whether animals are actually conscious of their actions, and whether in this consciousness there is any element which is at variance with the usual concepts of animal behaviour current among physiologists and also many ecologists. There is definite evidence that animals often migrate in response to stimuli which cannot be called danger signals but which appear to be unpleasant to them (Elton, 1930). Whether in this behaviour we can discern feelings akin to aesthetic feelings or whether they are to be looked upon as mechanical aspects of mental balance, cannot be decided. The whole question of animal behaviour in relation to the choice of habitats and habits in general is of profound importance both in theoretical science and in practical economic biology."

These are matters that we cannot yet solve, but it is important that we should not continue to ignore their existence. A major difficulty lies in the absence of an objective terminology. The use of vaguely defined terms is associated with the uncritical humanizing tendencies of many naturalists, who in turn give strong avoiding reactions to the carefully objective and perhaps overcorrected point of view of critical modern students.

Recognition of community of interests between the general and comparative phases of psychology and of ecology calls for commendation of the modern tendency toward objective terminology in both subjects, as well as in general biology and other phases of science. General anthropomorphic concepts and language are to be avoided, admitting that other considerations such as clarity and brevity or entrenched usage may sometimes require exception. It is unfortunate to have to use a Greek or Latin root meaning "loving," for example, to denote an ecological relation, when the English form would be objectionable or ridiculous. This is a language ideal that is frequently difficult to apply even with conscious and conscientious effort. There is a severe strain when one is convinced (*a*) that the Cartesian doctrine is essentially unsound, (*b*) that scientific writing should be simple, clear, and direct, and (*c*) that even the words used should not carry partially hidden suggestions unsupported by direct evidence.

A binding principle in ecology, as in many other phases of biology, deals with the integration of individual units into larger wholes. Cells of more complex animals combine into tissues, organs, and systems, and yet all this complexity develops from a single cell. Even at the cell level, certain cells living in close association with each other—as in lichens, for example—may not be germinally related. All ecological communities lack the germinal continuity characteristic of populations of single species and particularly characteristic of colonial animals like sponges or many hydroids, or the typical societal colonies of social bees, wasps, or ants. Interspecific populations also obviously lack germinal continuity. Their evolution is traced to a combination of ecology and genetics that will be outlined in the section on Evolution.

The relationships between these ecological categories may be traced either by the type method or by the principles treatment attempted in the present book. Neither approach is automatically preferable. The cataloguing of one category after another gives a readily indexed treatment that orders the details in a workable manner, but may conceal the underlying principles. The approach through principles may confuse the issue so far as facts are concerned and may be unsatisfactory for those interested primarily in a catalog of existing data.

The type treatment deals directly with the ecology of the oceans, one after another, of bays and gulfs, of the fresh water, and of the land. The principles treatment draws evidence now from one and now from another type of habitat, and then passes on to repeat the process with another principle. The two approaches continually tend to become mixed when the documentation of principles is given in any detail. Recognition of the existence of a physical environment as contrasted with a biotic environment illustrates the principles approach; even when the physical environment is broken down into component parts, the treatment continues to present principles, when, within the subdivisions such as temperature, light, and moisture, the discussion centers about principles such as the temperature "laws," Bergmann's rule, and Corioli's force.

A fresh definition of the community concept is offered in the present work: In large, the major community may be defined as a natural assemblage of organisms which, together with its habitat, has reached a survival level such that it is relatively independent of adjacent assemblages of equal rank; to this extent, given radiant energy, it is self-sustaining.

This definition places special restrictions on a term that has often been a useful catch-all, correctly applicable to any ecological assemblage ranging from the inhabitants of a small clod of earth to the animals and plants living in the northern evergreen forests of the world. Under the older usage, "community" might refer to a simple ecological unit illustrated by a thin mat of floating algae as well as to the complicated, multistoried tropical rain-forest (J. R. Carpenter, 1938). A practical solution seems to be to recognize the usage of the term "community" both in the restricted sense indicated by our definition, and in the extended loose sense. It will occasionally be necessary, under the conditions, to add or to imply "s.s." or "s.lat.," "in a strict sense" or "in a broad sense." We have wished to avoid further implementation of the facetious definition of ecology as being that phase of biology primarily abandoned to terminology.

There are two fundamental approaches to ecological communities that are best presented by considering the two extremes. As biocoenoses, they may be organized primarily by the interrelations of the plants and animals as associates; in contrast, the basic organization may rest on the common habitat in which the constituent organisms serve primarily as indicators and secondarily as associated individuals. Both types of communities exist in fairly pure form, and there are closely graded interconnections. The biota of the desert presents many aspects of a community controlled by its physical habitat, and the oyster bed is a classical example of a biotically controlled biocoenosis. Both types present many different orders of complexity and size; one of the larger of these, the biome, requires further mention.

The biome, represented by the northern coniferous forest in North America, includes three major plant associations: viz., the spruce-pine forest of Alaska and northwestern Canada; the spruce-balsam fir forest of northern Canada from the Mackenzie River through Labrador and southward; and the pine-hemlock forest of southeastern Canada, the region around Lake Superior, and northern Michigan. The climax dominants of the last two associations are radically different, but they resemble each other closely in having a large number of identical animal constituents that characteristically range through both.

Shelford and Olsen (1935, p. 395) list the common animals of the coniferous forest biome, pointing out that they range through the three major plant associations without conspicuous change. Their analysis shows the importance of the animals in defining biotic units and the weaknesses inherent in biome concepts based solely on data concerning plants. The vegetation is not the sole key to the biome. Furthermore, the pine-hemlock community has a clear unity with the transcontinental spruce-balsam fir forest and even with the Alaskan spruce-pine association. This unity is based on subclimax stages and on animal constituents some of which may be relatively unimportant ecologically.

The universality of the biome concept meets a severe test in the geographic fragmentation of the major biotic formations. New Guinea and northern Australia, for example, tend to be separated by plant geographers into two areas (Scrivenor et al., 1943). Contrariwise, most students of animal distribution unite the two into a common major zoogeographic region. The concept of the biome, like many other ecological generalizations, must be accepted with proper reservations and adjusted to the historical problems involved.

Ecological formations are not static. Given time, the advance and retreat of